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Effects of alternating temperature on cactus seeds with a positive photoblastic response

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A B S T R A C T

Temperature is an important factor governing cactus seed germination. Particularly, alternating regimes can have positive, neutral and negative effects on germination. We studied the effects of constant and alternating temperatures on the germination of positive photoblastic seeds of six cactus species native to Argentina. Seeds of all species failed to germinate in darkness, irrespective of temperature regimes. Seed germination was significantly affected by temperature. For constant temperature, *Cereus hankeanus*, *Echinopsis atacamensis*, *E. terscheckii* and *Parodia aureicentra* showed a higher proportion of maximum germination than *E. ancistrophora* and *Gymnocalycium saglionis*. In *E. atacamensis* and *E. terscheckii*, the effect of alternating temperature was neutral, as no differences were registered among the maximum germination values obtained for both temperature regimes. The other species showed reduced germination under alternating temperatures in relation to the maximum values obtained at constant temperatures, indicating a negative effect of temperature alternation. In addition, our results confirm the idea that alternating temperatures do not promote the germination of positive photoblastic cactus seeds in darkness.

1. Introduction

Temperature is one of the most important environmental factors that affect the timing of emergence, the overall population rate and the percentage of germinating seeds (Baskin and Baskin, 2014; Probert, 2000). The seeds of desert plants germinate over a wide range of temperatures, with a maximum percentage between 15 °C and 25 °C (Baskin and Baskin, 2014; Rojas-Aréchiga and Vázquez-Yanes, 2000). It has been suggested that alternating temperatures would be more favorable for germination than constant temperatures because seeds in natural conditions are submitted to daily fluctuations in this environmental factor (Baskin and Baskin, 2014).

The seeds of cactus species germinate between 17 °C and 34 °C, with optimal values at approximately 25 °C and are affected by low and high extreme values (Ortega-Baes and Rojas-Aréchiga, 2007; Ortega-Baes et al., 2011). In relation to alternating temperatures, three response types are possible in cacti and other species: positive, neutral and negative (Yang et al., 2003; Ortega-Baes and Rojas-Aréchiga, 2007; Ortega-Baes et al., 2011). These types of responses may be attributed to the limited number of temperature regimes used in previous studies (Ortega-Baes et al., 2011). In this sense, for the cactus *Echinopsis schickendantzii*, no differences in germination were found between the stimulatory effects of constant and alternating temperatures when a wide range of temperatures were used (Ortega-Baes et al., 2011). Even though species that inhabit arid environments would be the most sensitive to non-constant temperatures (Baskin and Baskin, 2014), this might not be so evident in cacti because seedling establishment generally occurs under nurse plants where the amplitude of soil temperature fluctuations is less extreme (Godínez-Alvarez et al., 2003; Ortega-Baes et al., 2011).

Alternating temperatures can substitute the light requirements for germination in positive photoblastic species (Mahmoud et al., 1983, 1984; Pons, 2000). Although positive photoblastism seems to be a relatively common feature in the cactus family (Ortega-Baes et al., 2010; Flores et al., 2011), few studies have evaluated whether alternating temperatures can substitute the light requirements for germination in these species (Rojas-Aréchiga and Vázquez-Yanes, 2000; Ortega-Baes and Rojas-Aréchiga, 2007; Ortega-Baes et al., 2010). So far, results indicate that alternating temperatures do not substitute the light requirements in cactus seeds; however, these evaluations have only been

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made over a limited range of alternating temperatures (Ortega-Baes and Rojas-Aréchiga, 2007; Ortega-Baes et al., 2010).

In this paper, we studied the effects of constant and alternating temperatures on seed germination in six species of cactus from Argentina, which were distributed in arid and semiarid regions. Specifically, we formulated the following questions: 1) Does the germination response to alternating temperatures (negative, neutral or positive) depend on the temperature level the seeds are exposed to, or is it a species-specific response? 2) Does alternating temperature substitute seed light requirements in positive photoblastic seeds?

2. Materials and methods

In January 2013, at least five fruits were collected from a minimum of three individuals for each species. Seeds were extracted from fruits, dried and stored in paper bags in the dark until the experiments began (February 2013). The studied species were *Cereus hankeanus*, *Echinopsis ancistrophora*, *E. atacamensis*, *E. terscheckii*, *Gymnocalycium saglionis* and *Parodia aureicentra*, all of which are native of the northwest of Argentina (Ortega-Baes et al., 2012). These species have positive photoblastic seeds (Ortega-Baes et al., 2010; Flores et al., 2011).

To evaluate the effects of constant and alternating temperatures on seed germination, a factorial experiment was performed (6 × 8 x 2) where the factors evaluated were species identity (six levels), temperature (eight levels: 30/20, 25/15, 25/10, 25/5, 30, 25, 20 and 15 °C) and light regime (two levels: white light and darkness). For each treatment, four replicates of 25 seeds were sown on the surface of 1% agar in water in Petri dishes and incubated with an 8 h-light/16 h-dark photoperiod. In the alternating temperature regimes, the light period coincided with the highest temperature. Germination was defined as radicle protrusion through the seed coats by > 1 mm and the proportion of germinated seeds was recorded daily for 30 days. 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 (Ortega-Baes et al., 2010). According to this method, all seeds were considered viable for this study.

2.1. Statistical analysis

Because no seeds germinated in the dark, we adjusted a linear model that considered the effect of the species, temperature and their interaction on the proportion of germinated seeds (p), and modeled the heterogeneity of variance among species. The data were transformed using an arcsine of the square root of p and the means were compared using a *post hoc* DGC test (Di Rienzo et al., 2002). Statistical analyses were conducted using the statistical software INFOSTAT (2009).

3. Results

For all the studied species, no seeds germinated in darkness under the considered temperature regimes. The proportion of germinated seeds was significantly affected by temperature ($F = 107.15$, $p < 0.001$), species ($F = 142.41$, $p < 0.001$) and their interaction ($F = 23.90$, $p < 0.001$). For constant temperature, the highest germination was registered in *C. hankeanus* (20 and 25 °C), *E. atacamensis* (20 °C), *E. teschecki*i (25 °C) and *P. aureicentra* (15 °C and 20 °C; Fig. 1). In *E. ancistrophora* the highest values for the germination proportion was registered at 20, 25 and 30 °C, while for *G. saglionis* the highest value of germination was recorded at 20 °C (Fig. 1). In all species, the lowest proportion of germination was registered at 15 °C and/or 30 °C, with the exception of *E. atacamensis*.

For alternating temperatures, the highest germination was registered in *E. atacamensis* (25/10, 25/15 and 30/20 °C) and in *E. terscheckii* (25/15 °C; Fig. 1). The lowest germination was registered at 25/5 °C (*E. ancistrophora*, *E. terscheckii* and *G. saglionis*) and at 25/10 °C (*G. saglionis*; Fig. 1). No significant differences between the highest values at constant and alternating temperatures were registered in *E. atacamensis* and *E. terscheckii* (Fig. 1). For the rest of the species, the maximum germination values obtained at alternating temperatures were always significantly lower than those obtained at constant temperature (Fig. 1).

4. Discussion

In general, the highest proportion of germinated seeds was recorded for constant temperatures at 20 and/or 25 °C. Our results coincide with those reported for other cactus species which indicated that the optimum temperature was approximately 25 °C. Except for *E. atacamensis*, germination was affected by extreme temperatures (15 and/or 30 °C), as has been registered for other species (Rojas-Aréchiga and Vázquez-Yanes, 2000; Yang et al., 2003; Ortega-Baes et al., 2011). According to our results, the responses of the studied species to alternating temperatures can be classified as neutral or negative. Thus, in *E. atacamensis* and *E. terscheckii*, there were no differences between the maximum values obtained at constant temperature and those obtained at alternating temperatures, while in the other species, the response was always negative. Therefore, the response of cactus seeds to alternating temperatures seems to be species-specific (Yang et al., 2003; Ortega-Baes et al., 2011).

The results registered at 30/20 °C showed that 30 °C is not a risky temperature for seed viability, even though they were exposed to this temperature for 8 h every day for 30 days. On the other hand, the results obtained at 25/5 and 25/10 °C suggest a negative effect of such cold temperatures on cacti seed germination, probably because these temperatures could induce dormancy. In contrast, in *E. atacamensis* and *P. aureicentra,* positive germination response to these cold temperatures could be related to the habitats where they are distributed, which are characterized by greater daily fluctuations in temperature, even during the rainy season.

Our results suggest that temperature is a factor that might regulate seed germination in natural conditions because it was lower in alternating temperature treatments, at least in some species. Cactus species undergo fluctuations in daily temperature and seedling establishment is generally associated with nurse plants or rocks, which cause the minimum temperatures to be higher and the maximum temperatures to be lower compared to bare soil (Godínez-Alvarez et al., 2003). Thus, these results support the idea that the seeds should germinate better under conditions of relatively stable temperatures (Ortega-Baes et al., 2011).

An important aspect of alternating temperature regimes is their interaction with the germination response to light in positive photoblastic species because these temperatures can induce germination in darkness (Probert, 2000). Positive photoblastism seems to be a common feature in cactus species because most of the studied species exhibit this type of behavior to light (Ortega-Baes et al., 2010; Flores et al., 2011). Our results confirm previous studies that classified the studied species as positive photoblastic (Ortega-Baes et al., 2010; Flores et al., 2011) and agree that alternating temperatures do not promote germination in darkness in cactus species with positive photoblastic seeds (Ortega-Baes and Rojas-Aréchiga, 2007; Ortega-Baes et al., 2010).

In summary, we recorded that in some species, alternating temperatures may have similar promoting effects on seed germination that constant temperatures (neutral behavior), while in other species, germination is affected by this temperature regime (negative behavior). Therefore, our results suggest that the response of cactus seeds to an alternating temperature regime would be species-specific. In addition, our results confirm the idea that alternating temperatures do not promote germination of cactus seeds in darkness. Cactus seeds seem to germinate better under relatively stable temperature conditions; this would explain to some degree why cactus establishment is greater

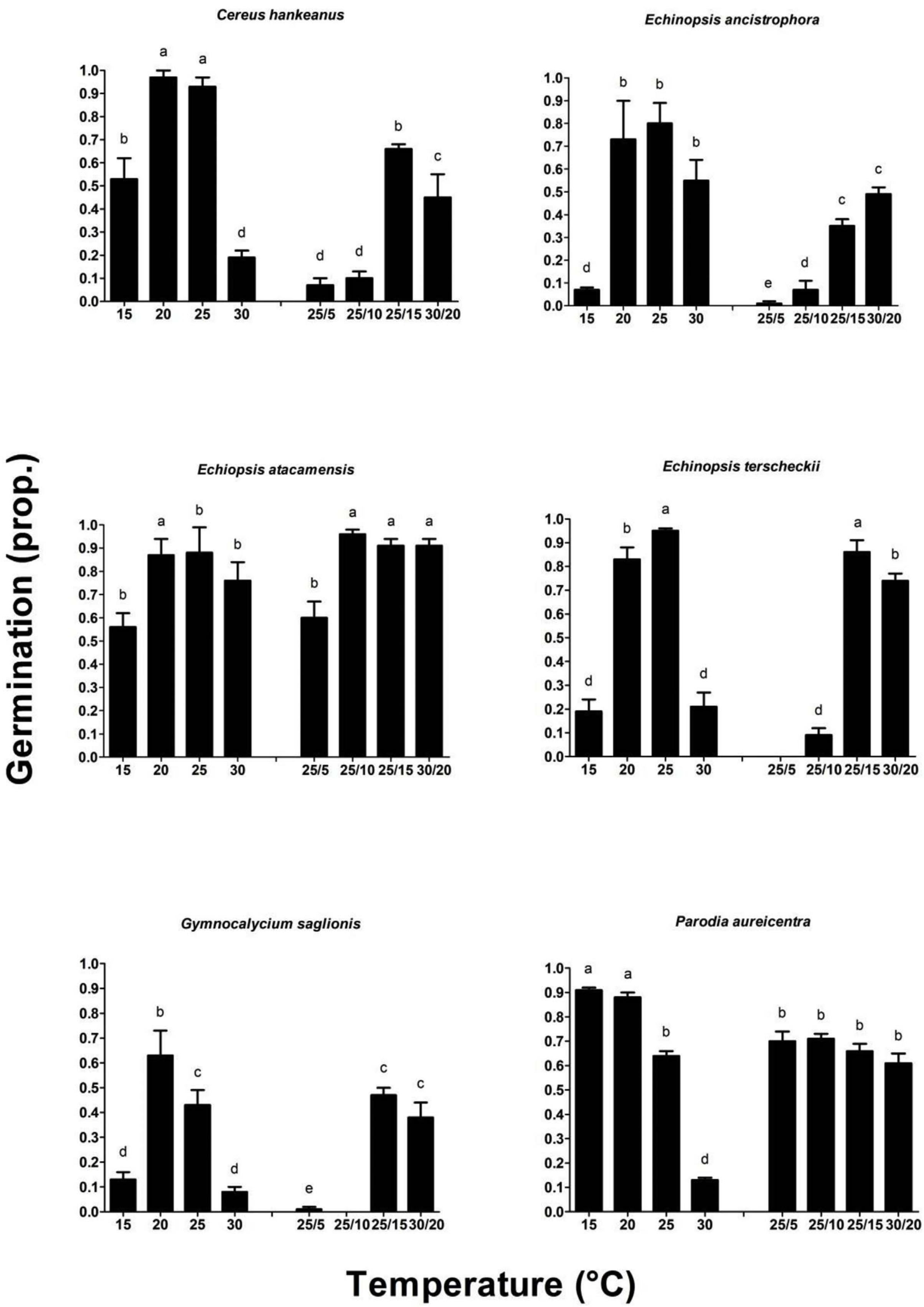

Fig. 1. Germination proportion (mean ± standard error) of six cactus species at constant and alternating temperatures. Different letters indicate significant differences in the mean value of the transformed variable for the combination of species x temperature according to a DGC test.

under nurse plants or rocks than in bare soil. Further studies should test this idea in field experiments and analyze the effects of this factor together with others that have been considered relevant to cactus seedling establishment (Godínez-Alvarez et al., 2003).

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