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Are cactus growth forms related to germination responses to light? A test using *Echinopsis* species

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ABSTRACT

In this study, we investigated the effect of light regimen (white light vs. darkness) on the germination of 12 species of the *Echinopsis* genus (tribe Trichocereeae, Cactaceae). This genus presents a variety of growth forms and relatively small and uniform seed size. These traits allowed us to test, within the same linage and removing seed mass effect, the hypothesis that the germination response to light (indifferent to light or positive photoblastic) is related to growth form. Our results reject this hypothesis since no seeds germinated in darkness, so all of the species can be classified as being positively photoblastic. The proportion of seed germination with white light was significantly different among cactus growth forms. Columnar cacti (arborescent, creeping and short) showed a greater proportion of seed germination than barrel and globose cacti. The germination rate differed among growth forms and species. At constant temperatures, creeping columnar cacti presented a significantly higher germination rate than the other growth forms. With alternating temperatures, columnar cacti showed higher germination rates than the other growth forms. The low proportion of seeds that germinated for some species indicates that they show seed dormancy. Our results suggest that germination responses to light in the cactus family could be related to seed mass and phylogenetic constraints.

1. Introduction

Seed germination is an important process in the plant life cycle. Several studies have focused on the relationship between germination responses and different plant traits such as life form, seed mass, regeneration strategy, rarity, and lineage, among others (Flores and Briones, 2001; Luna and Moreno, 2009; Luna et al., 2007; Ramírez-Padilla and Valverde, 2005; Rojas-Aréchiga et al., 1997). Life form has been associated with germination responses to light (Luna and Moreno, 2009; Rojas-Aréchiga et al., 1997), temperature (Flores and Briones, 2001; Jurado et al., 2000) and soil water potential (Flores and Briones, 2001). For example, succulent plants (i.e., cacti) have been shown to germinate at higher temperatures than the shrubs that inhabit the same arid regions (Flores and Briones, 2001).

Cacti are conspicuous elements of the arid and semi-arid environments of the Western Hemisphere. In recent years, important advances have been made in understanding different aspects of their biology (Godínez-Alvarez et al., 2003; Hunt, 2006; Nobel, 2002; Ortega-Baes and Godínez-Alvarez, 2006; Ortega-Baes et al., 2010; Rojas-Aréchiga and Vázquez-Yanes, 2000; Seal et al., 2009; Terrazas and Arias, 2003). Seed germination and seedling establishment are considered to be critical stages in the cactus life cycle and are thought to be mainly affected by soil water availability (Godínez-Alvarez et al., 2003). However, a great number of studies conducted with several cacti species belonging to different life forms have indicated that seed germination is also affected by light and temperature (Benítez-Rodríguez et al., 2004; Flores et al., 2006; Ortega-Baes and Rojas-Aréchiga, 2007; Rojas-Aréchiga et al., 1997, 1998; Rojas-Aréchiga and Vázquez-Yanes, 2000).

Studies of the effects of different light regimes on cactus seed germination have demonstrated that cactus species are either positively photoblastic or indifferent to light (Benítez-Rodríguez et al., 2004; Flores et al., 2006; Ortega-Baes and Rojas-Aréchiga, 2007; Rojas-Aréchiga et al., 1997; Rojas-Aréchiga and Vázquez-Yanes, 2000). It has been suggested that light responses could be related to different cactus growth forms (life forms; Rojas-Aréchiga et al., 1997).

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However, the relationship between cactus growth form and response to light is not obvious (Rojas-Aréchiga et al., 1997). All cacti are succulent plants; therefore, the response to light should be similar among cacti, but should vary with respect to other life forms (e.g., shrubs, trees). We considered it unlikely that seeds of globose cacti (or barrel cacti) have different germination responses to light than those of columnar cacti, unless there was another trait correlated with the growth form that was actually affecting the germination response to light. Germination response to light is more likely to be closely related to seed mass in cacti. However, this could also be the result of phylogenetic constraints.

The aim of our study was to determine the effects of the light regimen (white light vs. darkness) on seed germination in 12 cactus species of the *Echinopsis* genus. This is a South American genus of the tribe Trichocereeae (subfamily Cactoideae) that contains a high diversity of species with different growth forms, including globose, barrel, and columnar (Gibson and Nobel, 1986; Hunt, 2006). In addition, *Echinopsis* species have small seeds with little seed mass variation (0.696 ± 0.204; Seal et al., 2009). The wide variety of growth forms in the *Echinopsis* genus allows us to test, within the same lineage in Cactaceae and removing the potential effects of seed mass, the hypothesis that the germination response to light (indifferent to light or positive photoblastic) is related to the growth form (Rojas-Aréchiga et al., 1997). If the growth form is linked to the germination response to light, we would expect differences in germination behavior among different forms. Barrel and globose cacti have been shown to have a positive photoblastic response (Benítez-Rodríguez et al., 2004; Flores et al., 2006; Rojas-Aréchiga et al., 2008, 1997; Ruedas et al., 2000;), while columnar cacti can be either indifferent to light or positively photoblastic (Rojas-Aréchiga et al., 1997; Ortega-Baes and Rojas-Aréchiga, 2007). However, we believe that if lineage and seed mass effects are removed, there are no differences in the germination responses to light among cactus growth forms.

2. Materials and methods

2.1. Seed collection

From January to March 2007, ten fruits were collected from five individuals in Salta Province (Argentina), except for seeds of *Echinopsis candicans*, which were collected in La Pampa province (Argentina). Seeds were extracted from fruits, dried, stored at 5 ± 2 °C and sowed two months after harvest. Species names included in this study are listed in Table 1 and were named according to Hunt (2006). Site collection locations are not listed for protection purposes. Species were classified according to their growth forms: globose, barrel and three columnar types. The three columnar types were as follows: 1) *arborescent columnar*, in which individuals show a main erect and long axis (~15 m of height) and medial or terminal branching; 2) *short columnar*, in which individuals present one or many short axes (~1 m of height); and 3) *creeping columnar*, in which stems grow parallel to the soil surface, with the stem apical region erected. We recorded seed mass for each of the species (four lots of 25 seeds each, per species; Table 1).

2.2. Light effects

Light effects on seed germination were evaluated under two temperature regimes, constant (25 °C) and alternating temperatures (30/20 °C). Although many species germinate optimally at specific constant temperatures, it is frequently beneficial to use alternating temperatures. Seed testing associations frequently use a daily alternating temperature cycle of 30 °C/20 °C for tropical species (ISTA, 2008). However, the germination response to alternating temperatures may be negative for many cactus species. Consequently, it is more suitable to replicate the same experiment at constant and alternating temperatures (Ortega-Baes and Rojas-Aréchiga, 2007).

The light treatments were white light (8 h light/16 h dark) and darkness. For each species, four replicates of 25 seeds per treatment were sown on the surface of 1% agar in Petri dishes and were placed in temperature- and light-controlled incubators. At the alternating temperature, the light period coincided with the higher temperature. Germination was recorded daily for 30 days, and the emergence of the radicle was scored as germination. Darkness was achieved by wrapping Petri dishes in two pieces of aluminum foil, and germination was recorded at the end of the experiment. At the end of the germination assays, the viability of non-germinated seeds was analyzed. Seeds were cut longitudinally and embryos were observed under a stereoscopic microscope. Seeds were considered to be viable if their embryos were white and turgid. According to this method, all seeds were considered viable for this study. The response variables were the proportion of germinating seeds and the germination rate ($1/t_{50}$).

2.3. Statistical analysis

To calculate germination rates, germination progress curves were plotted for each temperature regime. Subsequently, the time

Table 1
Species, seed mass (mean ± standard deviation) and germination response (proportion and $1/t_{50}$ (d^{-1}); mean ± standard error) for 12 *Echinopsis* species (Cactaceae) of different life forms. Statistical differences between treatments are indicated by different letters.

Growth form	Species	Seed mass (g)	Seed germination proportion		$1/t_{50}$ (d^{-1})	
			25 °C	20/30 °C	25 °C	20/30 °C
Globose	*Echinopsis albispinosa*	0.0214 ± 0.0007	0.400 ± 0.083^{A}	0.510 ± 0.085^{B}	0.050 ± 0.0003^{A}	0.102 ± 0.009^{B}
	E. ancistrophora	0.0195 ± 0.0007	0.390 ± 0.019^{A}	0.490 ± 0.025^{B}	0.089 ± 0.008^{B}	0.043 ± 0.0001^{A}
	E. haematantha	0.0184 ± 0.0005	0.280 ± 0.065^{A}	0.220 ± 0.038^{A}	0.092 ± 0.011^{B}	0.086 ± 0.025^{B}
Creeping columnar	*E. angelesiae*	0.0131 ± 0.0004	0.590 ± 0.082^{B}	0.570 ± 0.025^{B}	0.115 ± 0.001^{C}	0.108 ± 0.021^{B}
	E. thelegona	0.0115 ± 0.0004	0.930 ± 0.034^{C}	0.940 ± 0.035^{D}	0.150 ± 0.000^{D}	0.156 ± 0.001^{C}
Arborescent columnar	*E. atacamensis*	0.0187 ± 0.0007	0.850 ± 0.070^{C}	0.900 ± 0.026^{D}	0.117 ± 0.001^{C}	0.158 ± 0.009^{C}
	E. terscheckii	0.0172 ± 0.0007	0.840 ± 0.000^{C}	0.740 ± 0.035^{C}	0.116 ± 0.00003^{C}	0.109 ± 0.021^{B}
Short columnar	*E. candicans*	0.0108 ± 0.0006	0.820 ± 0.038^{C}	0.820 ± 0.042^{C}	0.089 ± 0.001^{B}	0.145 ± 0.002^{C}
	E. schickendantzii	0.0100 ± 0.0002	0.880 ± 0.028^{C}	0.950 ± 0.010^{D}	0.112 ± 0.004^{C}	0.136 ± 0.002^{C}
	E. walterii	0.0082 ± 0.0002	0.660 ± 0.026^{B}	0.820 ± 0.048^{C}	0.052 ± 0.001^{A}	0.083 ± 0.002^{B}
Barrel	*E. leucantha*	0.0182 ± 0.0023	0.160 ± 0.028^{A}	0.120 ± 0.049^{A}	0.080 ± 0.015^{B}	0.043 ± 0.001^{A}
	E. thionantha	0.0093 ± 0.0007	0.450 ± 0.066^{A}	0.500 ± 0.068^{B}	0.114 ± 0.001^{C}	0.068 ± 0.025^{AB}

taken (t) to reach 50% of the final proportion of germinated seeds at each temperature was estimated (t_{50}), and the reciprocal ($1/t_{50}$) was plotted against the temperature (Bewley and Black, 1994). The effects of light on the final proportion of seeds that germinated and the germination rate were examined with alternating and constant temperature experiments using an unbalanced ANOVA on arcsine-transformed data, which considered species as being nested in the growth form factor. Means were compared using a *post hoc* DGC test (Di Rienzo et al., 2002). Treatments in which the proportion of seeds that germinated was zero for all replicates were not included in the ANOVA. Statistical analyses were conducted using the statistical program INFOSTAT (2007).

3. Results

None of the seeds germinated in darkness under any of the temperature regimes. The proportions of seeds that germinated with white light were significantly different among the cactus growth forms (constant temperature: $F_{4,36} = 42.83$, $p < 0.001$; alternating temperature: $F_{4,36} = 53.18$, $p < 0.001$) and cactus species (constant temperature: $F_{7,36} = 6.44$, $p < 0.0001$; alternating temperature: $F_{7,36} = 12.90$, $p < 0.0001$; Table 1). Under both temperature regimens, arborescent columnar, short columnar and creeping columnar life forms showed the greatest proportions of germinating seeds relative to barrel and globose cacti (Table 1). Under both temperature regimens, *Echinopsis leucantha* and *Echinopsis haematantha* showed the lowest proportion of germinating seeds (Table 1).

With both constant and alternating temperatures, germination rates were different among the growth forms (constant temperature: $F_{4,36} = 35.09$, $p < 0.001$; alternating temperature: $F_{4,36} = 12.61$, $p < 0.0001$; Table 1) and among the cactus species (constant temperature: $F_{7,36} = 16.92$, $p = 0.0001$; alternating temperature: $F_{7,36} = 4.69$, $p < 0.0009$; Table 1). At constant temperature, the creeping columnar growth form presented a significantly higher germination rate (i.e. seeds germinated more rapidly) than the barrel and globose forms. With alternating temperatures, arborescent columnar, creeping columnar and short columnar growth forms presented higher germination rates than the others (Table 1). The highest germination rate was recorded for *Echinopsis thelegona* under a constant temperature regimen and for *E. thelegona*, *Echinopsis atacamensis*, *Echinopsis schickendantzii* and *E. candicans* under an alternating temperature regimen (Table 1). The lowest germination rate (i.e. seeds germinated more slowly) was recorded for *Echinopsis albispinosa* and *Echinopsis walteri* under a constant temperature and for *E. leucantha* and *Echinopsis ancistrophora* under alternating temperatures (Table 1).

4. Discussion

Like other cacti, *Echinopsis* species were positively photoblastic, i.e., seed germination is regulated by light. This behavior has been documented for other cactus species in North and South American deserts (Flores et al., 2006; Ortega-Baes and Rojas-Aréchiga, 2007; Rojas-Aréchiga and Vázquez-Yanes, 2000). The results obtained in this study do not support the hypothesis once proposed by Rojas-Aréchiga et al. (1997) that the germination response to light could be related to cactus growth forms. The results indicated that the species may respond to light in the same way independently of their growth form. Even though the number of species studied may seem reduced, the relation stated is not determined by the number of species considered, but by their type of behavior. Only one species of each growth form which does not differ in the type of response is enough to discard the idea of Rojas-Aréchiga et al. (1997).

Our results indicate that light responses in the *Echinopsis* genus could be related to phylogenetic constraints because all species tested showed the same response to light. However, the results obtained could also be related to seed mass. The germination response to light has been related to seed size, indicating that small seeds have a positive photoblastic response (Flores et al., 2006; Galíndez et al., 2009). *Echinopsis* species have small seeds (see Table 1; Seal et al., 2009); therefore, the light response recorded could be related to this seed trait. Thus, it is important to determine whether the type of light response *per se* is the result of phylogenetic inertia and/or the result of seed size.

The light requirements for germination and small seed size might be related to the ability to form a persistent seed bank (Bowers, 2000; Flores et al., 2006; Rojas-Aréchiga and Batis, 2001), which could be hypothesized for the species we have studied. de Viana (1999) previously demonstrated a short-term persistent seed bank for *E. atacamensis,* and preliminary studies have shown that the globose cacti *E. ancistrophora* and *E. albispinosa* have at least a short-term persistent seed bank (Ortega-Baes, unpublished data).

Our results showed differences in germination under white light treatments among growth forms and species. This could be due to the effects of storage (at 5 ± 2 °C during two months). Some cactus seeds acquire dormancy during storage, whilst other cactus species need an after-ripening period to reach higher germination percentages, which is achieved under storage. However, the germination behavior of cactus species in this study does not differ from one registered with non storage seeds of the same species (Ortega-Baes et al., in press). Variations in germination response to white light among cactus species have been related to seed mass (columnar cacti; Loza-Cornejo et al., 2008), but our results did not show this relationship. In our study, cactus species with statistically similar values of germination proportion are found at the extreme positions within the seed size range of studied species (see Table 1).

For 58% of the species studied, the proportion of germinated seeds was less than 0.7, indicating that seeds of these species may have dormancy (Flores et al., 2006). These species mainly belong to globose and barrel growth forms; this would suggest that columnar growth forms of the *Echinopsis* genus produce non-dormant seeds. The presence of seed dormancy in the cactus family has been recorded in globose (Flores et al., 2006, 2008), articulated (Mandujano et al., 2005; Orozco-Segovia et al., 2007), barrel (Godínez-Alvarez and Valiente-Banuet, 1998; Rojas-Aréchiga et al., 1997) and columnar growth forms (Ortega-Baes et al., in press; Rojas-Aréchiga et al., 1997); therefore, relationships between seed dormancy and cactus growth forms can be discarded.

It has been indicated that alternating temperatures are more favorable for seed germination because seeds under natural conditions experience daily temperature fluctuations (Baskin and Baskin, 1998). However, several studies on cactus seed germination have found negative (Ortega-Baes and Rojas Aréchiga, 2007; Rojas-Aréchiga et al., 2001, 1998), neutral (De la Barrera and Nobel, 2003; Godínez-Alvarez and Valiente-Banuet, 1998; Ramírez-Padilla and Valverde, 2005; Ruedas et al., 2000) or positive responses (Fearn, 1974, 1981; Godínez-Alvarez and Valiente-Banuet, 1998) to alternating temperature regimes. Our results indicate all three responses, suggesting that the response to alternating temperature in our study is species-specific. An important aspect of alternating temperature regimens is their interaction with the germination response to light in photoblastic species since these temperatures can induce germination in darkness (Probert, 1992). Our results agree with other authors in that photoblastic cactus species do not germinate with alternating temperatures; however, it would be useful test other alternating temperatures as well (Ortega-Baes and Rojas Aréchiga, 2007).

In summary, *Echinopsis* species have positive photoblastic seeds regardless of their growth form, which does not support the hypothesis of Rojas-Aréchiga et al. (1997). Some species may have dormant seeds, especially those of the globose and barrel growth forms. The results suggest that germination responses to light in the cactus family could be related to seed mass and phylogenetic constraints. More comprehensive studies including different lineages and seed mass variations should be conducted to test this idea.

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