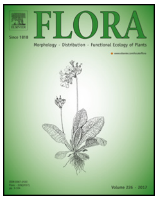
Flora 227 (2017) 18–24

Contents lists available at ScienceDirect

Flora

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



Combined effect of water potential and temperature on seed germination and seedling development of cacti from a mesic Argentine ecosystem

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ARTICLE INFO

Article history:
Received 24 June 2016
Received in revised form 5 December 2016
Accepted 8 December 2016
Edited by Hermann Heilmeier
Available online 10 December 2016

Keywords:
Climate change
Germination characteristics
Seedling traits
Cactaceae
Córdoba Mountains

ABSTRACT

Global climatic change will be associated with an increase of droughts and heat waves, which can affect seed germination and plant population dynamics. Cactus species from mesic ecosystems are likely to be more affected by these events than species from arid ecosystems. The aim of the study was to assess the combined effect of water potentials and temperatures on seed germination and seedling traits in six globose cactus species from Córdoba Mountains: *Echinopsis candicans*, *Gymnocalycium bruchii*, *G. capillense*, *G. mostii*, *G. quehlianum* and *Parodia mammulosa*. A factorial experiment was performed in which four water potential levels (0, −0.2, −0.4 and −0.6 MPa) were combined with two temperature levels (25 and 32 °C). Germination (%) and mean germination time (T_{50}) were recorded and seedling shape (width and length) was measured. In general, a decrease in water potential and an increase in temperature resulted in low germination, with different behaviors among species. At 32 °C and low water potentials, germination was low or null for almost all species. There was not a clear trend in the response of T_{50} to the treatments. Seedling development was highly and negatively affected by the combination of factors, particularly at low water potentials. The responses of the analyzed cactus species to low water potential were similar to those of cactus species from more arid ecosystems. Our results suggest that the studied species would be severely affected by changes in temperature and precipitation as predicted under a climate change scenario.

1. Introduction

Seed germination is a critical stage in the life-cycle of most plant species (Baskin and Baskin, 2001a). In slow growing species, like succulents, seed germination plays an important role in maintaining population dynamics (Godínez-Álvarez et al., 2003). Rainfall in arid and semiarid ecosystems is extremely variable in space and time, and droughts are common; thus, the soil is rarely maintained at its field water capacity (McGinnies, 1979; Whitford, 2002). In these environments, succulent species, such as cacti, developed germination strategies to cope with these constraints (Dubrovsky, 1996; Rojas-Aréchiga and Vázquez-Yanes, 2000). Even though most non-epiphytic cacti species inhabit arid or semiarid areas, many species inhabit more mesic environments such as those in southern Brazil, Uruguay and Córdoba Mountains in Argentina (Dutra Saraiva and Souza, 2012; Gurvich et al., 2014). The germination biology of cactus species from mesic environments is not well known (Gurvich et al., 2008 De la Rosa-Manzano and Briones, 2010); it has been suggested that cacti from those environments would not be adapted to germinate at drier conditions (Contreras-Quiroz et al., 2016).

Water availability and temperature are the most important factors in determining seed germination (Baskin and Baskin, 2014). Cacti from arid ecosystems, whose seeds are subjected to high temperatures and highly variable soil moisture, have likely developed adaptations to cope with these conditions. For example, cactus species from arid environments germinate well at high water potentials and some of them can germinate at relatively low water potentials (up to −0.8 or −1 MPa; De la Barrera and Nobel, 2003;

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http://dx.doi.org/10.1016/j.flora.2016.12.003

Guillén et al., 2011). Germination of some species is higher at lower water potentials than at field capacity (Flores and Briones, 2001). Many arid zone cacti can germinate at rather high temperatures (Gurvich et al., 2008; Pérez-Sánchez et al., 2011). However, few studies have analyzed the combined effect of these two factors (Ramírez-Padilla and Valverde, 2005; Meiado et al., 2010; Simão et al., 2010). Bauk et al. (2017) studied one species along an elevation gradient in central Argentina and found that the combination of high temperatures and low water potentials has strong negative effects on germination: populations at higher altitudes (cooler and wetter climatic conditions) were more strongly affected by the combination of high temperature and low water potential than lower-elevation populations. Global climate change is expected to increase not only mean values of climate parameters, but also the frequency of extreme events (McCarthy et al., 2001; Gurvich et al., 2002). Particularly, droughts and heat waves are expected to increase in number and duration, which could have profound effects on seeds in the soil and on plant population dynamics (Ooi et al., 2009). These effects are expected to be very important for cactus species from mesic environments, as they would be less adapted to heat and drought than species from arid environments.

Recent studies have found inter- and intraspecific differences in the size and shape of cactus seedlings (Sosa Pivatto et al., 2014; Bauk et al., 2015; Flores et al., 2016). Species with heavy seeds not only present large seedlings but also are usually columnar in shape (Sosa Pivatto et al., 2014), which might be advantageous for light capture. Bauk et al. (2015) found intraspecific differences in seedling shape in *Gymnocalycium monvillei* along an elevation gradient. These studies highlight that seedling traits are important in determining the early success of individuals. However, none of them analyzed how environmental conditions during germination, such as different temperatures and water potentials, can affect seedling traits (Flores et al., 2016).

The Córdoba Mountains region in central Argentina is an important center of cactus diversity and endemism (Gurvich et al., 2006, 2014). The climate of the Mountains is mesic in terms of temperature and precipitation (De Fina, 1992; Contreras-Quiroz et al., 2016). The aim of this study was to analyze the combined effect of water potential and temperature on germination characteristics (germination percentage and mean germination time, T_{50}) and seedling shape of six globose cactus species. Our main hypothesis is that seed germination and seedling traits of cactus species from a mesic environment would be negatively affected by high temperatures and low water potentials.

2. Materials and methods

2.1. Studied species and study area

We analyzed seed germination for six common cactus species that grow in Córdoba Mountains: *Echinopsis candicans* (Salm-Dyck) Hunt, *Gymnocalycium bruchii* (Spegazzini) Hosseus, *G. capillense* (Schick) Hosseus, *G. mostii* (Gürke) Britton & Rose, *G. quehlianum* (F. Haage ex Quehl) Vaupel ex Hosseus and *Parodia mammulosa* (Lemaire) Taylor. Representative species of different genera were selected based on their abundance in the area. All *Gymnocalycium* species are endemic to Córdoba Mountains, whereas the other species have a wider geographical distribution, being endemic to Argentina. Seed collection sites were close to the city of Capilla del Monte (30°52′09″S, 64°33′30″W). Mean annual temperature and precipitation are 16.5 °C and 750 mm (De Fina, 1992; Giorgis et al., 2015). Climate is warm temperate with dry winters and hot summers (Wca) according to Köppen-Geiger classification system (Kottek et al., 2006). Daily maximum temperatures during the warm season, when germination and establishment occurs, vary between 23 and 28 °C. Vegetation of the area is a mosaic of shrublands and grasslands, cacti species are mainly found in rocky outcrops (Gurvich et al., 2014). All species flower from spring to early summer, and fruits are mature from summer to early autumn (Gurvich et al., 2008; Giorgis et al., 2015). Mature fruits from 20 individuals (one or two fruits per individual) were collected from each species from December to February. Seeds were air-dried and stored in the laboratory at ambient conditions until the start of the experiments, four months after collection.

2.2. Germination experiment

We performed a factorial experiment in which four water potential treatments (0, −0.2, −0.4 and −0.6 MPa) were combined with two temperature levels (25 and 32 °C). The water potential values chosen are within the range of those reported during the rainy season for different soil types in semi-arid ecosystems (i.e., from −0.34 to −0.80 MPa; Ramírez-Padilla and Valverde, 2005). These temperatures were selected because 25 °C is the optimal germination temperature for these species (Gurvich et al., 2008) and also because it is close to the maximum mean temperature of the warmer months (De Fina, 1992), and 32 °C simulates a high temperature scenario expected for the region (Nuñez, 2006). The water potential of polyethylene glycol (PEG) solutions at the different temperatures was determined following Villela et al. (1991). Temperature treatments were performed in different germination chambers simultaneously. PEG 6000 was dissolved in distilled water and placed in a shaker bed at 20 °C for 16 h. Petri dishes of 0 MPa treatment contained 2 ml distilled water each. The water potentials of PEG solutions at each temperature were verified using a dew point micro-voltmeter (HR33T; Wescor Inc., Logan, UT, USA).

Seeds were set to germinate in Petri dishes. There were five Petri dishes per treatment with 20 seeds for each species. Each dish included filter paper and a PEG 6000 solution, which is harmless to seeds and mimics variations in soil moisture availability (Hardegree and Emmerich, 1994; De Villalobos and Peláez, 2001; Zeng et al., 2010). Seeds were set to germinate in germination chambers under a 12-h photoperiod. All dishes were sealed with plastic wrap to prevent evaporation. Germination was evaluated daily for 30 days; this time period exceeds that suggested by Baskin and Baskin (2001b) of about two weeks, because most of the seeds germinate within 10 days or less. We also used this time span to simulate the expected number of germinated seeds after a single rainfall event (Jurado and Westoby, 1992; Flores and Briones, 2001; Tobe et al., 2001). Protrusion of the radicle was the criterion for seed germination. The evaluated response variables were final germination percentage and mean germination time (T_{50}). T_{50} was calculated as:

$$T_{50} = \frac{\sum n_i t_i}{\sum n_i}$$

Where: n_i is the number of seeds newly germinated at time $_i$ and t_i is the period elapsed from the beginning of the germination test, expressed as number of days (Ellis and Roberts, 1978).

2.3. Seedling measurements

Thirty days after germination, seven seedlings per treatment were measured following Sosa Pivatto et al. (2014). Digital photographs were taken of each seedling, and seedling height and width were measured using BIO7 software.

2.4. Statistical analyses

To analyze germination percentage we performed generalized linear models, assuming binomial error distribution and using *Logit*

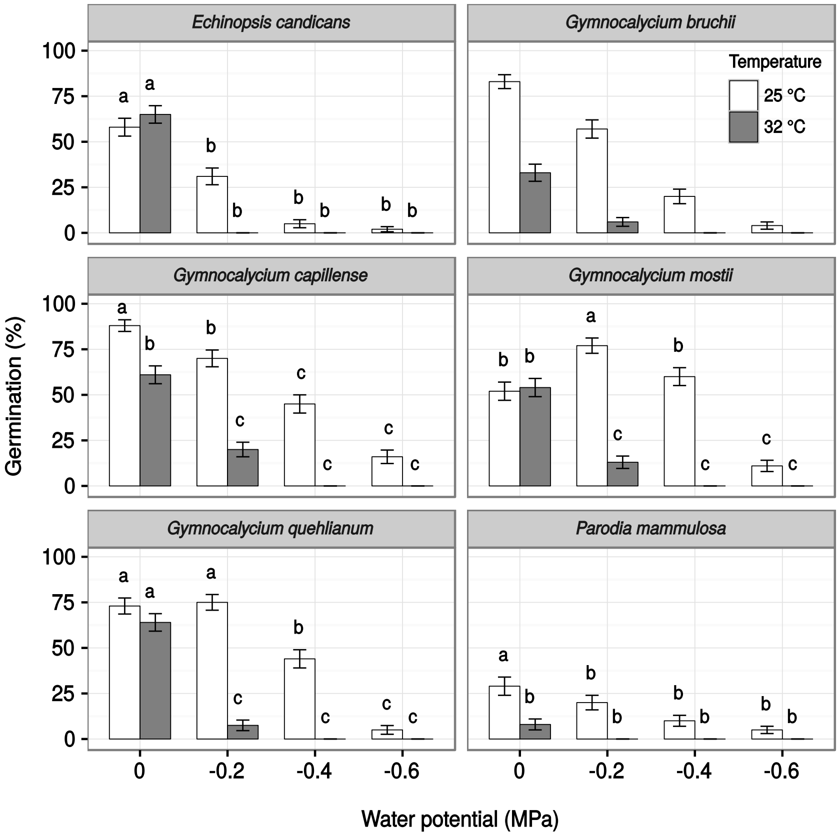

Fig. 1. Germination percentage (% and standard error, n = 5) of the analyzed species: (a) *Echinopsis candicans*, (b) *Gymnocalycium bruchii*, (c) *G. capillense*, (d) *G. mostii*, (e) *G. quehlianum* and (f) *Parodia mammulosa,* under four water potentials (0 control, −0.2, −0.4 and −0.6 MPa) and at two temperatures (25 and 32 °C). Different letters indicate significant differences for factor interaction effect (DGC *post hoc* test, $p < 0.05$). Interaction was not significant for *G. bruchii*; however principal factors present significant effect on this species (see main text for detailed results).

link function. We evaluated the effect of temperature and water potential, and of their interaction. For T_{50} we performed the analysis only for replicates with germination ≥ 20%. Because germination was null at some levels of temperature and water potential, we considered the combination of both explanatory variables as one factor (different combinations of the explanatory variables are different levels). We performed a linear model (one-way ANOVA) and when errors did not meet the homoscedasticity assumption, we added a variance function to the model.

Since in many treatments germination was low and some seeds germinated but did not develop, we obtained seedling trait data for only three treatments: 25 °C/0 MPa, 25 °C/−0.2 MPa and 32 °C/0 MPa. To analyze these results we performed linear models using the combination of both variables as one factor. When necessary, we added variance function to meet homoscedasticity assumption.

To explore differences among treatments in all analyses, we performed a *post-hoc* DGC test (Di Rienzo et al., 2002) when we found significant effect of factors or interactions. All statistical analyses were performed using Infostat v. 2015 (Di Rienzo et al., 2015; http://www.infostat.com.ar).

3. Results

We found a significant interaction effect of temperature and water potential on germination percentage in all species but *G. bruchii* ($p < 0.05$, see Appendix 1 in Supplementary material for complete model details). In general, germination percentage was higher at high water potentials (i.e. 0 MPa, sometimes −0.2 MPa) and at 25 °C (sometimes also at 32 °C; Fig. 1). No germination was recorded at −0.4 or −0.6 MPa at 32 °C. We did not find a significant effect of interaction of factors on germination percentage of *G. bruchii*. However, we found a significant effect of each principal factor ($p < 0.0001$). The pattern was similar to other species: germination was significantly higher at 25 °C (0.338 ± 0.037) than at 32 °C (0.000 ± 0.009) and significantly higher at 0 MPa (0.608 ± 0.041) than at lower water potentials (at −0.2 MPa, 0.225 ± 0.041; at −0.4 MPa, 0.000 ± 0.015 and at −0.6 MPa, 0.000 ± 0.006).

The effects of temperature × water potential interaction on T_{50} were different among species (see Appendix 2 Supplementary material). *G. bruchii*, *G. mostii* and *P. mammulosa* did not show an effect of treatments on T_{50} ($p > 0.05$). For *E. candicans*, T_{50} was low at 25 °C/0 MPa (fastest germination) and high at 25 °C/−0.2 MPa and 32 °C/0 MPa (Fig. 2). For *G. capillense*, T_{50} was low (i.e. fast germination) at 25 °C/0 MPa, 32 °C/0 MPa, and 32 °C/−0.2 MPa, and high (i.e. slow germination) in the other treatments (Fig. 2). Finally, *G. quehlianum* T_{50} was higher at 25 °C/−0.4 MPa (slower germination) than in the other treatments (25 °C/0 and −0.2 MPa, and 32 °C/0 MPa).

The effect of light and water potential on seedling height and width was statistically significant for all species ($p < 0.05$, see Appendix 2 Supplementary material). In addition, all species showed a similar response pattern (Fig. 3). The smallest length and width values of seedlings of all species were recorded at 25 °C/−0.2 MPa (Fig. 3). In general, seedlings were taller at 32 °C/0 MPa than at 25 °C/0 MPa (in *G. bruchii*, *G. capillense* and *G. quehlianum;* Fig. 3). Only *P. mammulosa* seedlings were taller at 25 °C/0 MPa than at 32 °C/0 MPa. Seedling width was smaller at the 25 °C/0 MPa than at 32 °C/0 MPa only in *E. candicans*, whereas no dif-

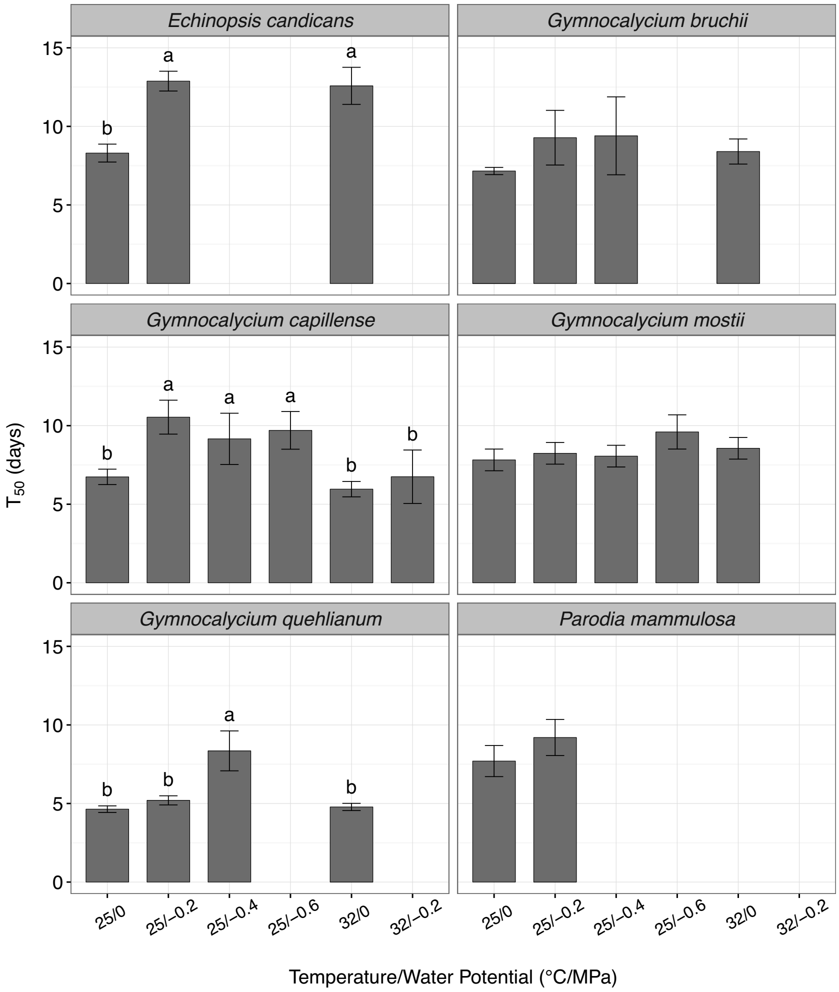

Fig. 2. Mean germination time (T_{50} and standard error) of the analyzed species: (a) *Echinopsis candicans*, (b) *Gymnocalycium bruchii*, (c) *G. capillense*, (d) *G. mostii*, (e) *G. quehlianum* and (f) *Parodia mammulosa*, under four water potentials (0 control, −0.2, −0.4 and −0.6 MPa) at 25 and 32 °C. T_{50} was not calculated when germination was less than 20%. Different letters indicate significant differences among treatments (DGC *post hoc* test, $p < 0.05$).

ferences were recorded between these treatments for other species (Fig. 3).

4. Discussion

For all but one species (*G. mostii*) maximum germination was obtained in distilled water (0 MPa), and low water potentials (mainly −0.4 and −0.6 MPa) reduced germination. Similar results have been found for another mesic cactus species: *Rhipsalis baccifera* from humid montane forest in Mexico (de la Rosa-Manzano and Briones, 2010). However, similar patterns were observed for cacti from dry and semiarid environments as well: *Stenocereus queretaroensis* from West Central Mexico (De la Barrera and Nobel, 2003); *Neobuxbaumia tetetzo*, *N. mezcalensis* and *N. macrocephala* from Tehuacan Valley (Ramírez-Padilla and Valverde, 2005); *Cereus jamacaru* subsp. *jamacaru* from Brazil (Meiado et al., 2010); *Stenocereus pruinosus* from Tehuacan Valley (Guillén et al., 2011); *Pilosocereus arrabidae* from Brazil (Martins et al., 2012); and *Stenocereus stellatus* from Tehuacan Valley, Mexico (Rodríguez-Morales et al., 2013).

The germination pattern of *G. mostii* (highest germination at −0.2 MPa) was also a common pattern found in the literature for cacti from arid environments, e.g. for *Neobuxbaumia tetetzo* and *Pachycereus hollianus* (Flores and Briones, 2001), as well as *Polaskia chichipe*, *Myrtillocactus schenckii*, *Escontria chiotilla*, and *Polaskia chende* (Guillén et al., 2011), all these species from Tehuacan Valley. For the latter species, total germination was relatively high in treatments from 0 to −0.8 MPa, and it was nearly 40% even in the treatment testing the lowest water potential (−1.0 MPa). Overall, in agreement with results reported in the literature, our results suggest that there is not a clear pattern of germination response to low water potentials in cactus species from arid or mesic environments. Response seems to be species-specific and even intraspecific differences were detected (Flores and Briones, 2001; Ramírez-Padilla and Valverde, 2005; Bauk et al., 2017). These patterns could be related to the microenvironmental conditions of the areas which species, or populations, inhabit (Contreras-Quiroz et al., 2016) as well as to taxon origin (Anderson, 2001; Charles, 2009). Moreover, germination of cactus species is more affected by low water potentials than germination of some species of other growth forms. In a review of 243 plant species of different growth forms and origins, Dürr et al. (2015) found that many species can germinate well in a range of water potentials from −1.0 to −1.5 MPa; at these values, most cactus species do not germinate or present a very limited germination. These results suggest that tolerance to dry conditions during cactus germination and early development is uncoupled from the high tolerance of adult plants.

In agreement with previous investigations in the study area, we found that some species could germinate well at high temperatures (Gurvich et al., 2008). These results are consistent with other

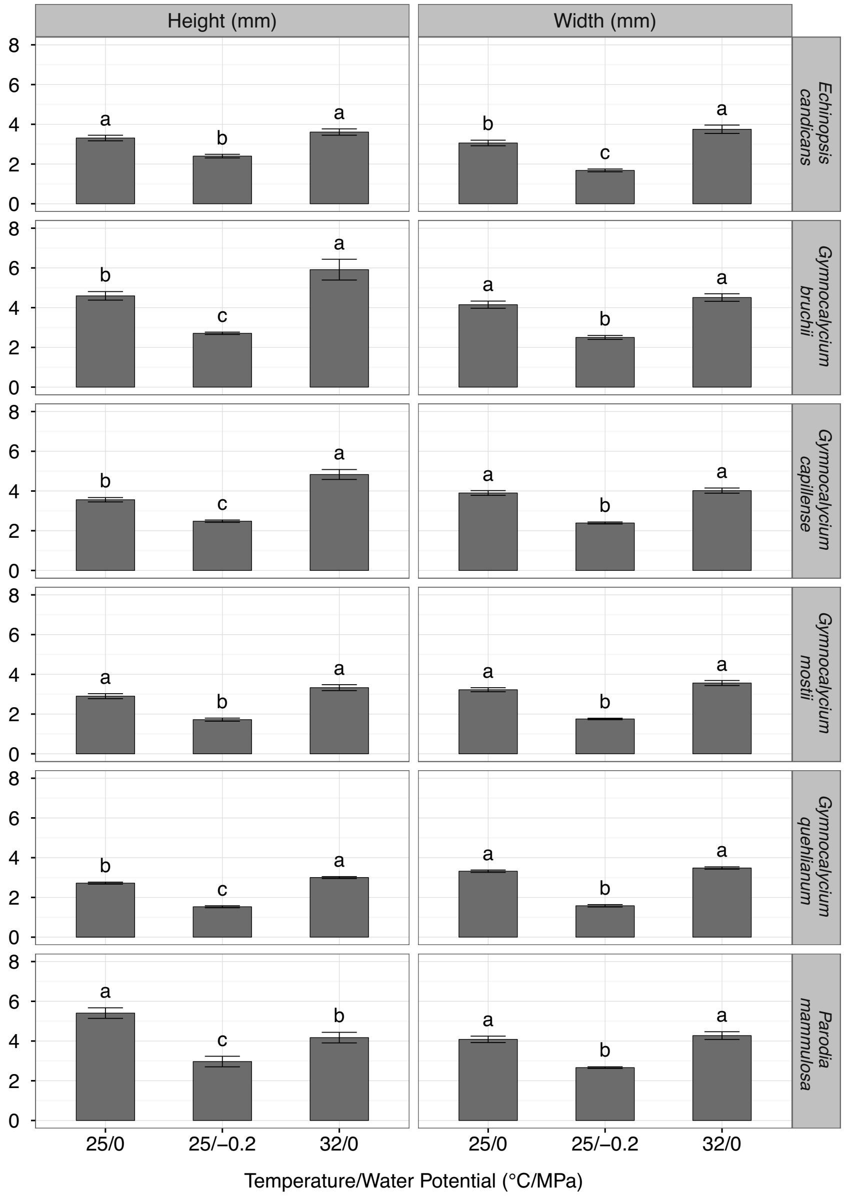

Fig. 3. Seedling height and width (mm and standard error) of the analyzed species: (a) *Echinopsis candicans*, (b) *Gymnocalycium bruchii*, (c) *G. capillense*, (d) *G. mostii*, (e) *G. quehlianum* and (f) *Parodia mammulosa.* These measurements were only taken in three treatments, 25 °C/0 MPa, 25 °C/−0.2 MPa and 32 °C/0 MPa. Different letters indicate significant differences among treatments ($p \leq 0.05$).

studies of cacti, in which although best germination occurs at ca. 25 °C, many species germinate well up to 40 °C (Rojas-Aréchiga and Vázquez-Yanes, 2000; De la Barrera and Nobel, 2003). However, the combination of high temperature and low water potential deeply affected germination; this result was not previously recorded in the literature (Kaufmann and Ross, 1970). The combination of both factors is similar to the situation in field conditions; in this case, there would be a decrease in the germination window of species, which could alter species demography (Godínez-Álvarez et al., 2003).

We also found different behaviors among species. For example, *G. mostii* and *G. quehlianum* exhibited a high germination at −0.2 MPa, and were less affected by the high temperature than the other species. *E. candicans* presented high germination at 32 °C and high water potential in comparison with the other species, but was strongly affected by low water potentials. These results suggest that different cactus species would respond differentially to environmental changes. The differences among species could be related to microenvironmental variations and taxon origin. For example, *G. mostii* inhabits more open and rocky outcrops than the other species; hence, its seeds are likely subjected to warmer and drier conditions (Gurvich et al., 2006). In a recent study, *G. mostii* was the only species of the area that presented hydration memory (Contreras-Quiroz et al., 2016). *Gymnocalycium quehlianum* belongs to the Trichomosemineum subgenus; species of this group inhabit low areas in west-central Argentina (Monte Desert and arid Chaco biogeographical regions), where conditions are much warmer and drier than in the surrounding mountain areas where other species of the genus are found (Charles, 2009). In Córdoba Mountains this species occurs between 400 and 1200 m a.s.l., being more abundant at lower altitudes (Pamela Martino, unpublished data).

Even though all the studied species presented some germination at low water potentials, seedling development was negatively affected. Thirty days after germination, only seedlings of the −0.2 MPa/25 °C treatment were alive. This means that even if species had the ability to germinate at low water potential, the stress imposed to seedlings would affect their growth and survival. Similar results were found by Kin et al. (2015), who analyzed seedling growth of *Pterocactus tuberosus* germinated under different water potentials. These results suggest that under field conditions seedling establishment would be negatively affected by these stressful conditions.

5. Conclusion

This research adds new information about the effects of combined high temperatures and low water potential on the germination and seedling growth of cacti from Central Argentina. We found that germination under low water potentials of cacti from mesic ecosystems was similar to that of species from arid ecosystems, and that response was species-specific. We also found a very important effect of the combination of low water potentials and high temperatures, which negatively affected seed germination. Seedling development was much more negatively affected by treatments than germination, and this could seriously limit seedling establishment (Flores et al., 2004; Pérez-Sánchez et al., 2015). This result is particularly relevant in relation to climate change expected in the area. Actual tendencies indicate an increase of both temperatures and precipitation in the region (de la Casa and Nasello, 2012). The balance of both factors would determine species establishment: if temperature increment is high and precipitation is low, a failure of seedling establishment is expected.

Acknowledgments

This work was supported by grants from Consejo Nacional de Investigaciones Científicas y Técnicas of Argentina (CONICET, PIP 11220110100873) and the Research Committee of the Cactus and Succulent Society of America. DE Gurvich and G Funes are researches at CONICET. Jorgelina Brasca assisted with the English version of the manuscript. The comments of two anonymous reviewers greatly improved the quality of the article.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.flora.2016.12.003.

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