Journal of the Professional Association for Cactus Development

Water deficit and extreme temperatures inhibit seed germination of *Echinocereus cinerascens* (DC.) Lem.

Beatriz Quiroz-González[1], Ana Gabriela Flores-Vargas[2], H. Azael Ramírez-Tobias[3], Cecilia B. Peña-Valdivia[4], J. Alonso Alcalá-Jáuregui[2] and Hugo M. Ramírez-Tobias[2‡]

[1] Associate researcher (project 321352) at Universidad Autónoma de San Luis Potosí, Facultad de Agronomía y Veterinaria; and Instituto Politécnico Nacional, Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR) Unidad Oaxaca, C. Hornos 1003, Santa Cruz Xoxocotlán 71230, Oaxaca, Mexico.
[2] Universidad Autónoma de San Luis Potosí, Facultad de Agronomía y Veterinaria, Carretera San Luis - Matehuala Km. 14.5, Ejido Palma de la Cruz 78321, Soledad de Graciano Sánchez, S.L.P., Mexico.
[3] Student at Instituto Politécnico Nacional. Escuela Superior de Cómputo. Av. Juan de Dios Bátiz s/n esq. Av. Miguel Othón de Mendizabal 07738. Ciudad de México, México.
[4] Programa de Posgrado en Botánica, Colegio de Postgraduados, Montecillo, Estado de México. 56264. México.

‡Corresponding author: hugo.ramirez@uaslp.mx

Abstract. Cactus *Echinocereus cinerascens* is a cactus of ecological and cultural importance in the Mexican Plateau; however, fundamental knowledge regarding its seed germination remains scarce. This study evaluated germination response under different temperatures (10, 18, 25, and 30 °C) and water potentials (well-hydrated, -0.5, -1.0, and -1.5 MPa), using filter paper as substrate. Germination was recorded over time, and germination parameters were analyzed. The seeds achieved germination percentages exceeding 95 % under well-hydrated conditions at 18 and 25 °C within 10 to 17 days. In contrast, no germination was recorded at 10 °C, as well as at 30 °C under moisture restriction (-0.5 to -1.5 MPa). Progressive substrate dehydration significantly reduced the germination percentage and increased the time to the onset of germination and time to 50% germination, with median values falling below 20% and exceeding 15 and 20 days, respectively, at -1.5 MPa. These effects were exacerbated when combined with higher temperatures. Furthermore, temperature and hydration levels that deviate from optimal conditions increased variability in germination variables suggesting a bet-hedging strategy. Seed germination of *E. cinerascens* is remarkable under temperature and moisture levels but dehydration and unfavorable temperatures inhibit it. Sexual propagation of this species, based on seed germination, is a viable method.

Keywords: *Cactaceae, Mexican Plateau, temperature regimes, water potential*

Cite: Quiroz-González, B.Q., Flores-Vargas, A.G., Ramírez-Tobias, H.A., Peña-Valdivia, C.B., Alcalá-Jáuregui, J.A. and Ramírez-Tobias, H.M. 2026. Water deficit and extreme temperatures inhibit seed germination of *Echinocereus cinerascens* (DC.) Lem. *Journal of the Professional Association for Cactus Development. 28*:270-281. https://doi.org/10.56890/jpacd.v28i.625.

Associate Editor: Ana Gisela Reyes-Alvarado

Technical Editor: Tomás Rivas-Garcia

Received date: 05 May 2026
Accepted date: 26 June 2026
Published date: 22 August 2026

Introduction

The family Cactaceae is native to the Americas, comprising approximately 120 genera and between 1,450 and 1,870 species (Hernández *et al.*, 2004; Hunt *et al.*, 2006; Nyffeler and Eggli, 2010). Mexico holds a prominent global position in terms of the richness and diversity of its cactus flora, harboring nearly 60 genera, and 670 species, 80% of which are endemic (Guzmán *et al.*, 2003). This plant family is distinguished by its horticultural potential as fruit and industrial crops, while their ornamental use confers it significant economic importance in international trade (Mizrahi *et al.*, 1997).

One important species is the *alicoche* (*Echinocereus cinerascens* (DC.) Lem.), a cactus native to the scrublands of the arid zones within the Mexican Plateau (Bravo-Hollis and Sánchez-Mejorada, 1991), and endemic to Mexico (Torres-Colín

et al., 2017). The fruits of this plant are harvested for seasonal consumption and are highly valued by rural populations, even reaching local commercial markets. Its ethnobotanical significance, edible and medicinal, has been documented (Torres-Colín *et al.*, 2017). Besides, research indicates the presence of phenethylamine-type alkaloids (tyramine, 3-methoxytyramine, hordenine, 3,4-dimethoxyphenethylamine, and anhalidine) with stimulant, antidepressant, bronchodilatory, and hallucinogenic effects (Bruhn and Sánchez-Mejorada, 1977). Furthermore, pigments derived from *E. cinerascens* have shown potential applications in the food industry, medicine, and agriculture (Elias *et al.*, 2018).

Despite their importance, cacti face substantial challenges due to environmental stressors, such as increases in mean annual temperatures and heatwaves, and greater duration, frequency, and intensity of droughts. Additional threats include wildfires, land-use change, illegal poaching for trade, and the introduction of invasive species (Bezerra-Silva *et al.*, 2024; Hultine *et al.*, 2023; Velázquez *et al.*, 2010). Due to their unique biological characteristics, this plant, like others in their taxonomic group, are highly vulnerable to disturbances. This susceptibility is due to the high habitat specificity, low growth rates, and long life cycles, resulting in low establishment success (Bezerra-Silva *et al.*, 2024; Mandujano *et al.*, 2010). Consequently, all species within the Cactaceae are listed under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Leonor and Sierra, 2011) and *E. cinerascens* is listed in the IUCN Red List of Threatened Species, as it faces significant threats (Torres-Colín *et al.*, 2017).

Regarding its conservation and management, studies have documented findings on the propagation of *E. cinerascens*. Successful results have been reported using in vitro propagation on MS medium starting from axillary buds (Elias *et al.*, 2015). Its seeds exhibited low germination rates compared to other cacti, such as *Myrtillocactus geometrizans* and *Stenocereus dumortieri*, in agar-based germination experiments, even though its fruits contain approximately ten times more seeds (Rojas-Aréchiga and Mandujano, 2013). While asexual propagation results in Cactaceae are promising due to the potential for producing large quantities of individuals, their clonal origin results in high homogeneity, which may confer disadvantages when facing environmental stressors.

The low seed germination documented for *E. cinerascens* on agar (Rojas-Aréchiga and Mandujano, 2013) pose a challenge that calls for further exploration of seed-based propagation, considering environmental factors and alternative germination methods. Recent evidence within the genus *Echinocereus* also indicates that germination performance can be substantially modified by seed pretreatments, as acid scarification increased germination percentage and germination speed in different populations of *E. stramineus* (González-Fernández *et al*., 2025). Gurvich *et al.* (2017) studied the germination of six cactus species using filter paper as a substrate at different temperatures and water potentials. They found that germination percentages varied from 25 to 80% among species and were significantly affected by the interaction between these factors. Germination studies are critical for the success of plant conservation programs, as they represent an indispensable tool for the propagation of wild species (Barrios *et al.*, 2024). The present study aimed to evaluate the germination response of *E. cinerascens* seeds under varying temperatures and substrate moisture levels, to identify thermal and hydric thresholds that may constrain seedling establishment under future climatic conditions and to provide baseline information for ex situ propagation and seed conservation efforts.

Materials and Methods

Plant material

Fruits of *E. cinerascens* at physiological maturity were collected from the Altiplano Potosino (22°23'16'' N, 100°46'20'' W; 1840 m) in August 2021. The fruits were kept at room temperature (average 25 °C) for 5 days, after which the seeds were extracted and stored at 4 °C for 11 months. Prior to applying the treatments, the seeds were surface sterilized with 10 % sodium hypochlorite for 3 min, rinsed with deionized water, and sown on filter paper, after which they were assigned to their respective treatment.

Description of treatments

The experiments were carried out under a two-way factorial design using temperature and substrate water potential as factors. The levels of the first factor were 10, 18, 25, and 30 ºC and those for the second one were a control treatment (~0 MPa), –0.5, –1.0, and –1.5 MPa. This resulted in 16 treatment combinations. Each treatment was assessed with five replicates, each replicate comprising 20 seeds.

The experimental units were placed in rooms whose temperature was controlled using a laboratory's temperature regulation system, consisting of a MIDEA® mini-split inverter system and a COMENERGY evaporator. Prior to each temperature trial, room temperature levels were tested and monitored with a HOBO® MX1101 data logger (Bourne, Massachusetts, USA). The substrate water levels were created by using polyethylene glycol 8000 (Sigma), an osmotic agent with a molecular weight of 8000 that enables the simulation of drought stress during germination (Khan *et al.*, 2001).

The water potential levels were maintained over time as follows; the initial weight of each observation unit was recorded at the beginning of the experiment and every other day. When a weight difference with respect to the initial value was recorded, distilled water was added to restore the initial weight. This compensated for water loss and maintained the polyethylene glycol concentration on the filter paper, which served as the substrate throughout the entire experiment. All treatments were evaluated under a 12 h light/12 h dark photoperiod, for 30 days.

Evaluated variables

The course of germination over time was assessed thorough the accumulative germination. Also, the following germination parameters were analyzed: time to the onset of germination, time to the 50% germination (T_{50}), and germination percentage. A seed was considered germinated when the emergence of the embryo through the seed coat was observed.

The time to the onset of germination was defined as the average time at which germination occurred in each treatment, and results were expressed in days.

The T_{50}, which represents the rate of germination per unit of time, was calculated as follows:

$$T_{50} = \frac{\sum n_i t_i}{\sum n_i}, \quad [1]$$

where n_i is the number of seeds that germinated on day i, and t_i is the number of days after sowing. Results were expressed in days.

https://www.jpacd.org Electronic ISSN: 1938-6648

Germination percentage (*GP*) was registered at the end of the experiment and was calculated as follows:

$$GP = \frac{Germinated\ seed\ count}{Sound\ seed\ count} \times 100, \quad [2]$$

Cumulative germination (*CG*) represents the total number of seeds germinated from day 1 to day *n*, and it was calculated using the following equation:

$$CG = \sum_{i=1}^{n} Seeds\ germinated\ at\ day\ i \times 100, \quad [3]$$

Results were expressed as percentage of germinated seeds.

Experimental design and statistical analysis

A completely randomized design with a factorial arrangement of treatments was applied. The main effects of water potential and temperature, as well as their interaction, were evaluated by using parametric factorial analysis of variance or, alternatively, the Scheirer–Ray–Hare test, depending on the normality of data. Normality was evaluated by using Shapiro-Wilks test. When significant effects were detected, multiple post-hoc comparisons were conducted using Dunn's test with Holm correction and Tukey's test. For the analysis of *CG* over time, the Friedman test was applied to nonparametric repeated-measures data, followed by post-hoc Wilcoxon tests with a Holm correction. All statistical analyses were performed using R version 4.4.0 (R Core Team®, 2026).

Results and Discussion

The best response with almost 100 % seed germination was observed at 25 ºC with the high level of humidity in the substrate (0 MPa), it lasted 12 days (Figure 1). The temperature and humidity conditions that generated the best germination response of *E. cinerascens* partially coincides to those indicated as optimal for several species of the Cactaceae family (Barrios *et al.*, 2020). The range for optimal germination documented is 20 to 30 ºC but the best seed germination of this species was observed between 18 and 25 ºC but not at 30 ºC. Moreover, the median accumulated germination reached at least 75 % at -0.5 MPa with its low level (Q1), 60 and 50% at 18 and 25 ºC. According to optimal documented levels, -0.4 MPa diminished germination percentage less than 60 %.

Time course of cumulative germination

The combination of low water potential with various germination temperatures allowed us to observe an inverse relationship between both environmental variables throughout the germination process. At 25 ºC and 0 MPa seeds started to germinate on day 5 and reached the maximum germination percentage by day 12. The reduction of temperature, from 25 to 18 ºC, together with the high humidity (0 MPa), promoted a faster initiation of germination (3 days) but a slower one, so that the maximum percentage of germination occurred on day 21, though similar germination percentages were reached. Likewise, the maximum level of cumulative germination decreased as the water potential of the substrate declined, but the decrease was lower with higher temperature (25 ºC) than with 18 ºC (Figure 1). Some studies have addressed the combined effects of temperature and substrate moisture on

https://www.jpacd.org Electronic ISSN: 1938-6648

germination in cultivated plants (Khaeim *et al.*, 2022) and in cacti (Flores *et al.*, 2017; Gurvich *et al.*, 2017). However, their analyses have mainly focused on parameters such as maximum germination. Alvarado and Bradford (2002) examined germination over time and reported that potato seeds required a longer time to initiate germination as substrate water potential decreased, with no change in this pattern across different germination temperatures (14, 16, and 18 °C), which contrasts with the results of our study.

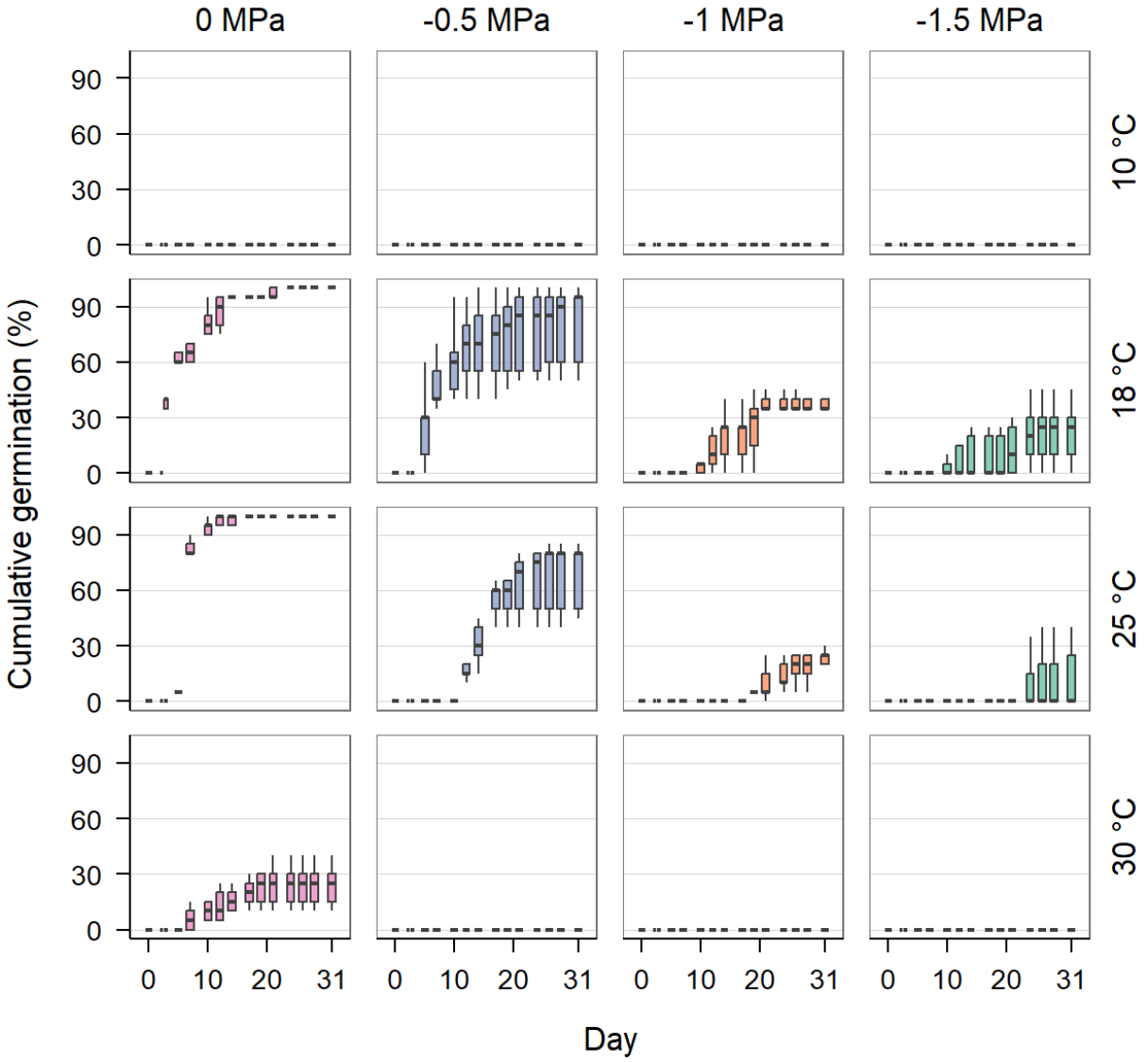

Figure 1. Effect of water potential [control (~0 MPa), -0.5, -1, -1.5 MPa] on the cumulative germination of *Alicoche* (*E. cinerascens*) seeds subjected to temperatures of 10, 18, 25 and 30 °C. The boxes represent the quartiles (Q1, Q2=median, Q3). and the whiskers symbolize the non-outlier range. Friedman Chi-squared = 116.84; $P < 2.2x10^{-16}$.

The apparently better response of germination dynamics observed at 18 °C combined with −0.5, −0.1, and −1.5 MPa, compared to 25 °C (Figure 1), it is likely due to lower temperatures promoting a more humid atmosphere. Under such atmospheric humidity levels, seeds lose less moisture, and although germination proceeds more slowly due to the cooler temperature, at the end, a higher final germination

https://www.jpacd.org Electronic ISSN: 1938-6648

percentage is achieved. In contrast, higher temperatures promoted a faster germination rate —more evident in the combinations of 0 and −0.5 MPa at 18 and 25 °C— but resulted in a lower final proportion of germinated seeds. These ungerminated seeds may remain in a state of low metabolic activity and become reactivated if additional moisture is available, as has been demonstrated for seeds of several *Agave* species (Ramírez-Tobías *et al.*, 2014). Although it has been indicated that the characteristics of seeds, which affect the ability to absorb and lose water to the atmosphere, are different between species and between seeds of the same species (Ramírez-Tobias *et al.*, 2014), the processes of moisture loss from the germination substrate to the seed, and from both surfaces to the atmosphere, are phenomena that should be analysed in future research.

Germination of seeds of *E. cinerascens* exhibits high sensitivity to both low temperatures and high temperatures when combined with substrate desiccation. Seeds did not germinate at 10 or 30 °C combined to -0.5 MPa or drier conditions (Figure 1). Nobel (1988) states that cactus seeds from subtropical deserts do not tolerate temperatures below 12 °C. Similarly, it has been reported that barrel cacti such as *Ferocactus flavovirens*, *F. robustus*, *F. recurvus*, and *Echinocactus platyacanthus* fail to germinate at 10 °C but do so from 15 °C onwards (Rojas-Aréchiga and Vázquez-Yanes, 2000). The absence of germination at 10 °C may be attributed to a reduction in initial imbibition due to increased water viscosity (Koornneef *et al.*, 2002; Ramírez-Tobias *et al.*, 2012), lower hydrolytic enzyme activity, decreased membrane fluidity, and limited cell expansion required for radicle emergence (Bewley *et al.*, 2013). Conversely, the negative effect of high temperatures on germination is associated to enzyme denaturation, membrane alteration, and thermos-inhibition (Lima and Meiado, 2025). Besides, it might be due to the impossibility of the species for triggering molecular repairs mechanisms that produce protecting products such as heat shock proteins (Visscher *et al.*, 2022).

Parameters of the germination process

The water potential significantly affected the evaluated parameters of germination while temperature affected the percentage of germination and the time to 50 % germination (Table 1). The reduction of the substrate water potential decreased the germination percentage and increased both the time to germination onset and the time to 50 % germination (Figure 2). These effects on germination parameters may be attributed to the accumulation of abscisic acid (ABA), a phytohormone that inhibits cell elongation and reduces the mobilization of reserves toward the embryo, thereby preventing radicle emergence (Silva *et al.*, 2020).

Table 1. Results of the statistical analysis of the effect of different temperatures (18, 25 and 30 ºC) and water potentials [-1.5, -1.0, -0.5 and control moisture treatment (0 MPa)] on parameters of the germination process of *E. cinerascens*.

Source of variation	**Germination percentage**		**Time to the onset of germination**		**Time to 50% germination**	
	***H*†**	***P***	***H***	***P***	***F***	***P***
Temperature	25.48	<0.01	5.88	>0.05	5.99	<0.05
Water potential	22.02	<0.001	26.32	<0.001	31.15	<0.001
Interaction	3.45	>0.05	1.02	>0.05	2.50	>0.05

†*H* and *F* are the test statistics applied (Scheirer–Ray–Hare test and Fisher's *F* test, respectively).

A

https://www.jpacd.org Electronic ISSN: 1938-6648

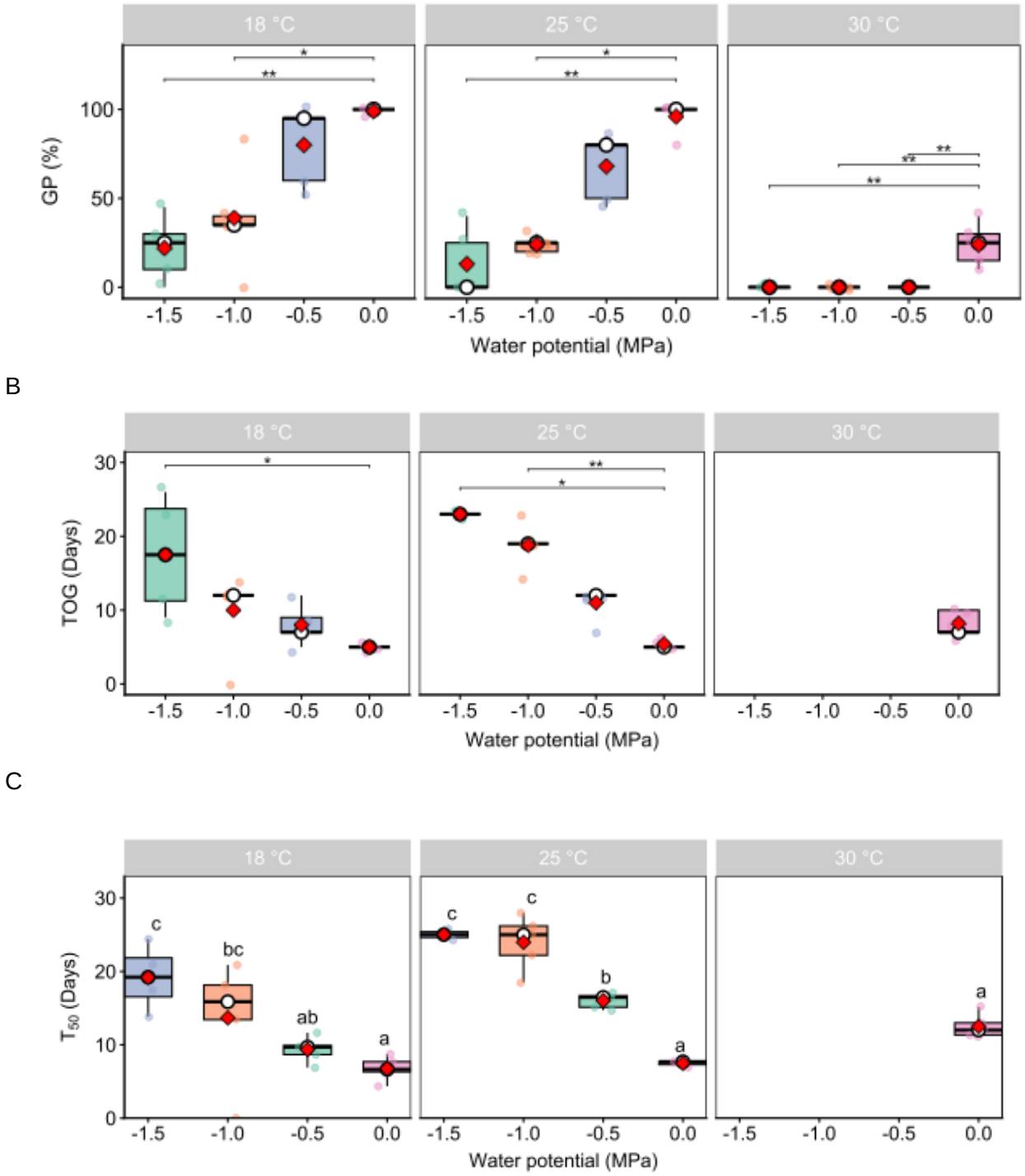

Figure 2. Effect of temperature and water deficit on the cumulative germination percentage (A), the time to the onset of germination (B) and the time to 50 % germination (C) of *E. cinerascens* seeds. Boxes represent quartiles (Q1; Q2=median, is the bold central line; Q3), red diamonds are the arithmetic mean, dots denote outliers, and whiskers symbolize the non-outlier range. Horizontal lines with asterisks (*p<0.05 and **p<0.01) represent differences according to Dunn´s test and different letters represent differences according to Tukey test (α=0.05). Each treatment consisted of five replicates, with 20 seeds per replicate.

https://www.jpacd.org Electronic ISSN: 1938-6648

Notwithstanding the response of germination parameters to the decline in available substrate moisture, a germination percentage of approximately 30 % was achieved at -1.5 MPa (Figure 2A). This represents a water potential level typically considered critical for most crop plants. Water stress tolerance may be linked to the mucilaginous secretory layer of the seeds, which efficiently absorbs water and distributes it across the seed surface. This feature has previously been reported in plant species from desert environments. It has been attributed to a possible effect of cellular structure denaturation (Pérez-Sánchez *et al.*, 2011). This mechanism enhances water uptake and facilitates germination under conditions of minimal moisture availability (Bregman and Graven, 1997). Thus, germination of *E. cinerascens* seeds appears to exhibit a slowing-down process as an adaptive adjustment to moisture-restricted conditions, even under highly limiting water availability.

The modification of substrate moisture and temperature toward unfavorable levels induced an increased variation of the response germination parameters. Under those conditions, germination occurred over a prolonged period, in contrast to optimal conditions (25 °C and 0 MPa), where germination was concentrated within shorter timeframes. At 18 and 25 °C and at 0 MPa, the median germination percentage was close to 100 % with minimal variability. However, at -0.5 MPa, the germination percentage showed a variation of approximately 30 % points (Figure 2A). Similarly, the variation in time-to-germination onset was minimal at 25 °C, as well as at 18 °C under 0 MPa. At 18 °C, this variation increased as water potential declined, reaching an interquartile range (Q1–Q3) of nearly 12 days (Figure 2B). The variation in time to 50 % germination also increased as water potential decreased, though less conspicuously (Figure 2C).

The mentioned variability response observed in those response germination parameters may be associated with a bet hedging ecological strategy that mitigates risk by dispersing the emergence of individuals (in this case, seedlings) over time. In annual plants of the Sonoran Desert, it has been mathematically demonstrated that delayed germination reduces long-term variance in reproductive success (Gremer and Venable, 2014). These findings suggest that seed germination in *E. cinerascens* exhibits temporal dispersal as an adaptive trait under adverse environmental conditions, which may function to decrease risk against high environmental stochasticity.

The genus *Echinocereus* is the third most species-rich genus in the family Cactaceae (Sánchez *et al.*, 2014). With this study, the number of species in which the germination process has been documented has risen to five (out of 60 species). However, the indicated progress is still marginal if one takes into account that understanding the process of seed germination is a way to promote the preservation of cactus species (Rojas-Aréchiga and Vázquez-Yanes, 2000). These results provide useful baseline information for predicting limitations in seedling establishment under future climatic conditions and for designing *ex situ* propagation or seed conservation protocols based on optimal thermal and moisture requirements.

Conclusions

Echinocereus cinerascens seeds exhibit germination rates near 100 % at temperatures of 18 °C and 25 °C under optimal substrate moisture (0 MPa), with germination occurring within 10 to 17 days. Germination is inhibited by suboptimal temperatures, and this inhibition is exacerbated when coupled with increasing substrate dehydration. Suboptimal temperatures and moisture conditions increase response variability in germination parameters.

https://www.jpacd.org Electronic ISSN: 1938-6648

The inability to germinate at high temperatures (30 °C) suggests that *E. cinerascens* could be highly vulnerable to climate change scenarios involving increased temperatures and reduced water availability during the germination season.

ETHICS STATEMENT

Not applicable.

CONSENT FOR PUBLICATION

Not applicable.

AVAILABILITY OF SUPPORTING DATA

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

COMPETING INTERESTS

The authors declare that they have no competing interests.

FUNDING

We thank Consejo Nacional de Humanidades, Ciencia y Tecnología (now as Secretaría de Ciencia, Humanidades, Tecnología e Innovación-SECIHTI) for funding project #321352, “Strengthens the UASLP botanical garden system for biocultural preservation and ethnobiological knowledge exchange.

AUTHOR CONTRIBUTIONS

Conceptualization, H.M.R.-T.; methodology, H.M.R.-T.; software, B.Q.-G., and H.A.R.-T.; validation, H.M.R.-T., and B.Q.-G.; formal analysis, H.A.R.-T., and B.Q.-G.; investigation, A.G.F.-V., H.M.R.-T., and B.Q.-G.; resources, H.M.R.-T.; data curation, B.Q.-G. and H.A.R.-T.; writing—original draft preparation, A.G.F.-V., H.M.R.-T., and B.Q.-G.; writing—review and editing, H.M.R.-T., C.B.P.-V., J.A.A.-J., and B.Q.-G.; visualization, H.M.R.-T., C.B.P.-V., and B.Q.-G.; supervision; H.M.R.-T., and B.Q.-G.; project administration, H.M.R.-T.; funding acquisition, H.M.R.-T.

ACKNOWLEDGMENTS

To the CONAHCYT (now SECIHTI), which through the project (321352) entitled "Strengthening the Botanical Garden System of the UASLP for conservation and visualization" supported this project. To the students Jesús María Jacobo Serna and Elizabeth Ibarra Roque, and to Dr. Idrissa Diédhiou for their support during the experimentation process. To Dr. Exequiel Ezcurra to improve the readability of the manuscript.

References

Alvarado, V. and Bradford, K.J. 2002. A hydrothermal time model explains the cardinal temperatures for seed germination. *Plant, Cell & Environment. 25*(8):1061-1069. https://doi.org/10.1046/j.1365-3040.2002.00894.x

Barrios, D., Sánchez, J.A., Flores, J. and Jurado, E. 2020. Seed traits and germination in the Cactaceae family: A review across Americas. *Botanical Sciences. 98*(3):417-440. https://doi.org/10.17129/botsci.2501

Barrios, D., Sánchez, J. and González-Torres, L. 2024. Germination, seed traits, and seedling vigor of *Pilosocereus robinii* (Cactaceae) from northwestern Cuba. *Journal of the Botanical Research Institute of Texas. 18*(2):433-444. https://doi.org/10.17348/jbrit.v18.i2.1372

Bewley, J.D., Bradford, K.J., Hilhorst, H.W.M. and Nonogaki, H. 2013. Germination. In Seeds: Physiology of Development, Germination and Dormancy, 3rd Edition (pp. 133-181). Springer New York. https://doi.org/10.1007/978-1-4614-4693-4_4

Bezerra-Silva, A., Albuquerque-Lima, S., Gomes, V.G.N., Fagundes, A.C. de A., Gomes, M.T.D., Silva, M.T. da, Machado, I.C. and Funch, L.S. 2024. When are cacti found with flowers and fruits? Estimation of the reproductive phenology of the genus Xiquexique based on herbarium data. *Diversity. 16*(2):79. https://doi.org/10.3390/d16020079

Bravo-Hollis, H. and Sánchez-Mejorada, H. 1991. Las Cactáceas de México: Volúmenes II y III. Universidad Nacional Autónoma de México.

Bregman, R. and Graven, P. 1997. Subcuticular secretion by cactus seeds improves germination by means of rapid uptake and distribution of water. *Annals of Botany. 80*(4):525-531. https://doi.org/10.1006/anbo.1997.0471

Bruhn, J.G. and Sánchez-Mejorada, H. 1977. Phenethylamines from *Echinocereus cinerascens* and Pilosocereus [*Cephalocereus] chrysacanthus*]. *Phytochemistry. 16*(5):622-623. https://doi.org/10.1016/0031-9422(77)80041-1

Elias, H., Mat-Taha, R., Hasbullah, N.A., Othman, R., Mahmad, N., Saleh, A. and Abdullah, S. 2018. Detection and quantification of natural pigments extracted from callus of *Echinocereus cinerascens*. *Pigment & Resin Technology*. 47(6):464-469. https://doi.org/10.1108/PRT-10-2017-0083

Elias, H., Taha, R.M., Hasbullah, N.A., Mohamed, N., Manan, A.A., Mahmad, N. and Mohajer, S. 2015. The effects of plant growth regulators on shoot formation, regeneration and coloured callus production in *Echinocereus cinerascens in vitro*. *Plant Cell, Tissue and Organ Culture (PCTOC). 120*(2):729-739. https://doi.org/10.1007/s11240-014-0641-z

Flores, J., Pérez-Sánchez, R.M. and Jurado, E. 2017. The combined effect of water stress and temperature on seed germination of Chihuahuan Desert species. *Journal of Arid Environments. 146*:95-98. https://doi.org/10.1016/j.jaridenv.2017.07.012

Gremer, J.R. and Venable, D.L. 2014. Bet hedging in desert winter annual plants: Optimal germination strategies in a variable environment. *Ecology Letters. 17*(3):380-387. https://doi.org/10.1111/ele.12241

González-Fernández, R., Quiñonez-Martínez, M., Osuna-Ávila, P. and Valero-Galván, J. 2025. Study on fruit and seed morphology and morphometry, seed phytochemicals, and germination characterization in three populations of *Echinocereus stramineus* (Cactaceae) at Ciudad Juárez Municipality, Chihuahua, Mexico. *Journal of the Professional Association for Cactus Development*. 27:35-55. https://doi.org/10.56890/jpacd.v27i.574

Gurvich, D.E., Pérez-Sánchez, R., Bauk, K., Jurado, E., Ferrero, M.C., Funes, G. and Flores, J. 2017. Combined effect of water potential and temperature on seed germination and seedling development of cacti from a mesic Argentine ecosystem. *Flora. 227*:18-24. https://doi.org/10.1016/j.flora.2016.12.006

Guzmán, U., Arias, S. and Dávila, P. 2003. Catálogo de Cactáceas Mexicanas. Universidad Nacional Autónoma de México / Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Hernández, H.M., Gómez-Hinostrosa, C. and Goettsch, B. 2004. Checklist of Chihuahuan desert Cactaceae. *Harvard Papers in Botany. 9*(1):58-68.

Hultine, K.R., Hernández-Hernández, T., Williams, D.G., Albeke, S.E., Tran, N., Puente, R. and Larios, E. 2023. Global change impacts on cacti (Cactaceae): Current threats, challenges and conservation solutions. *Annals of Botany. 132*(4):671-683. https://doi.org/10.1093/aob/mcad040

Hunt, D.R., Taylor, N. and Charles, G. 2006. The New Cactus Lexicon. dh books.

Khaeim, H., Kende, Z., Jolánkai, M., Kovács, G.P., Gyuricza, C. and Tarnawa, Á. 2022. Impact of temperature and water on seed germination and seedling growth of maize (*Zea mays* L.). *Agronomy. 12*(2):397. https://doi.org/10.3390/agronomy12020397

Khan, S., Khyber, K. and Mexal, J.G. 2001. Germination of soybean seed primed in aerated solution of polyethylene glycol (8000). *Journal of Biological Sciences. 1*(3):105-107. https://doi.org/10.3923/jbs.2001.105.107

Koornneef, M., Bentsink, L. and Hilhorst, H.W.M. 2002. Seed dormancy and germination. *Current Opinion in Plant Biology. 5*(1):33–36. https://doi.org/10.1016/S1369-5266(01)00219-9

Leonor, D.C. and Sierra, J. 2011. Las cactáceas mexicanas y los riesgos que enfrentan. *Revista Digital Universitaria. 12*(1):1-23.

Lima, A. and Meiado, M.V. 2025. Increasing temperatures negatively affect seed hydration memory during the germination of two cactus species under water deficit condition. *Plant Ecology. 226*(3):279-293. https://doi.org/10.1007/s11258-025-01490-5

Mandujano, M.d.C., Carrillo-Angeles, I., Martínez-Peralta, C. and Golubov, J. 2010. Reproductive Biology of Cactaceae. In Ramawat, K. (ed.), Desert Plants (pp. 197–230). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-02550-1_10

Mizrahi, Y., Nerd, A. and Nobel, P.S. 1997. Cacti as Crops. In Horticultural Reviews (Vol. 18, pp. 291-319). John Wiley & Sons, Inc. https://doi.org/10.1002/9780470650608.ch6

Nobel, P.S. 1988. Environmental biology of agaves and cacti. Cambridge University Press.

Nyffeler, R. and Eggli, U. 2010. A farewell to dated ideas and concepts: Molecular phylogenetics and a revised suprageneric classification of the family Cactaceae. *Schumannia. 6*:109-149.

Pérez-Sánchez, R., Jurado, E., Chapa-Vargas, L. and Flores, J. 2011. Seed germination of Southern Chihuahuan Desert plants in response to elevated temperatures. *Journal of Arid Environments. 75*(10):978-980. https://doi.org/10.1016/j.jaridenv.2011.04.020

Ramírez-Tobias, H.M., Peña-Valdivia, C.B., Aguirre R., J.R., Reyes-Agüero, J.A., Sánchez-Urdaneta, A.B. and Valle G.S. 2012. Seed germination temperatures of eight Mexican Agave species with economic importance. *Plant Species Biology. 27*(2):124-137. https://doi.org/10.1111/j.1442-1984.2011.00341.x

Ramírez-Tobías, H.M., Peña-Valdivia, C.B., Trejo, C., Aguirre, R.J.R. and Vaquera, H.H. 2014. Seed germination of Agave species as influenced by substrate water potential. *Biological Research. 47*(1):11-11. https://doi.org/10.1186/0717-6287-47-11

Rojas-Aréchiga, M. and Mandujano, M.C. 2013. Aspectos sobre la germinación de *Myrtillocactus geometrizans*, *Stenocereus dumortieri* y *Echinocereus cinerascens*. *Cactáceas y Suculentas Mexicanas. 58*(4):100-111.

Rojas-Aréchiga, M. and Vázquez-Yanes, C. 2000. Cactus seed germination: A review. *Journal of Arid Environments. 44*(1):85-104. https://doi.org/10.1006/jare.1999.0582

Sánchez, D., Arias, S. and Terrazas, T. 2014. Phylogenetic relationships in Echinocereus (Cactaceae, Cactoideae). *Systematic Botany. 39*(4):1183-1196. https://doi.org/10.1600/036364414X683831

Silva, J.H.C.S., de Azerêdo, G.A. and Targino, V.A. 2020. Resposta germinativa de sementes de cactáceas colunares sob diferentes regimes de temperatura e de potencial hídrico. *Scientia Plena. 16*(12):123101. https://doi.org/10.14808/sci.plena.2020.123101

Torres-Colín, R., Parra, J.G., Cruz, L.A., Ramírez, M.P., Gómez-Hinostrosa, C., Bárcenas, R.T. and Hernández, H.M. 2017. Flora vascular del municipio de Guadalcázar y zonas adyacentes, San Luis Potosí, México. *Revista Mexicana de Biodiversidad. 88*(3):524-554. https://doi.org/10.1016/j.rmb.2017.06.012

Velázquez, A., Mas, J.F., Díaz-Gallegos, J.R., Mayorga-Saucedo, R., Alcántara, P.C., Castro, R., Fernández, T., Bocco, G., Ezcurra, E. and Palacio, Y.J.L. 2010. Mapping land cover changes in Mexico, 1976-2000 and applications for guiding environmental management policy. *Singapore Journal of Tropical Geography. 31*(2):152-162. https://doi.org/10.1111/j.1467-9493.2010.00398.x

Visscher, A.M., Latorre Frances, A., Yeo, M., Yan, J., Colville, L., Gomez Barreiro, P. and Pritchard, H.W. 2022. Comparative analyses of extreme dry seed thermotolerance in five Cactaceae species. *Environmental and Experimental Botany. 186*:104514. https://doi.org/10.1016/j.envexpbot.2021.104514