Environmental and Experimental Botany 71 (2011) 79–88

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Seeds photoblastism and its relationship with some plant traits in 136 cacti taxa

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ARTICLE INFO

Article history:
Received 9 April 2010
Received in revised form 17 October 2010
Accepted 28 October 2010

Keywords:
Cactaceae
Photoblastism
Plant traits
Seed dormancy
Seed germination

ABSTRACT

Seed germination triggered by light exposure (positive photoblastism) has been determined in quantitative studies for numerous plant families and species. For Cactaceae, positive photoblastism is thought to be associated with life form and seed mass, but this association has never been evaluated. To explore hypotheses on associations between seed mass, seed dispersal, seed dormancy, life form, taxa and plant height with Relative Light Germination (RLG) in Cactaceae, we evaluated the effect of light on seed germination of 136 taxa. The taxa studied are native to several countries: México, Chile, Argentina, Brazil, Perú, USA, and Venezuela. Seed traits contrasted with RLG were life form, seed mass, seed dispersal, seed dormancy, adult plant height and taxon. We found some differences between RLG among taxa; Cacteae, Pachycereeae and Trichocereeae had higher RLG than Notocacteae. RLG was lower for seeds from taller than for shorter taxa, and lower for taxa with heavier seeds than for taxa with lighter seeds. Dispersal syndrome groups varied with RLG. RLG did not differ between cylindrical and globose taxa. Trends found here were in agreement with expectations for small-seeded species to have a light requirement to germinate more often than large-seeded species. This is the first time that cactus height is related to photoblastism. It is possible that seeds from tall plants are larger and thus have the capacity to produce taller seedlings than those from small plants, and that seedlings from large seeds with more resources have the ability to emerge from greater soil depths than those from small seeds.

1. Introduction

Light is one of the most important environmental signals to which the life cycle of a plant may respond to in any environment (Gutterman, 1993). The effect of light on seed germination has been studied for many species of Cactaceae (Rojas-Aréchiga et al., 1997; Rojas-Aréchiga and Vázquez-Yanes, 2000; Flores et al., 2006; Gurvich et al., 2008; Ortega-Baes et al., 2010a), a common family across arid and semiarid ecosystems of the Americas (Ortega-Baes and Godínez-Álvarez, 2006; Ortega-Baes et al., 2010b). Positive photoblastism or the promotion of seed germination by exposure to light has been documented for several cacti species, but others show no light requirement for germination (Balboa, 1983; Flores et al., 2006). Across plant families, the seeds of positively photoblastic species are often dormant (Thompson and Grime, 1979; Grime et al., 1981; Rees, 1993; Pons, 2000) and small in size (Grime et al., 1981; Pons, 1991, 2000; Rokich and Bell, 1995; Milberg et al., 2000; Fenner and Thompson, 2005). Since smaller plants tend to have smaller seeds (Westoby et al., 1992), we hypothesize that smaller plants produce positively photoblastic seeds. From the literature, one study can be found comparing plant height to photoblastism, in which Kyereh et al. (1999) found that most photoblastic species of Ghanaian forest trees were short.

Other plant attributes thought to be associated with positive photoblastism include life form (Rojas-Aréchiga et al., 1997; Morgan, 1998; Bell et al., 1999; Rojas-Aréchiga and Vázquez-Yanes,

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doi:10.1016/j.envexpbot.2010.10.025

Table 1
Cacti species from seven countries and their germination in light and darkness and other traits (life form, seed mass, seed dispersal, seed dormancy, adult plant length and taxon). RLG is Relative Light Germination calculated as RLG = Gl/(Gd + Gl), where Gl = germination percentage in light, and Gd = germination percentage in darkness. RLG represents a range of values varying from 0 (germination only in darkness) to 1 (germination only in light).

Species with dormant seeds	Light	Darkness	RLG	Seed mass (mg)	Taxon	Dispersal syndrome	Plant length (cm)	Life form	Country	References
Ariocarpus bravoanus ssp. *bravoanus*	66	0	1	0.920	Cacteae	Hydrochory	3	Rosetophyllous	México	Flores et al. (2006)
Ariocarpus bravoanus ssp. *hintonii*	36	0	1	0.910	Cacteae	Hydrochory	3	Rosetophyllous	México	Flores et al. (2006)
Ariocarpus kotschoubeyanus	56	1	0.982	0.770	Cacteae	Hydrochory	3	Rosetophyllous	México	Flores et al. (2006)
Ariocarpus retusus	53	0	1	0.890	Cacteae	Hydrochory	25	Rosetophyllous	México	Flores et al. (2006)
Ariocarpus scaphirostris	54	0	1	ND	Cacteae	Hydrochory	3	Rosetophyllous	México	Mandujano et al. (2007)
Astrophytum capricorne	64	0	1	1.800	Cacteae	Hydrochory	25	Globose	México	Samperio-Ruiz (2007)
Astrophytum ornatum	10	0	1	2.144	Cacteae	Hydrochory	100	Globose	México	New data
Aztekium ritteri	33	0	1	0.500	Cacteae	Synzoochory	3	Globose	México	Maiti et al. (1994)
Copiapoa cinerea ssp. *haseltoniana*	51	28	0.646	0.728	Notocacteae	Endozoochory	150	Globose	Chile	New data
Copiapoa eremophila	51	28	0.646	ND	Notocacteae	Endozoochory	150	Globose	Chile	New data
Copiapoa gigantea	15	19	0.441	ND	Notocacteae	Endozoochory	150	Globose	Chile	New data
Copiapoa grandiflora	30	18	0.625	0.497	Notocacteae	Endozoochory	50	Globose	Chile	New data
Copiapoa longistaminea	50	54	0.481	0.289	Notocacteae	Endozoochory	100	Globose	Chile	New data
Cylindropuntia leptocaulis	28	10	0.737	ND	Cereeae	Endozoochory	180	Cylindrical	México	Rojas-Aréchiga et al. (in press)
Discocactus zenthneri	4	0	1	ND	Trichocereeae	Endozoochory	7	Globose	Brazil	Veiga-Barbosa et al. (2010)
Echinocereus enneacanthus	42	0	1	0.47758	Cacteae	Endozoochory	200	Cylindrical	USA	New data
Echinocereus reichenbachii	14	0	1	0.579	Pachycereeae	Endozoochory	40	Globose	USA	New data
Echinocereus stramineus	62	1	0.984	0.366	Pachycereeae	Endozoochory	45	Globose	USA	New data
Echinopsis ancistrophora	44	1	0.978	0.822	Trichocereeae	Synzoochory	9.5	Globose	Argentina	New data
Echinopsis haematantha	34	0	1	0.792	Trichocereeae	Synzoochory	12	Globose	Argentina	New data
Echinopsis thionantha	41	0	1	0.374	Trichocereeae	Endozoochory	24	Cylindrical	Argentina	New data
Echinopsis tubiflora	51	0	1	2.100	Trichocereeae	Synzoochory	75	Cylindrical	Argentina	Ortega-Baes et al. (2010a)
Epiphyllum anguliger	68	0	1	1.400	Hylocereeae	Endozoochory	1200	Cylindrical	México	Zimmer and Büttner (1982)
Epithelantha micromeris	33	0	1	0.620	Cacteae	Endozoochory	30	Globose	México	Flores et al. (2006)
Eriosyce confinis var. *kunzei*	41	2	0.953	0.77692	Notocacteae	Unassisted	15	Globose	Chile	New data
Eriosyce curvispina	40	0	1	0.343	Notocacteae	Unassisted	25	Globose	Chile	New data
Eriosyce engleri	22	0	1	0.925	Notocacteae	Unassisted	30	Globose	Chile	New data
Eriosyce subgibbosa ssp. *clavata*	56	0	1	0.52	Notocacteae	Unassisted	100	Globose	Chile	New data
Eriosyce subgibbosa var. *litoralis*	31	0	1	0.54	Notocacteae	Unassisted	100	Globose	Chile	New data
Escobaria emskoetteriana	59	0	1	0.536	Cacteae	Endozoochory	10	Globose	México	Maiti et al. (1994)
Ferocactus cylindraceus	62	0	1	2.222	Cacteae	Endozoochory	300	Globose	USA	New data
Gymnocalycium bruchii	38	0	1	1.320	Trichocereeae	Synzoochory	3.5	Globose	Argentina	Gurvich et al. (2008)
Gymnocalycium capillaense	55	0	1	ND	Trichocereeae	Synzoochory	8	Globose	Argentina	Gurvich et al. (2008)
Gymnocalycium mihanovichii	61	2	0.968	ND	Trichocereeae	Synzoochory	5	Globose	Argentina	Zimmer and Büttner (1982)
Gymnocalycium monvillei	20	0	1	0.300	Trichocereeae	Synzoochory	8	Globose	Argentina	Gurvich et al. (2008)
Gymnocalycium monvillei ssp. *monvillei*	17	0	1	0.300	Trichocereeae	Synzoochory	12	Globose	Argentina	Brencher et al. (1978)
Gymnocalycium saglionis	33	0	1	0.179	Trichocereeae	Endozoochory	15	Globose	Argentina	New data
Gymnocalycium schickendantzii	15	0	1	0.184	Trichocereeae	Synzoochory	10	Globose	Argentina	New data
Lophophora diffusa	51	3	0.944	0.966	Cacteae	Endozoochory	7	Globose	México	Trujillo-Hernández (2002)
Lophophora williamsii	67	11	0.859	0.509	Cacteae	Endozoochory	7	Globose	México	Trujillo-Hernández (2002)
Maihueniopsis camachoi	50	9	0.847	4.704	Opuntioideae	Endozoochory	5	Globose	Chile	New data
Maihueniopsis ovata	65	44	0.596	9.308	Opuntioideae	Endozoochory	10	Globose	Chile	New data
Mammillaria aureilanata	42	0	1	1.100	Cacteae	Endozoochory	7.5	Globose	México	Flores et al. (2006)
Mammillaria napina	24	0	1	ND	Cacteae	Endozoochory	5	Globose	México	Rodríguez-Ortega et al. (2006)
Mammillaria orcuttii	68	0	1	0.360	Cacteae	Endozoochory	15	Globose	México	Flores et al. (2006)
Mammillaria pectinifera ssp. *solisioides*	23	0	1	ND	Cacteae	Endozoochory	4	Globose	México	Rodríguez-Ortega et al. (2006)
Mammillaria plumosa	51	0	1	0.290	Cacteae	Endozoochory	7	Globose	México	Flores et al. (2006)
Mammillaria polythele ssp. *polythele*	69	0	1	0.16	Cacteae	Endozoochory	60	Globose	México	Zimmer (1969a)
Mammilloydia candida	46	0	1	0.590	Cacteae	Endozoochory	30	Globose	México	Flores et al. (2006)
Melocactus curvispinus ssp. *caesius*	50	0	1	0.500	Cereeae	Endozoochory	30	Globose	Venezuela	Arias and Lemus (1984)
Mila caespitosa ssp. *caespitosa*	45	0	1	0.173	Trichocereeae	Endozoochory	30	Globose	Perú	New data
Myrtillocactus geometrizans	63	0	1	0.691	Pachycereeae	Endozoochory	400	Cylindrical	México	New data
Neoraimondia arequipensis ssp. *roseiflora*	56	9	0.862	0.934	Browningieae	Endozoochory	1000	Cylindrical	Perú	New data
Opuntia microdasys	35	8	0.814	ND	Opuntioideae	Endozoochory	100	Articulated	México	Rojas-Aréchiga et al. (in press)
Opuntia rastrera	40	10	0.8	ND	Opuntioideae	Endozoochory	50	Articulated	México	Rojas-Aréchiga et al. (in press)

Opuntia sulphurea	5	0	1	6.998	Opuntioideae	Synzoochory	30	Articulated	Argentina	New data
Opuntia tomentosa	20	0	1	16	Opuntioideae	Endozoochory	70	Articulated	México	Olvera-Carrillo et al. (2003)
Opuntia violacea	12	0	1	15.11	Opuntioideae	Endozoochory	100	Articulated	México	Rojas-Aréchiga et al. (in press)
Pachycereus hollianus	65	60	0.52	4.520	Pachycereeae	Endozoochory	500	Cylindrical	México	Rojas-Aréchiga et al. (1997)
Pachycereus pecten-aboriginum	40	38	0.513	9.606	Pachycereeae	Endozoochory	800	Cylindrical	México	New data
Pilosocereus arrabidae	60	0	1	0.984	Cereeae	Endozoochory	400	Cylindrical	Brazil	Martins (2007)
Pilosocereus catingicola ssp. *salvadorensis*	47	0	1	ND	Cereeae	Endozoochory	400	Cylindrical	Brazil	Meiado et al. (2008)
Polaskia chichipe	50	0	1	0.519	Pachycereeae	Endozoochory	400	Cylindrical	México	New data
Selenicereus grandiflorus	54	4	0.931	1.660	Hylocereeae	Endozoochory	500	Cylindrical	México	New data
Stenocereus eruca	32	0	1	1.328	Pachycereeae	Endozoochory	300	Cylindrical	México	Yang (1999)
Stenocereus gummosus	68	0	1	1.174	Pachycereeae	Endozoochory	150	Cylindrical	México	New data
Stenocereus stellatus	65	0	1	0.800	Pachycereeae	Endozoochory	400	Cylindrical	México	Rojas-Aréchiga et al. (1997)
Turbinicarpus alonsoi	41	0	1	0.270	Cacteae	Hydrochory	11	Globose	México	Flores et al. (2006)
Turbinicarpus gielsdorfianus	68	0	1	0.460	Cacteae	Hydrochory	7	Globose	México	Flores et al. (2006)
Turbinicarpus horripilus	57	0	1	ND	Cacteae	Hydrochory	18	Globose	México	Matías-Palafox (2007)
Turbinicarpus laui	48	0	1	0.800	Cacteae	Hydrochory	1.5	Globose	México	Flores et al. (2006)
Turbinicarpus lophophoroides	8	0	1	0.900	Cacteae	Hydrochory	3.5	Globose	México	Flores et al. (2006)
Turbinicarpus pseudopectinatus	5	5	0.5	0.740	Cacteae	Hydrochory	3	Globose	México	Flores et al. (2006)
Turbinicarpus schmiedickeanus ssp. *jauernigii*	37	0	1	0.520	Cacteae	Hydrochory	3	Globose	México	Flores et al. (2006)
Turbinicarpus schmiedickeanus ssp. *rubriflorus*	69	0	1	0.510	Cacteae	Hydrochory	3	Globose	México	Flores et al. (2006)
Turbinicarpus valdezianus	57	0	1	0.43	Cacteae	Hydrochory	3	Globose	México	Rojas-Aréchiga et al. (2008)
Species with non-dormant seeds										
Ariocarpus trigonus	94	0	1	1.400	Cacteae	Hydrochory	25	Rosetophyllous	México	Flores et al. (2006)
Astrophytum myriostigma	86	12	0.878	1.566	Cacteae	Hydrochory	25	Globose	México	New data
Carnegiea gigantea	97	0	1	1.184	Pachycereeae	Endozoochory	1600	Cylindrical	USA	McDonough (1964)
Cereus hankeanus	94	0	1	1.800	Cereeae	Endozoochory	360	Cylindrical	Argentina	New data
Cereus jamacaru	95	2	0.979	ND	Cereeae	Endozoochory	1000	Cylindrical	Brazil	Prisco (1966)
Cereus repandus	93	0	1	3.28	Cereeae	Endozoochory	1000	Cylindrical	Venezuela	Yang (1999)
Cleistocactus acanthurus ssp. *faustianus*	82	0	1	0.293	Trichocereeae	Endozoochory	30	Globose	Perú	New data
Cleistocactus hyalacanthus	90	0	1	0.216	Trichocereeae	Endozoochory	100	Cylindrical	Argentina	New data
Coleocephaleocereus fluminensis	100	0	1	0.25	Cereeae	Endozoochory	300	Cylindrical	Brazil	Genofre-Salles (1987)
Copiapoa cinerea ssp. *columna-alba*	72	44	0.621	0.315	Notocacteae	Endozoochory	130	Globose	Chile	New data
Corryocactus brevistylus	85	1	0.988	0.886	Pachycereeae	Endozoochory	500	Cylindrical	Chile	New data
Coryphanta radians	90	0	1	0.129	Cacteae	Endozoochory	8	Globose	México	New data
Coryphantha delaetiana	80	55	0.593	0.330	Cacteae	Endozoochory	6	Globose	México	Zimmer (1969b)
Coryphantha potosiana	72	37	0.661	0.2	Cacteae	Endozoochory	15	Globose	México	Zimmer (1969b)
Cylindropuntia imbricata	47	73	0.392	7.96	Opuntioideae	Endozoochory	300	Cylindrical	USA	New data
Echinocactus grusonii	88	0	1	0.770	Cacteae	Endozoochory	200	Globose	México	Zimmer (1969a)
Echinocactus platyacanthus	74	0	1	2.627	Cacteae	Endozoochory	250	Cylindrical	México	New data
Echinocactus texensis	82	0	1	1.8	Cacteae	Endozoochory	20	Globose	México	Maiti et al. (1994)
Echinopsis angelesiae	92	0	1	0.500	Trichocereeae	Endozoochory	100	Cylindrical	Argentina	New data
Echinopsis atacamensis	97	21	0.822	0.757	Trichocereeae	Endozoochory	1000	Cylindrical	Chile	New data
Echinopsis atacamensis ssp. *pasacana*	77	4	0.951	0.66	Trichocereeae	Endozoochory	1000	Cylindrical	Argentina	Zimmer (1969a)
Echinopsis bolligeriana	94	1	0.989	1.105	Trichocereeae	Endozoochory	200	Cylindrical	Chile	New data
Echinopsis candicans	82	0	1	0.0108	Trichocereeae	Endozoochory	60	Cylindrical	Argentina	Ortega-Baes et al. (2010a)
Echinopsis chiloensis spp. chiloensis	95	57	0.625	0.727	Trichocereeae	Endozoochory	800	Cylindrical	Chile	New data
Echinopsis chiloensis ssp. *litoralis*	98	24	0.803	0.667	Trichocereeae	Endozoochory	200	Cylindrical	Chile	New data
Echinopsis chiloensis ssp. *skottsbergii*	94	21	0.817	0.572	Trichocereeae	Endozoochory	200	Cylindrical	Chile	New data
Echinopsis coquimbana	90	0	1	1.133	Trichocereeae	Endozoochory	100	Cylindrical	Chile	New data
Echinopsis huascha	78	3	0.963	ND	Trichocereeae	Endozoochory	100	Cylindrical	Argentina	Zimmer (1969a)
Echinopsis leucantha	80	14	0.851	0.780	Trichocereeae	Endozoochory	35	Cylindrical	Argentina	New data
Echinopsis schickendantzii	85	1	0.988	0.409	Trichocereeae	Endozoochory	25	Cylindrical	Argentina	New data
Echinopsis terscheckii	95	0	1	0.550	Trichocereeae	Endozoochory	1200	Cylindrical	Argentina	New data
Echinopsis thelegona	93	0	1	1.200	Trichocereeae	Endozoochory	200	Cylindrical	Argentina	Ortega-Baes et al. (2010a)
Echinopsis walterii	82	6	0.932	0.800	Trichocereeae	Endozoochory	16	Cylindrical	Argentina	Ortega-Baes et al. (2010a)
Eriosyce aurata	78	8	0.907	4.024	Notocacteae	Unassisted	90	Globose	Chile	New data

Table 1 (*Continued*)

Species with dormant seeds	Light	Darkness	RLG	Seed mass (mg)	Taxon	Dispersal syndrome	Plant length (cm)	Life form	Country	References
Eriosyce chilensis	94	9	0.913	0.498	Notocacteae	Unassisted	100	Globose	Chile	New data
Eriosyce eriosyzoides	83	0	1	0.686	Notocacteae	Unassisted	40	Globose	Chile	New data
Eriosyce heinrichiana	98	3	0.97	0.388	Notocacteae	Unassisted	2	Globose	Chile	New data
Eriosyce napina	94	44	0.681	0.408	Notocacteae	Unassisted	3	Globose	Chile	New data
Eriosyce occulta	75	45	0.625	0.495	Notocacteae	Unassisted	1	Globose	Chile	New data
Eriosyce paucicostata	89	21	0.809	0.372	Notocacteae	Unassisted	30	Globose	Chile	New data
Eriosyce subgibbosa	95	3	0.969	0.524	Notocacteae	Unassisted	100	Globose	Chile	New data
Eriosyce subgibbosa ssp. *castanea*	81	0	1	0.53	Notocacteae	Unassisted	100	Globose	Chile	New data
Eriosyce taltalensis	89	21	0.809	0.387	Notocacteae	Unassisted	8	Globose	Chile	New data
Escontria chiotilla	76	0	1	0.66	Pachycereeae	Endozoochory	700	Cylindrical	México	Martínez-Cárdenas et al. (2003)
Espostoa melanostele	94	0	1	0.334	Trichocereeae	Endozoochory	200	Cylindrical	Perú	New data
Eulychnia acida	99	71	0.582	0.699	Notocacteae	Endozoochory	400	Cylindrical	Chile	New data
Eulychnia acida f. procumbens	97	84	0.536	0.699	Notocacteae	Endozoochory	700	Cylindrical	Chile	New data
Eulychnia breviflora	100	95	0.513	0.583	Notocacteae	Endozoochory	700	Cylindrical	Chile	New data
Eulychnia castanea	100	89	0.529	0.761	Notocacteae	Endozoochory	100	Cylindrical	Chile	New data
Ferocactus flavovirens	80	0	1	ND	Cacteae	Endozoochory	100	Globose	México	Rojas-Aréchiga et al. (1997)
Ferocactus glaucescens	86	0	1	0.500	Cacteae	Endozoochory	45	Globose	México	Zimmer (1969a)
Ferocactus hamatacanthus	83	0	1	ND	Cacteae	Endozoochory	60	Globose	México	Maiti et al. (1994)
Ferocactus histrix	75	0	1	0.296	Cacteae	Endozoochory	110	Globose	México	New data
Ferocactus latispinus ssp. *spiralis*	70	0	1	0.261	Cacteae	Endozoochory	30	Globose	México	Rojas-Aréchiga et al. (1997)
Ferocactus peninsulae	91	0	1	2.170	Cacteae	Endozoochory	250	Globose	México	Yang (1999)
Ferocactus robustus	70	0	1	0.498	Cacteae	Endozoochory	100	Globose	México	Rojas-Aréchiga et al. (1997)
Ferocactus wislizeni	75	1	0.987	2.551	Cacteae	Endozoochory	300	Globose	USA	New data
Gymnocalycium spegazzinii	88	0	1	0.215	Trichocereeae	Synzoochory	12	Globose	Argentina	New data
Haageocereus acranthus	79	0	1	0.445	Trichocereeae	Endozoochory	200	Cylindrical	Perú	New data
Haageocereus chilensis	98	2	0.98	0.655	Trichocereeae	Endozoochory	100	Cylindrical	Chile	New data
Haageocereus pseudomelanostele	91	0	1	0.352	Trichocereeae	Endozoochory	70	Cylindrical	Perú	New data
Haageocereus pseudomelanostele ssp. *auriespinus*	83	0	1	0.190	Trichocereeae	Endozoochory	70	Cylindrical	Perú	New data
Hylocereus setaceus	100	5	0.952	0.280	Hylocereeae	Endozoochory	100	Cylindrical	Brazil	Simão et al. (2007)
Hylocereus undatus	84	31	0.73	1.337	Hylocereeae	Endozoochory	500	Cylindrical	México	New data
Maihuenia poeppiggi	99	88	0.529	ND	Maihuenioideae	Endozoochory	10	Cushion	Chile	Zimmer (1973)
Mammillaria albilanata ssp. *albilanata*	95	20	0.826	0.270	Cacteae	Endozoochory	15	Globose	México	Zimmer (1969b)
Mammillaria bocasana	74	0	1	0.836	Cacteae	Endozoochory	10	Globose	México	New data
Mammillaria carnea	92	0	1	ND	Cacteae	Endozoochory	20	Globose	México	Benítez-Rodríguez et al. (2004)
Mammillaria crinita	97	0	1	0.230	Cacteae	Endozoochory	8	Globose	México	Flores et al. (2006)
Mammillaria formosa ssp. *chionocephala*	96	0	1	ND	Cacteae	Endozoochory	20	Globose	México	Zimmer and Büttner (1982)
Mammillaria haageana	90	0	1	0.212	Cacteae	Endozoochory	15	Globose	México	Benítez-Rodríguez et al. (2004)
Mammillaria hernandezii	87	0	1	ND	Cacteae	Endozoochory	2	Globose	México	Rodríguez-Ortega et al. (2006)
Mammillaria heyderi ssp. *gaumeri*	99	0	1	ND	Cacteae	Endozoochory	5	Globose	México	Cervera et al. (2006)
Mammillaria huitzilopochtli	90	28	0.763	ND	Cacteae	Endozoochory	15	Globose	México	Flores-Martínez and Manzanero-Medina (2003)
Mammillaria kraehenbuehlii	72	65	0.526	ND	Cacteae	Endozoochory	12	Globose	México	Flores-Martínez et al. (2002)
Mammillaria longimamma	86	2	0.977	2	Cacteae	Endozoochory	15	Globose	México	Zimmer (1969a)
Mammillaria magnimamma	95	15	0.864	0.260	Cacteae	Endozoochory	12	Globose	México	Ruedas et al. (2000)
Mammillaria mazatlanensis	90	0	1	0.242	Cacteae	Endozoochory	15	Cylindrical	México	Sánchez-Soto et al. (2010)
Mammillaria mystax	95	0	1	0.110	Cacteae	Endozoochory	15	Globose	México	Benítez-Rodríguez et al. (2004)
Mammillaria oteroi	77	0	1	ND	Cacteae	Endozoochory	3	Globose	México	Flores-Martínez and Manzanero-Medina (2003)
Mammillaria supertexta	95	0	1	ND	Cacteae	Endozoochory	13	Globose	México	Benítez-Rodríguez et al. (2004)
Mammillaria winterae	91	0	1	ND	Cacteae	Endozoochory	10	Globose	México	Maiti et al. (1994)
Mammillaria zeilmanniana	70	0	1	ND	Cacteae	Endozoochory	8	Globose	México	Zimmer (1969a)
Melocactus conoideus	80	0	1	ND	Cereeae	Endozoochory	10	Globose	Brazil	Rebouças and dos Santos (2007)

Melocactus peruvianus	77	0	1	0.308	Cereeae	Endozoochory	20	Globose	Perú	New data
Micranthocereus flaviflorus	96	0	1	ND	Cereeae	Endozoochory	75	Cylindrical	Brazil	Veiga-Barbosa et al. (2010)
Myrtillocactus schenkii	89	0	1	0.460	Pachycereeae	Endozoochory	500	Cylindrical	México	New data
Neobuxbaumia macrocephala	78	76	0.506	0.900	Pachycereeae	Endozoochory	1500	Cylindrical	México	Ramírez-Padilla and Valverde (2005)
Neobuxbaumia mezcalaensis	93	45	0.674	6.000	Pachycereeae	Endozoochory	1000	Cylindrical	México	Ramírez-Padilla and Valverde (2005)
Neobuxbaumia tetetzo	96	88	0.522	1.420	Pachycereeae	Endozoochory	1500	Cylindrical	México	Ramírez-Padilla and Valverde (2005)
Obregonia denegrii	81	0	1	0.553	Cacteae	Endozoochory	5	Globose	México	New data
Oreocereus celsianus	86	0	1	1.560	Trichocereeae	Synzoochory	200	Cylindrical	Perú	New data
Oreocereus hempelianus	81	0	1	0.937	Trichocereeae	Synzoochory	200	Cylindrical	Chile	New data
Pachycereus gaumeri	89	95	0.484	ND	Pachycereeae	Endozoochory	800	Cylindrical	México	Dorantes-Euan et al. (2003)
Pachycereus grandis	77	76	0.503	12.198	Pachycereeae	Endozoochory	2500	Cylindrical	México	New data
Pachycereus pringlei	94	90	0.511	5.000	Pachycereeae	Endozoochory	1100	Cylindrical	México	Yang (1999)
Parodia aureicentra	71	0	1	0.149	Notocacteae	Hydrochory	15	Globose	Argentina	New data
Parodia leninghausii	94	2	0.979	0.181	Notocacteae	Synzoochory	60	Cylindrical	Brazil	Zimmer and Büttner (1982)
Parodia maasii	96	0	1	ND	Notocacteae	Synzoochory	50	Globose	Argentina	Zimmer (1969a)
Parodia microsperma	100	0	1	0.046	Notocacteae	Hydrochory	20	Globose	Argentina	New data
Pelecyphora strobiliformis	74	0	1	0.443	Cacteae	Hydrochory	15	Globose	México	Flores et al. (2006)
Pereskia aculeata	76	76	0.5	ND	Pereskioideae	Endozoochory	300	True leaves shrub	Brazil	Pedroni and Sánchez (1997)
Pilosocereus chrysacanthus	75	60	0.556	ND	Cereeae	Endozoochory	400	Cylindrical	México	Rojas-Aréchiga et al. (1997)
Pilosocereus gounellei	97	9	0.915	ND	Cereeae	Endozoochory	400	Cylindrical	Brazil	Veiga-Barbosa et al. (2010)
Pilosocereus leucocephalus	93	86	0.52	ND	Cereeae	Endozoochory	500	Cylindrical	México	Miranda-Jácome (2008)
Polaskia chende	94	0	1	0.558	Pachycereeae	Endozoochory	400	Cylindrical	México	New data
Rebutia minuscula	74	0	1	ND	Trichocereeae	Synzoochory	4	Globose	Argentina	Zimmer (1969a)
Rhipsalis baccifera	83	2	0.976	0.2	Rhipsalideae	Epizoochory	400	Cylindrical	México	De la Rosa-Manzano and Briones (2010)
Stenocereus alamosensis	87.5	5	0.946	2.581	Pachycereeae	Endozoochory	400	Cylindrical	México	Sánchez-Soto et al. (2010)
Stenocereus griseus	90	3	0.968	1	Pachycereeae	Endozoochory	900	Cylindrical	Venezuela	Arias and Williams (1978)
Stenocereus pruinosus	94	46	0.671	1.890	Pachycereeae	Endozoochory	500	Cylindrical	México	New data
Stenocereus queretaroensis	84	0	1	2.27	Pachycereeae	Endozoochory	600	Cylindrical	México	De la Barrera and Nobel (2003)
Stenocereus thurberi	91	0	1	1.251	Pachycereeae	Endozoochory	800	Cylindrical	México	New data
Thelocactus conothelos ssp. *aurantiacus*	74	0	1	2.500	Cacteae	Endozoochory	12	Globose	México	Flores et al. (2006)
Thelocactus setispinus	77	28	0.733	0.760	Cacteae	Endozoochory	12	Globose	México	Zimmer (1969a)
Turbinicarpus schmiedickeanus	74	0	1	0.370	Cacteae	Hydrochory	3	Globose	México	Flores et al. (2006)
Turbinicarpus schmiedickeanus ssp. *klinkerianus*	80	0	1	0.710	Cacteae	Hydrochory	3	Globose	México	Flores et al. (2006)
Turbinicarpus schmiedickeanus ssp. *Flaviflorus*	86	0	1	0.350	Cacteae	Hydrochory	3	Globose	México	Flores et al. (2006)
Turbinicarpus schmiedickeanus ssp. *macrochele*	98	7	0.933	0.620	Cacteae	Hydrochory	3	Globose	México	Flores et al. (2006)
Turbinicarpus schmiedickeanus ssp. *schwarzii*	90	1	0.989	0.55	Cacteae	Hydrochory	3	Globose	México	New data

2000; Benítez-Rodríguez et al., 2004) and perenniality (light promotes the germination of annual species; De Villiers et al., 2002). Positive photoblastism is also considered to be associated with phylogeny (Morgan, 1998; Fenner and Thompson, 2005) and with temperature variation during seed development (Rojas-Aréchiga et al., 1997; Contreras et al., 2009). However, there is no consensus on the relationship between such plant traits and the light requirement for germination, nor between cacti traits and photoblastism.

Seed germination and establishment are key aspects in cacti biology (Godínez-Álvarez et al., 2003). In this study, we aim to understand better the relationship between the light requirement for germination and other plant traits for species of cacti. We analyzed Relative Light Germination (RLG; Milberg et al., 2000; Jiménez-Aguilar and Flores, 2010) values instead of germination percentages since seed batches differed in their dormancy level. RLG = Gl/(Gd + Gl), where Gl = germination percentage in light, and Gd = germination percentage in darkness. RLG represents a range of values varying from 0 (germination only in darkness) to 1 (germination only in light). Specifically we tested whether RLG was associated with: (i) seed size, assuming that small seeds are more frequently buried in the soil away from the light; (ii) seed dormancy; (iii) dispersal syndrome, because the mode of seed dispersal can influence the positioning of seeds within the soil and their contact with light; (iv) life form; following the suggestion from the literature that globose cacti need light to germinate and columnar cacti do not (Rojas-Aréchiga et al., 1997); (v) adult plant height, because taller plants tend to have larger seeds; and (vi) phylogeny.

2. Materials and methods

2.1. Study taxa

To explore the association between RLG and plant traits in taxa of cacti, we searched for information on the effect of light on seed germination from the published literature and found data for 110 taxa. We also included information for 86 taxa from our own data. Seeds were placed in Petri dishes containing agar for 30 d. There were four replicates per treatment, with 25 seeds in each. For incubation in darkness, Petri dishes were wrapped in double aluminum foil. All dishes were placed in a germination chamber under two conditions: a 14-h daily photoperiod (hereafter 'light') and continuous darkness at 25 °C, following Flores et al. (2006). To reduce temperature fluctuations, fluorescent lamps and air ventilation were used. At the end of the 30-d incubation period, we determined germination percentages. Information on all 196 taxa is presented in Table 1. The taxa studied are native to several countries: México (101 taxa), Chile (37 taxa), Argentina (28 taxa), Brazil (11 taxa), Perú (9 taxa), USA (7 taxa), and Venezuela (3 taxa).

2.2. Traits contrasted with RLG

Seed traits contrasted with RLG were seed mass, seed dormancy, seed dispersal syndrome and taxon. Other contrasted plant traits were life form and adult plant height.

Seed mass (Table 1) was obtained from Seal et al. (2009) and references therein. Seed dormancy is considered to be a very common adaptive plant strategy in unpredictable and harsh environments, such as arid and semiarid landscapes (Jurado and Flores, 2005). In this study, a taxon was considered to have dormant seeds when 30% of the seeds did not germinate without germination promoters (Flores et al., 2006). Using this criterion, the data were classified as 76 dormant taxa and 120 non-dormant taxa (Table 1). However, it is well known that as seeds of many species come out of dormancy, their germination responses with regard to light–dark can change (Flores et al., 2006). Therefore we used higher germination percentages (≥50% 103 taxa, ≥60% 95 taxa and ≥70% 83 taxa) as dormancy criteria to explore relationships with RLG.

Seed dispersal was classified according to Bregman (1988), based on fruit and seed structure into endozoochory or dispersal of seeds by animals after passage through the gut (137 taxa), epizoochory or the passive transport of seeds on the outside of the animal (1 taxa), synzoochory or deliberate transport of seeds externally by an animal (17 taxa), unassisted or the lack of dispersal structures (15 taxa), and hydrochoric or the displacement of seeds by water (26 taxa) (Table 1).

Taxa were grouped according to the shape of the plants into articulated (5 taxa), cylindrical (74 taxa), globose (109 taxa), rosetophyllous (6 taxa), true leaves shrub (1 taxa), and cushion (1 taxa) (Table 1). This information was obtained from Anderson (2001).

Taxa were grouped either as the subfamily Opuntioideae, Maihuenioideae and Pereskioideae, or into tribes within the subfamily Cactoideae to test for associations between traits and taxon. This information was obtained from Anderson (2001). Most taxa (73) belonged to the tribe Cacteae, followed by the tribes Trichocereeae (39 taxa), Notocacteae (29 taxa), Pachycereeae (25 taxa), Cereeae (14 taxa), Hylocereeae (4 taxa), Browningieae (1 taxon), and Rhipsalideae (1 taxon), and by the subfamilies Opuntioideae (8 taxa), Maihuenioideae (1 taxon), and Pereskioideae (1 taxon) (Table 1). In order to analyze the effects of taxa on RLG, we chose the four taxa with the higher number of taxa: Cacteae, Trichocereeae, Notocacteae, and Pachycereeae.

Adult plant height (Table 1) was obtained for all taxa from the literature (Anderson, 2001; Sotomayor et al., 2004).

2.3. Statistical analysis

We used PROC GLM in SAS 8.2 (SAS Institute Inc, 2005) to fit analysis of covariance to estimate the simultaneous effects on RLG of the following factors: taxon with four levels including Cacteae, Pachycereeae, Trichocereeae, and Notocacteae; dormancy with three levels including dormant, and non-dormant; dispersal syndrome with four levels including unassisted, synzoochoric, hydrochoric, and endozoochoric; and life form with two levels including cylindrical, and globose. Two covariates were included of seed mass ranging from 0.046 to 16 mg, and plant height ranging from 1 to 2500 cm. In order to avoid potential problems related to small sample sizes, analysis factor levels that were represented by at least 10 observations were only included. There were 196 taxa in our database, however for analyses we only used those traits that included 10 or more taxa ($n = 136$ observations, and $k = 10$ free parameters). Individual seeds were used as the sampling unit. Tests to explore different dormancy criteria were made with smaller sets of taxa (≥50% germination, ≥60% and ≥70%). Whenever significant differences among different levels of the same factor were found, we used Tukey tests to determine differences among individual levels of the factor. Finally, parameter estimates and their standard errors were used to estimate the effect of variation on values of individual variables on RLG while keeping the values of all other variables constant.

3. Results

3.1. Analyses for dormant and non-dormant seeds

The results of the analysis of covariance suggest that the overall combined effect of seed mass, seed dormancy, seed dispersal syndrome, taxon, life form, and adult plant height on RLG was significant ($r^2 = 0.4421$, $F = 9.907$, $P < 0.0001$). We found some differences between least square means RLG among taxa ($F = 15.9879$, $P < 0.0001$). The average RLG of Cacteae, Pachyc-

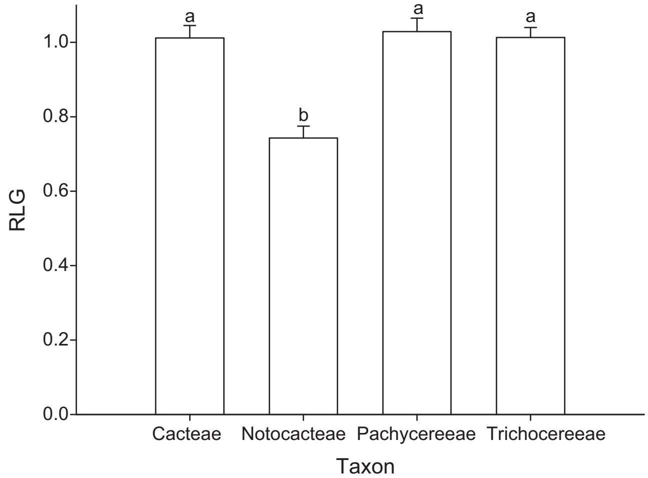

Fig. 1. Differences in least square means of RLG among taxa. Bars indicate mean ± standard error. Means with the same letter are not significantly different (analysis of covariance, $P < 0.0001$).

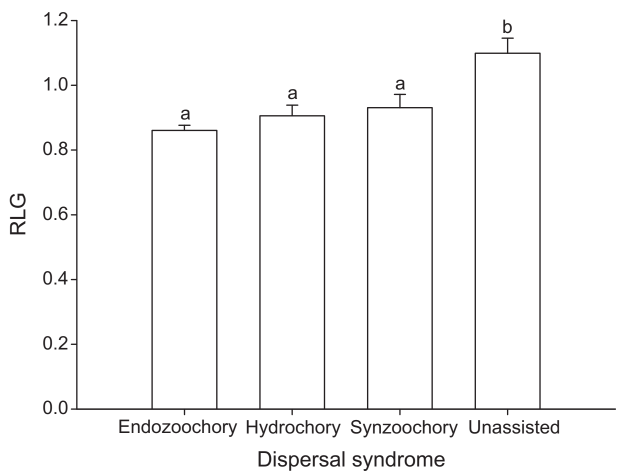

Fig. 2. Differences in least square means of RLG among dispersal syndrome groups. Bars indicate mean ± standard error. Means with the same letter are not significantly different (analysis of covariance, $P = 0.0002$).

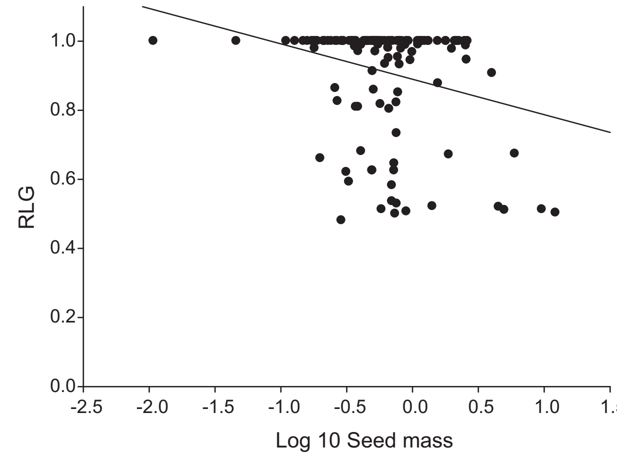

Fig. 3. Effect of seed mass on least square means of RLG (analysis of covariance, $P = 0.0016$).

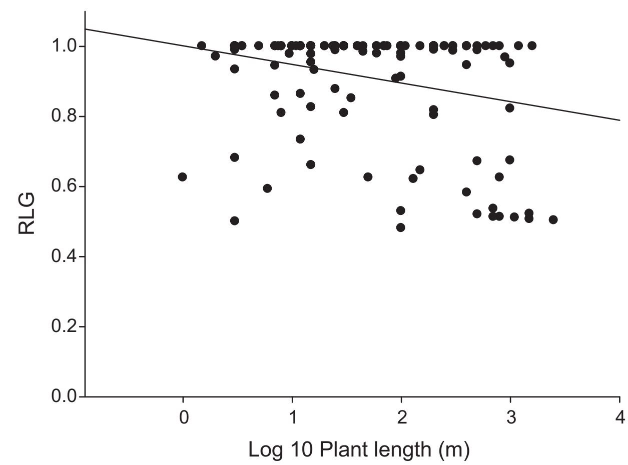

Fig. 4. Effect of plant length on least square means of RLG (analysis of covariance, $P = 0.0060$).

ereeae and Trichocereeae did not differ but was higher than for Notocacteae (Fig. 1). Mean RLG did not vary in mean between dormant (0.95 ± 0.02) and non-dormant taxa (0.94 ± 0.01, $F = 0.0118$, $P = 0.9138$).

Dispersal syndrome groups also varied on their average RLG values ($F = 6.9463$, $P = 0.0002$); average RLG was smaller for taxa with endozoochoric, synzoochoric and hydrochoric seeds compared to those with unassisted seeds (Fig. 2).

RLG was higher for taxa with lighter seed mass ($F = 10.3639$, $P = 0.0016$; Fig. 3). RLG also decreased linearly with increasing plant height ($F = 7.8113$, $P = 0.0060$, Fig. 4). RLG did not differ ($F = 0.34$, $P = 0.5637$) between cylindrical (0.96 ± 0.03) and globose taxa (0.94 ± 0.02).

3.2. Analyses for different dormant criteria

When considering different germination percentages for dormancy criteria, we found consistent differences between least square means RLG among taxon and plant height. However, dispersal and seed mass were only marginally different when considering taxa ≥60% germination, and not significant for those ≥70% germination (Table 2).

Table 2
Results of analyses of covariance estimating the simultaneous effects of several factors on RLG. Analyses were carried out for dormant and non-dormant taxa, and also for non-dormant taxa using different germination percentages as dormancy criteria.

	Dormant and non-dormant (136 taxa)	Germination ≥ 50% (103 taxa)	Germination ≥ 60% (95 taxa)	Germination ≥ 70% (83 taxa)
Taxon	$P < 0.0001^*$	$P < 0.0001^*$	$P < 0.0001^*$	$P < 0.0001^*$
Plant height	$P = 0.0060^*$	$P = 0.0098^*$	$P = 0.0113^*$	$P = 0.0070^*$
Dispersal Syndrome	$P = 0.0002^*$	$P = 0.0022^*$	$P = 0.0588$ N.S.	$P = 0.0963$ N.S.
Seed mass	$P = 0.0016^*$	$P = 0.0453^*$	$P = 0.0679$ N.S.	$P = 0.2683$ N.S.
Life form	$P = 0.5637$ N.S.	$P = 0.7216$ N.S.	$P = 0.4717$ N.S.	$P = 0.5227$ N.S.
Dormancy type	$P = 0.9138$ N.S.	N.T.	N.T.	N.T.

N.S. = not significant; N.T. = not tested.
* Significant effect.

4. Discussion

The effect of light on cacti seed germination has been evaluated in seven out of 34 countries where cacti occur naturally (Ortega-Baes and Godínez-Álvarez, 2006). Mexico is the country with the highest number of cactus species and endemic cactus species (Ortega-Baes and Godínez-Álvarez, 2006; Ortega-Baes et al., 2010b). Most of the taxa in this study (51.5% of 196 taxa) are from Mexico. Some South American countries have high cacti richness (Ortega-Baes and Godínez-Álvarez, 2006; Ortega-Baes et al., 2010b), however, there is very little research about the effect of light on cacti seed germination in these countries; Chile is the second country with cacti taxa studied (18.9%), followed by Argentina (14.3%), Brazil (5.6%), Peru (4.6%), USA (3.6%), and Venezuela (1.5%).

Seed responses to light are important for preventing the occurrence of germination in places and at times that are unfavourable for seedling establishment. Such responses might also be important for plants that establish under the shade of nurse plants like most cacti species do (Flores and Jurado, 2003; Godínez-Álvarez et al., 2003). RLG differed among taxa, plant height, dispersal syndrome, and seed mass when analyzing dormant and non-dormant taxa. We found that the response to light was associated with phylogeny, since Cacteae, Pachycereeae and Trichocereeae had higher RLG than Notocacteeae. Thus it is possible that the response to light is associated with common ancestors (Fenner and Thompson, 2005). However, we also found that RLG decreased with increasing plant height and seed mass, and it was also related to seed dispersal. Since each subfamily has species with different traits, we suggest that the effect of common ancestors is smaller than the effect of other traits. Plant height is considered an important trait in the evolution of plants (Falster and Westoby, 2003). Seeds from shorter cactus plants (and small seeds) have a stronger light requirement for germination than those from taller plants (and large seeds), similar to findings by Kyereh et al. (1999) for small stature genera of forest trees in Ghana. Thus, it is possible that seeds from tall plants have the capacity to produce taller seedlings than those from short plants.

Seed dormancy was unrelated to RLG. This is in contrast with other studies that suggest non-dormant seeds of cacti (Flores et al., 2006) and of other families (Thompson and Grime, 1979; Grime et al., 1981; Rees, 1993; Pons, 2000) are positively photoblastic. Perhaps future studies with a larger number of species might separate dormancy types and their effect on photoblastism. In this study when excluding dormant taxa using different germination percentages we found consistent differences between least square means RLG among taxon and plant height, but seed dispersal and seed mass were only marginally associated with RLG when considering taxa ≥60% germination, and not associated for those ≥70% germination. This reduction in significant associations could be result of a clear distinction between non-dormant taxa and taxa with seeds coming out of dormancy or just an artifact of a smaller sample size.

Seed dispersal and photoblastism were associated when analyzing dormant and non-dormant taxa, and for non-dormant taxa with ≥50% germination. RLG was smaller for taxa with endozoochoric, synzoochoric and hydrochoric seeds compared to those with unassisted seeds. These results suggest that germination of seeds dispersed by animals could be less dependent on light; perhaps because seeds may end up covered by dung. However, Vázquez Yanes and Orozco Segovia (1986) suggested that the passage through intestines of different dispersers may alter the optical properties of the seed coat and therefore the photoblastic response. In addition, it has been suggested that large seeds are generally more difficult to disperse than small ones, since big seeds need larger animals, stronger winds or more powerful propulsion than small seeds (Willson and Traveset, 2000). However, most cacti seeds (small and large) requiring light were animal-dispersed. This is similar to findings by Díaz and Cabido (1997) of vertebrate-dispersed seeds being common in cacti.

Life form and photoblastism were not related, coinciding with Ortega-Baes et al. (2010a), but in contrast to suggestions that life form is associated with photoblastism in Cactaceae (Rojas-Aréchiga et al., 1997). The latter authors argue for a relationship between a light requirement for germination and life form in seven cacti species of the Zapotitlán Valley in Southern Mexico. Probably, this relationship is a result of plant height, as globose cacti are in general shorter than columnar cacti. Perhaps light requirement is related to vertical distribution of temperature during the day, since daily temperature variations are larger closer to the ground and are smaller with increasing plant height (Lowry, 1978). Temperature during seed development has been found to affect seed response to light during germination (Contreras et al., 2009). Seeds of short cacti are more exposed to high temperatures than tall cacti. Thus, cacti temperature requirements could be associated with vertical distribution of environmental temperatures during seed development, as suggested by Rojas-Aréchiga et al. (1997).

There are few studies that deal with cactus seed mass and photoblastism. Maiti et al. (2003) and Flores et al. (2006) suggested that cactus seeds requiring light were small. A light requirement for germination of small seeds is probably very relevant because positive photoblastism is one of the physiological characteristics that could favour formation of a soil seed bank (Thompson et al., 1993, 2001; Hodkinson et al., 1998; Bowers, 2000; Rojas-Aréchiga and Batis, 2001). In contrast, cactus seeds that do not require light to germinate tend to be large. It is possible that seeds from large seeds produce seedlings that have the ability to emerge from greater soil depths than those from small seeds, since they have more resources. This, however, remains to be tested.

Acknowledgements

Financial support was obtained from SEMARNAT S-3406, SEP-CONACYT-44806, PAICYT, and UANL FCF PG. K. Thompson provided excellent advice on an early version of the manuscript. Some data were obtained during a Sabbatical leave of JF in the Cactus Seed Biology Monograph Project at the Millennium Seed Bank, Kew. The Millennium Seed Bank Project is supported by the Millennium Commission, The Wellcome Trust, Orange Plc., and Defra. The Royal Botanic Gardens, Kew, receive grant-in-aid from Defra.

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