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Germination of *Peniocereus greggii* (Engelm.) Britton & Rose is regulated by seed age and temperature, not scarification

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Abstract. *Peniocereus greggii* (Engelm.) Britton & Rose is a species listed as Subject to Special Protection (Pr) under Mexican standards, with significant ecological value in the Chihuahuan Desert, yet information regarding its propagation remains scarce. This study evaluated the effects of seed age (fresh *vs.* 7-year storage), temperature (constant 24 °C *vs.* fluctuating 30–37 °C), and scarification treatments (H_2SO_4 at 40% and 50%, mechanical incision, and control) on germination. A three-way ANOVA revealed significant differences for all factors and a significant interaction between seed age and scarification. Scarification alone did not improve germination; acid treatment (H_2SO_4) effectively inhibited germination, while mechanical incision underperformed the control. Germination was significantly higher in aged 2016 seeds than in 2022 seeds, and was strictly higher under a moderate, constant temperature (24 °C) than under fluctuating high temperatures. These results provide solid inferential evidence that *P. greggii* seeds possess physiological dormancy that is naturally alleviated by after-ripening. Consequently, artificial scarification is unnecessary and detrimental. For *ex situ* conservation, we recommend extended dry storage of seeds, followed by sowing under moderate temperature conditions (24 °C), and strictly avoiding physical or chemical modifications to the seed coat.

Keywords: *physiological dormancy, after-ripening, conservation, desert plants, seed propagation*

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Introduction

Cacti, members of the Cactaceae family, are keystone species in arid and semi-arid ecosystems due to their ecological, cultural, and economic importance (Flores and Macias, 2008). They provide essential ecosystem services, including soil stabilization and the support of trophic chains (Stavi, 2022). Indigenous communities have long used cacti for sustenance, traditional medicine, and construction materials, embedding these plants within their cultural practices and survival strategies (Pedrosa *et al.*, 2018; Ramirez-Rodriguez *et al.*, 2020).

Despite their importance, nearly 31% of cactus species are endangered due to habitat loss and illegal trade (Goettsch *et al*., 2015). While research has increased recently, encompassing phylogeny to germination (Barrios *et al*., 2022), it remains focused on ornamental species, often neglecting the germination and propagation of underutilized native species (Villavicencio *et al*., 2019).

This creates a significant gap in the ecological understanding required for effective conservation and restoration.

Peniocereus greggii, an endemic cactus of northern Mexico and southwestern United States, is a key component of these habitats. Known for its tuberous root and nocturnal blooming, it supports specialized biodiversity, including nocturnal pollinators such as bats and moths (Suzán *et al*., 1994; Fleming *et al*., 2023). The establishment and survival of *P. greggii* are highly dependent on the microclimatic shelter provided by native nurse shrubs (Muro-Pérez *et al*., 2012). Therefore, understanding the specific factors influencing its seed germination is vital for developing effective propagation and conservation strategies (Loweree and Carrasco, 2018).

In the context of seed ecology, many underutilized arid species present physiological dormancy, which can sometimes be coupled with a mechanically resistant seed coat that limits embryo growth (Baskin and Baskin, 2014). Given previous findings that seed scarification enhances germination in such species (Osuna-Ávila *et al*., 2025), this study examined whether scarification benefited *P. greggii*. In addition, the role of temperature, an established factor in cacti germination success (Rojas-Arechiga and Vazquez-Yanez, 2000), was evaluated to identify optimal propagation conditions. The aforementioned factors, together with seed age, were examined in relation to the germination rates of *P. greggii* seeds to determine appropriate conditions for seedling establishment. Based on seed morphology, general assumptions about seed viability, and the species' ecology, we hypothesized that: (1) germination rates would decrease in older seeds due to a loss of viability over time; (2) artificial scarification would enhance germination by overcoming the mechanical resistance of the hard, rugose seed coat; and (3) seeds would exhibit optimal germination under constant, moderate temperatures (24 °C) compared to fluctuating high temperatures, reflecting their adaptation to buffered microclimates under nurse canopies. Ultimately, this research aimed to contribute valuable data to the limited body of knowledge on *P. greggii* propagation, supporting conservation efforts and sustainable management practices within its native range.

Material and Methods

Experimental site

The experiment was conducted from June 14 to August 13, 2023, at the seed laboratory of the Facultad de Zootecnia y Ecología (FZyE), Universidad Autónoma of Chihuahua, located in Chihuahua, in Northern Mexico. The geographical coordinates of FZyE are 28º 35’ 10” North and 106º 06’ 38” West, with an altitude of 1550 m.

Study species

Peniocereus greggii (Engelm.) Britton & Rose, commonly known as "Arizona Queen of the Night" or "Huevo de venado", is a perennial cactus native to the arid regions of northern Mexico and the southwestern United States, with altitudes between 1200 and 1600 m (Pinkava, 1995). This species is characterized by a prominent, tuberous napiform root that serves as a primary energy reservoir, weighing up to 60 kg, and by slender, grayish stems that mimic dry branches for camouflage (Mauseth and Stone-Palmquist, 2001). *P. greggii* gets typically established under nurse plants such as *Larrea tridentata* and *Neltuma* spp., which provide an appropriate microclimate for seedling survival (Muro-Pérez *et al.*, 2012). The seeds are black, approximately 3-4 mm long, and have a hard, rugose testa (Muro-Pérez *et al.*, 2021).

Site of origin of the seeds

The seeds used in this study were collected from a natural population of *P. greggii* located in the San Onofre ejido, municipality of Satevó, Chihuahua, Mexico (Figure 1). Geographically, the site is situated between 28° 06' 03" N and 106° 11' 13" W, at an altitude of 1,368 m (INEGI, 2018). The climate is classified as very dry and semi-warm with warm summers (BWh), according to the Köppen system modified by García (2004). The average annual temperature ranges from 18 to 21 °C, with an annual precipitation range of 250-300 mm and a frost-free period of approximately 225 days (INEGI, 2018). The topography consists of low- to medium-hills with slopes ranging from 4 to 20%, characterized by deep alluvial soils. The local vegetation is a Xerophytic scrubland (Rzedowski, 2006) with *Neltuma glandulosa*, *Vachellia constricta*, *Fouquieria splendens*, *Mimosa aculeaticarpa*, and *Larrea tridentata* being the most frequently observed species in the study area.

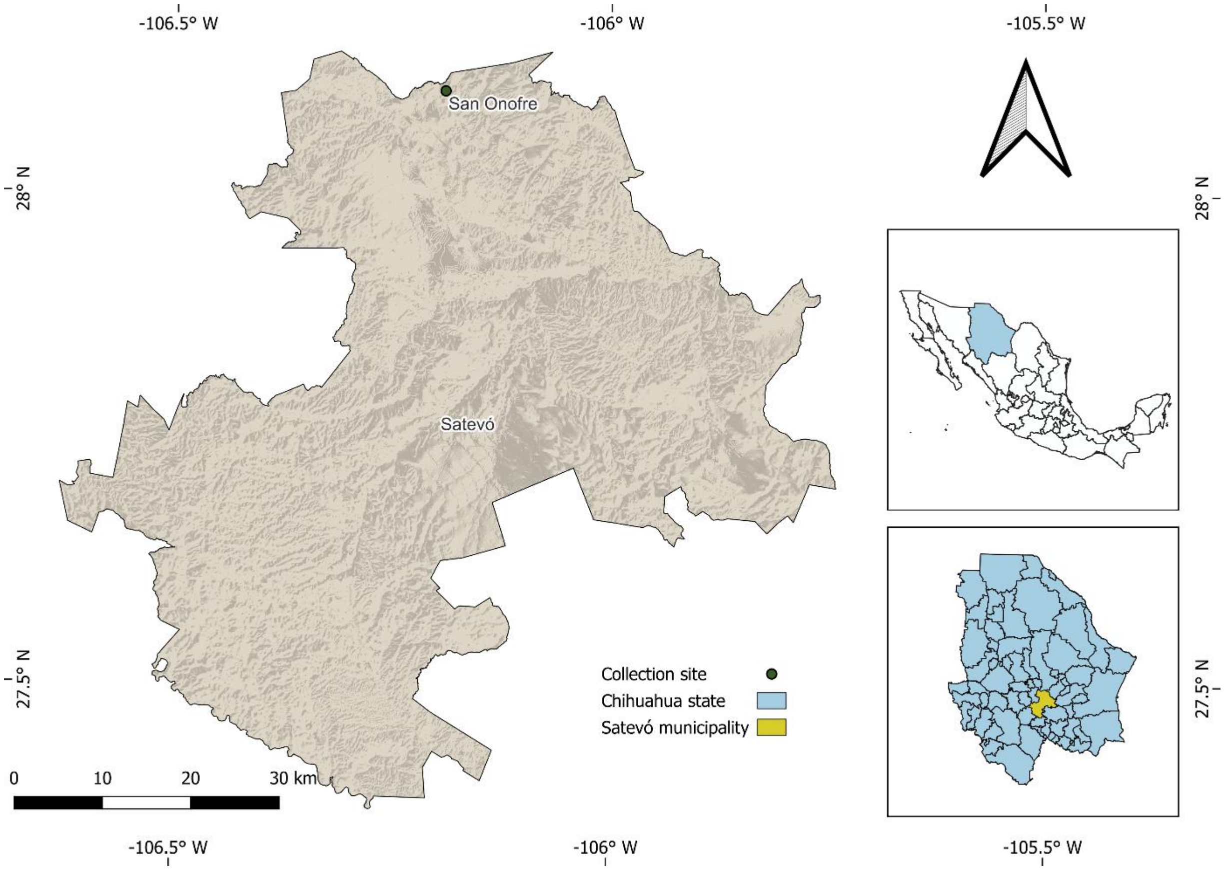

Figure 1. Geographic location of the collection site of *P. greggii* in the municipality of Satevó, Chihuahua, Mexico.

Seed material and processing

Two separate seed lots were used in this study to assess the effect of storage time (after-ripening) on germination: one harvested in the summer of 2016, and the other harvested in the summer of 2022. Both seed lots were provided by local landholders (*ejidatarios*) from the community of San Onofre. Following the methodology described by Gutiérrez (2015), seeds from 2016 were extracted from ripe fruits, separated from the mucilage using a strainer under running tap water, and air-dried. These seeds were stored in sterile glass jars at room temperature (25 ± 2 °C) in darkness at the Facultad de Zootecnia y Ecología (FZyE) facilities for six years. The 2022 seed lot was processed using the exact same cleaning and storage protocol to ensure consistency between samples.

Seed sterilization and scarification

Seeds were immersed in distilled water for 24 h to allow for imbibition. Following this process, were disinfected in a 20% sodium hypochlorite solution (Cloralex®) for 15 min, then rinsed three times with distilled water. The seeds were then placed on Whatman filter paper until completely dry and stored in plastic containers.

For the scarification trials, two sets of seeds were established, one for each harvest year (2016 and 2022). Within each set, four treatments were evaluated using 400 seeds per year (100 seeds per treatment): T1, immersion in a 50% sulfuric acid (H_2SO_4) solution for 6 min; T2, immersion in a 40% H_2SO_4 solution for 6 min; T3, mechanical scarification consisting of a 1 mm incision with a sterile scalpel in the micropyle region; and T4, an intact control group. After treatment, all seeds were rinsed with distilled water, dried on Whatman filter paper, and placed in sterile containers prior to the germination assays.

Substrate preparation and seeding

The germination substrate consisted of a 1:1:1 mixture of black tezontle (<0.5 mm) for moisture retention, silica sand to prevent waterlogging, and a commercial black soil (Nutrigarden®, Querétaro, Mexico) to enrich the mixture with organic matter. The mixture was homogenized and sterilized in a microwave oven (Sharp R21ltf) at maximum power for 10 min to eliminate potential pathogens.

The sterilized substrate was placed into 125 mL transparent plastic containers. Each container was modified with two perforations: a 3 mm drainage hole at the base and a 5 mm gas exchange vent in the lid. Ten seeds were placed on the substrate surface of each container using tweezers to avoid mechanical damage. Given that many Cactaceae seeds are photoblastic (Meiado *et al.*, 2016), they were left exposed to light. Each container constituted an experimental unit, with five replicates per treatment.

Irrigation was performed every three days or when the substrate surface appeared dry, watering to field capacity to ensure the substrate was moist but not waterlogged, as excessive moisture can rapidly lead to seed rot in Cactaceae species.

Germination trials

Germination assays were conducted under two distinct temperature regimes: a constant temperature of 24 ± 2 °C within a germination chamber (model VRD5AI, Torrey, Mexico) and a variable room temperature ranging from 30 °C to 37 °C, with a total of 800 seeds across all treatments. Germination, defined as the visible appearance of the radicle and hypocotyl through the seed coat, was recorded daily for 61 d, from June 15 to August 13, 2023.

Experimental design

The experimental trials followed the International Seed Testing Association (ISTA, 2021) guidelines, with modifications in the number of seeds per unit as recommended for wild taxa with limited seed availability (Baskin and Baskin, 2014; Rao *et al.*, 2007). A Completely Randomized Design (CRD) with a 2 × 4 × 2 factorial arrangement of fixed effects was employed, resulting in 16 treatment combinations. The factors evaluated were:

Factor A (Seed Age): Two levels (2016 and 2022). Factor B (Scarification): Four levels (T1: 50% H_2SO_4, T2: 40% H_2SO_4, T3: mechanical incision, and T4: intact control). Factor C (Incubation Temperature): Two levels (constant 24 °C and variable 30-37 °C).
The primary response variable was the Germination Percentage (GP), calculated at the end of the 61-day period as follows:

$$GP = \left(\frac{Number\ of\ germinated\ seeds}{Total\ number\ of\ seeds\ sown}\right) \times 100 \qquad [1]$$

Statistical analysis

Prior to analysis, germination percentage data were transformed using the arcsine square root function [arcsin($\sqrt{x}$/100)] to satisfy the assumptions of normality and homoscedasticity inherent to Analysis of Variance (ANOVA). The normality of the model residuals was verified using the Shapiro-Wilk test, while homoscedasticity was evaluated with Levene's test, and the independence of observations was confirmed using the Durbin-Watson test. Subsequently, data were analyzed using a three-way ANOVA. When significant differences were detected among multiple levels, a Tukey HSD test (α = 0.05) was used. In addition, a Welch's two-sample t-test (α = 0.05) was used for specific pairwise comparisons between two independent groups (e.g., comparing the natural germination of intact seeds between the two years of harvest). The mathematical model was defined as:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk} + \varepsilon_{ijkl} \qquad [2]$$

Where Y_{ijkl} represents the transformed germination percentage, μ is the overall mean, and α, β, and γ are the main effects of age, scarification, and temperature, respectively. The combinations of α, β, and γ represent their interactions, whereas ε_{ijkl} denotes the experimental error. As measures of precision and model fit, the coefficient of variation (CV) and coefficient of determination (R^2) were calculated. All analyses were performed using R (version 4.5.1) within RStudio (version 2025.09.0+387) and the *agricolae* package (de Mendiburu, 2021).

Results and Discussions

Germination of *P. greggii* was significantly influenced by seed age, temperature, and scarification treatments (Table 1). A significant interaction between seed age and scarification ($P < 0.05$) was observed, indicating that treatment effectiveness depends on seed physiological state. These results were obtained via a three-way ANOVA, as the data (after arcsine transformation) strictly fulfilled the assumptions of normality (Shapiro-Wilk, *P* = 0.082), homoscedasticity (Levene, *P* = 0.608), and independence of observations (Durbin-Watson, *P* = 0.482). The model demonstrated high precision (CV = 2.02) and explained 44.58% of the total variability ($R^2 = 0.445$). Although this coefficient of determination is moderate, such values are expected in ecological studies of wild plant populations. The remaining unexplained variability (~55%) suggests that seed germination in *P. greggii* is also driven by complex intrinsic or unmeasured microenvironmental factors, such as genetic variation, maternal effects, or specific moisture and light requirements (Baskin and Baskin, 2014; Barrios *et al*., 2020).

Table 1. Three-way analysis of variance (ANOVA) of the effect of seed age, temperature, and scarification treatment on the germination percentage of *P. greggii.*

Source of Variation	**Df**	**Sum Sq**	**Mean Sq**	**F-value**	***P*-value**
Age	1	0.2876	0.2876	6.107	0.016 *
Treatment	3	1.0894	0.3631	7.709	< 0.001 ***
Temperature	1	0. 2243	0.2243	4.762	0.032 *
Age × Treatment	3	0.6122	0.2041	4.3327	0.007 **
Age × Temperature	1	0.0162	0.0162	0.345	0.559
Treatment × Temperature	3	0.058	0.0193	0.410	0.746
Age × Treatment × Temperature	3	0.1372	0.0457	0.971	0.412
Residuals	64	3.0146	0.0471		

Note: Df = Degrees of freedom; Sum Sq = Sum of squares; Mean Sq = Mean squares. Significance codes: ***0.001, **0.01, *0.05.

Effect of seed age

In the intact control group (T4), seeds collected in 2016, after seven years of storage, registered significantly higher germination percentages than freshly harvested seeds from 2022 (Figure 2). Although this result may initially seem counterintuitive, it suggests that a portion of *P. greggii* seeds can maintain viability for extended periods under controlled conditions. The significantly higher germination in older seeds potentially indicates a reduction in physiological dormancy over time (after-ripening). However, it is important to note that viability tests (e.g., tetrazolium) were not performed on non-germinated seeds; therefore, it cannot be definitively determined whether the low germination percentages (around 30%) are due to physiological dormancy or a loss of seed viability during storage. Furthermore, since initial germination data for the 2016 lot are unavailable, it is acknowledged that differences in germination could be partially influenced by the intrinsic characteristics of each seed lot rather than solely by age. This result is consistent with findings from other Cactaceae; for instance, Kwack and Zimmer (1978) documented successful germination in aged seeds of *Maihuenia poeppigii*, suggesting that physiological changes during storage can enhance germinability. Similarly, Flores *et al*. (2005) reported germination success in over 83 cactus species after one year of storage, while Trujillo *et al*. (2014) observed that stored seeds of *Ferocactus townsendianus* remained viable for up to 10 years.

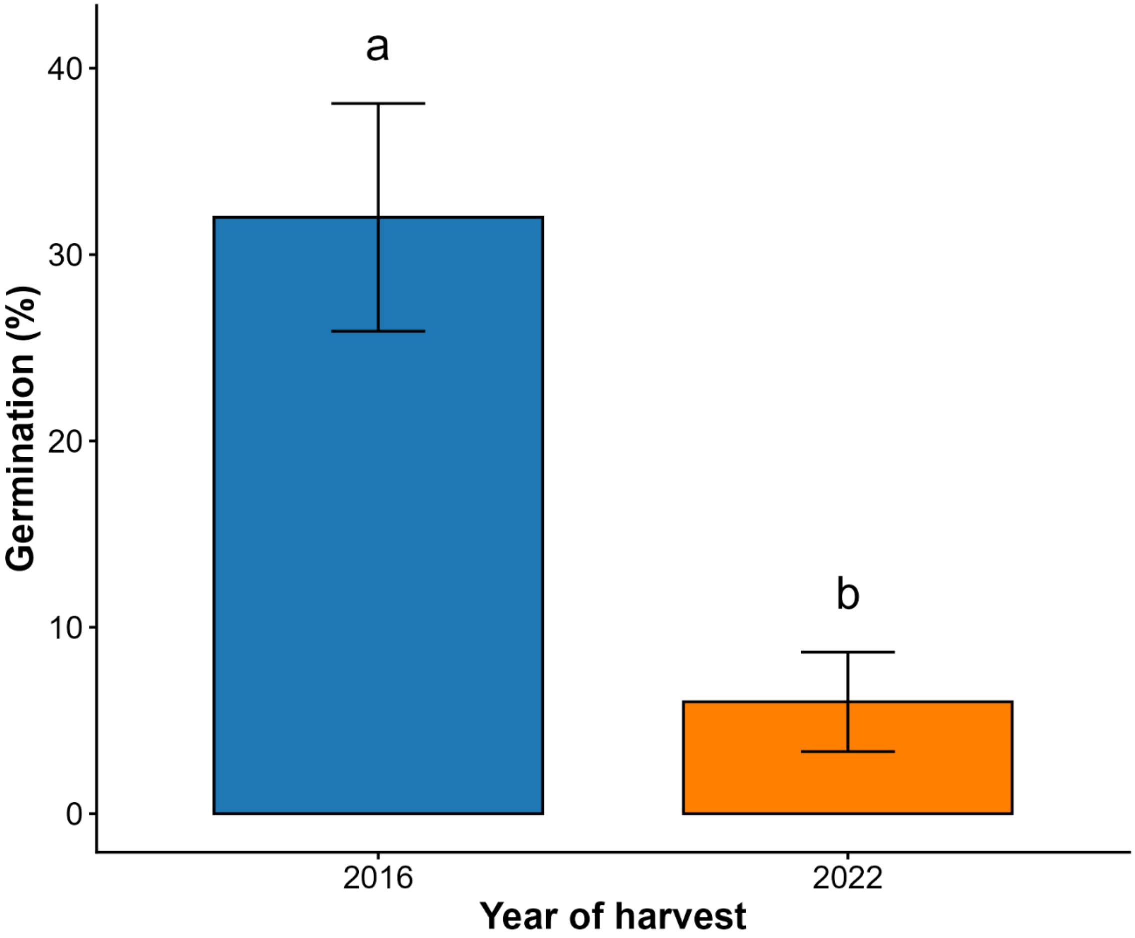

Figure 2. Final germination of *P. greggii* control seeds (non-scarified, T4) harvested in 2016 (blue) and 2022 (orange). The experiment was supervised for 61 days; however, the data presented correspond to the first 45 days, as germination ceased by day 42. Different letters above bars indicate significant differences according to Welch's t-test (P = 0.001). Bars represent means ± standard error.

The ability of *P. greggii* seeds to germinate after two distinct storage periods suggests the potential formation of persistent seed banks under natural conditions, as has been documented for other species (Kemp, 1989; Bowers, 2005). Our results could be interpreted as evidence of a bet-hedging strategy in which some seeds germinate under favorable conditions, while others remain dormant but viable. This type of strategy would potentially increase the likelihood of species persistence over time by allowing only a subset of the seed bank to germinate annually. Consequently, it is hypothesized that if harsh environmental conditions prevent seedling establishment, the seed bank might not be exhausted, securing a remnant of viable seeds for future favorable years. These insights are highly relevant given the existing knowledge gap regarding the capability of cactus species to form persistent seed banks (Cano-Salgado *et al*., 2012; Ordoñez-Salanueva *et al*., 2017).

Interaction between seed age and scarification treatments

The effectiveness of scarification treatments was significantly modulated by seed age (P = 0.007, Table 1). Therefore, the results are presented separately for each seed lot to avoid confounding the factors (Figure 3). In contrast to expectations based on the hard, rugose seed coat of *P. greggii*, neither chemical nor mechanical scarification improved germination compared to the Control (T4).

In the 2016 seeds, the control treatment achieved the highest germination percentage (~32 %), significantly outperforming all scarification methods. Consequently, the application of sulfuric acid (T1, T2) and mechanical incision (T3) effectively inhibited germination. A plausible explanation for this inhibition is that prolonged storage had already rendered the seed coat permeable through natural after-ripening. Therefore, the application of aggressive scarification methods to these aged seeds likely resulted in an overexposure of the internal tissues to the acid or mechanical stress, negatively affecting their germination capacity rather than promoting it.

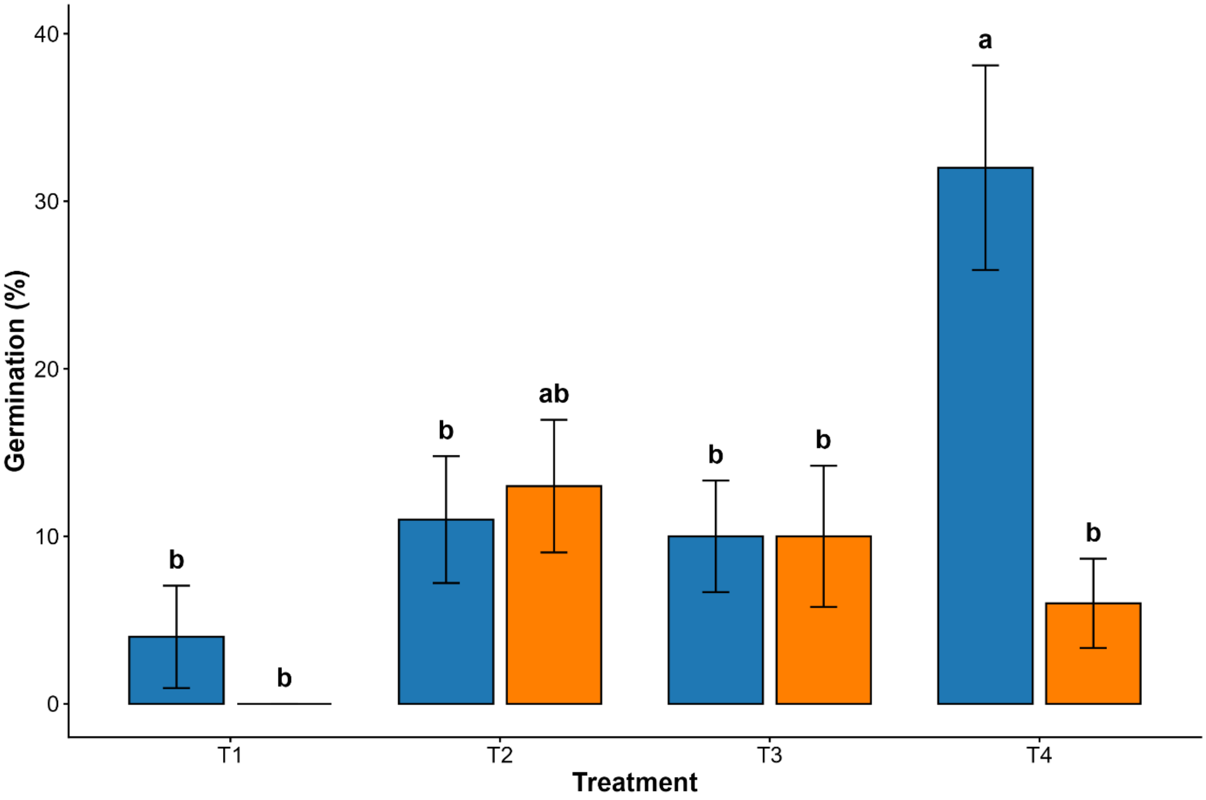

Figure 3. Interaction effect of seed age and scarification treatments on the germination percentage of *P. greggii*. Bars represent means ± standard error for seeds harvested in 2016 (blue) and 2022 (orange). Data are pooled across both temperature regimes (constant 24 °C and fluctuating 30–37 °C) as no significant interactions were detected for this factor. Treatments included: T1 (50% H_2SO_4 for 6 min), T2 (40% H_2SO_4 for 6 min), T3 (1 mm mechanical incision), and T4 (intact control). Germination was monitored for 61 days; however, data are presented for the first 45 days as germination ceased by day 42. Different letters indicate significant differences among all age-treatment combinations according to Tukey's HSD test ($P \leq 0.05$).

In contrast, germination was universally low (below 13%) in the 2022 seeds, regardless of the scarification method used. The failure of mechanical scarification (T3) on positively affecting the germination of *P. greggii* is particularly telling. In species where a hard seed coat acts as a primary barrier, artificially breaching the testa typically triggers immediate imbibition and germination, as demonstrated by the success of mechanical scarification in *Opuntia engelmannii* and *O. megacantha* (Gonzalez-Cortés *et al*., 2018), or in *Harrisia fragrans*, where scarification is mandatory for emergence (Dehgan and Pérez, 2005). The fact that *P. greggii* seeds neither respond to the direct opening of the seed coat (T3) nor to the erosion caused by acid (T2) strongly suggests the testa is naturally permeable to water and gases.

This response aligns *P. greggii* with other cactus species where the limiting factor is physiological rather than physical. For instance, Navarro-Carbajal *et al*. (2010) reported that for *Mammillaria mystax*, neither acid nor mechanical incision surpassed the control, confirming the absence of physical dormancy. Similarly, Godínez-Álvarez and Valiente-Banuet (1998) found that the vast majority of cacti in the Tehuacán Valley germinate freely without treatment. Therefore, the lack of a response to scarification in *P. greggii* indicates that natural abrasion is unnecessary for germination (Maiti *et al*., 1994) and provides solid inferential evidence of a physiological dormancy mechanism that cannot be broken by simply removing the physical barrier provided by the seed coat. These findings are consistent with other studies in Cactaceae reporting ecophysiological regulation of germination rather than purely physical dormancy mechanisms (Matus *et al*., 2022).

According to Kigel (1995), this type of dormancy is common among arid-zone species and serves as a temporal dispersion mechanism. By preventing all seeds from germinating simultaneously after a single rain event, physiological dormancy reduces the risk of massive mortality, ensuring that a portion of the seed bank remains available for future favorable conditions.

Effect of temperature

Given that the interactions between incubation temperature and both seed age (P = 0.559) and scarification treatment (P = 0.746) were not significant (Table 1), the main effect of temperature was analyzed independently by pooling the data across these factors. The analysis revealed that germination was significantly higher at a constant temperature of 24 °C than in the fluctuating 30-37 °C regime (P = 0.032; Figure 4).

While this difference might initially suggest a requirement for thermal stability, it is more likely driven by the absolute temperature values of the treatments. According to Barrios *et al*. (2020), the optimal germination range for the vast majority of Cactaceae species lies between 20 and 30 °C, whereas temperatures equal to or exceeding 35 °C typically do not promote germination. These results are consistent with recent findings for other cacti. For instance, Becker *et al*. (2020) reported that *Cereus hildmannianus* achieves maximum germinability at 25 °C, while Bacelar (2022) observed that eight endangered species from the Brazilian *Campo Rupestre* also share this specific thermal optimum, with germination declining sharply at higher temperatures.

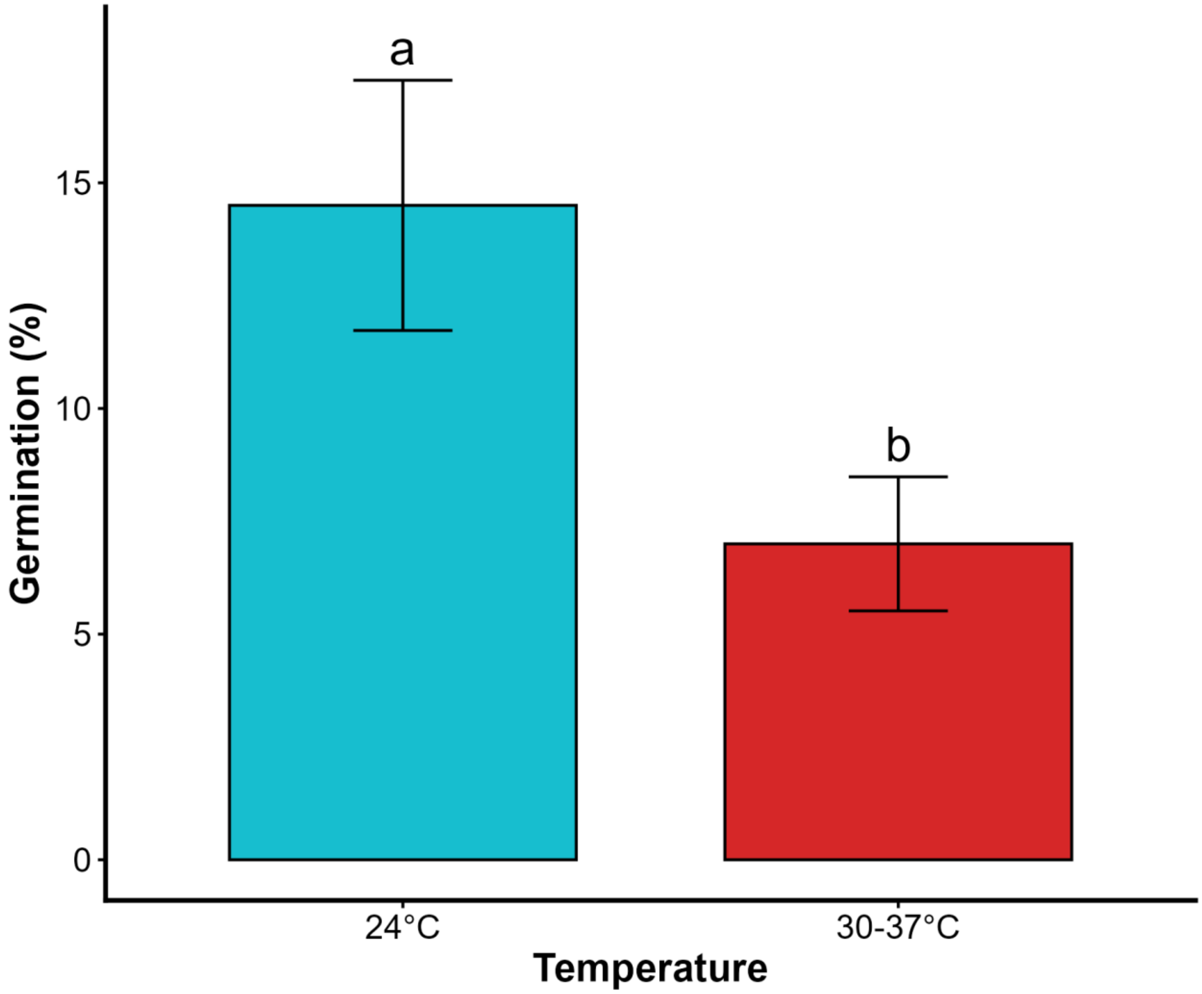

Figure 4. Effect of incubation temperature on the germination percentage of *P. greggii*. Bars represent means ± standard error, pooled across both seed ages (2016 and 2022) and all treatments (T1–T4), as no significant interactions were detected between temperature and these factors ($P > 0.05$). Different letters above bars indicate significant differences between the two thermal regimes based strictly on the main effect of the three-way ANOVA ($P = 0.032$).

Therefore, the reduced germination observed under the fluctuating regime is likely a direct consequence of heat stress induced by temperatures reaching 37 °C, rather than the fluctuation itself. As explained by Visscher *et al*. (2022), thermal stress in cactus seeds often triggers complex molecular repair mechanisms during imbibition (e.g., upregulation of Heat Shock Proteins), which may delay or arrest germination if the stress exceeds the seed's tolerance threshold.

Ecologically, the preference for moderate temperatures (e.g., 24 °C) and sensitivity to high heat are consistent with the species' association with nurse plants. Although some cactus species inhabiting open spaces benefit from fluctuating temperatures to sense canopy gaps (Ortega-Baes *et al*., 2011), *P. greggii* typically establishes itself beneath shrub canopies such as those of *Larrea tridentata* or *Neltuma* spp. These nurse plants create a buffered microenvironment, protecting seedlings from extreme diurnal temperature fluctuations and excessive heat (Muro-Pérez *et al*., 2012). Thus, the inability to germinate effectively at high temperatures (30-37 °C) likely represents an adaptive mechanism that prevents seedling emergence during periods of potentially lethal heat stress in the open desert.

Conclusions

In this study, the germination of *P. greggii* was significantly influenced by seed age, with older seeds (stored for seven years) achieving the best germination percentages. This provides solid inferential evidence that the species undergoes a natural after-ripening process to overcome physiological dormancy. Consequently, artificial scarification treatments are unnecessary and detrimental, as they effectively inhibit germination in aged seeds and fail to promote it in fresh ones.

Regarding environmental requirements, this study showed that *P. greggii* achieves the best germination at a moderate, constant temperature of 24 °C, whereas high-fluctuating regimes (30–37 °C) likely induce thermal inhibition. For effective *ex situ* conservation and propagation, it is recommended to store seeds for extended periods (dry storage) to allow natural dormancy release and to sow them under moderate temperature conditions, strictly avoiding physical or chemical modification of the seed coat.

ETHICS STATEMENT

Not applicable.

CONSENT FOR PUBLICATION

All the authors agreed on the publication of this version of the manuscript.

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

Not applicable.

AUTHOR CONTRIBUTIONS

Conceptualization, F.D.L-R., F.V-G., E.E.V-G. Methodology, F.D.L-R. Validation, N.G.A-P. Formal analysis, F.D.L-R. Investigation, F.D.L-R. Resources, F.D.L-R. and C.R.M-N. Writing—original draft preparation, F.D.L-R; Writing—review and editing, F.V-G., E.E.V-G., C.R.M-N., R.C-L., H.V-M. Visualization, F.D.L-R. Supervision, F.V-G. and E.E.V-G.

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