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NOTES AND INSIGHTS

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Tolerance to 1 year of drought: The role of seed hydration memory in the germination and early seedling development of *Xiquexique gounellei* subsp. *gounellei* under prolonged water deficit

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Abstract

Seed hydration memory can provide ecophysiological advantages, enhancing seedling competitiveness and influencing species establishment in environments with limited water availability. This study aimed to evaluate the effects of hydration–dehydration cycles (HD cycles) on seed germination and initial development of *Xiquexique gounellei* subsp. *gounellei* seedlings subjected to prolonged water deficit. Seeds were subjected to 0, 1, 2, and 3 HD cycles, each consisting of 5 h of hydration followed by 3 h of dehydration. The *Germination Memory Index* (GMI) was then calculated using daily germination data. After a 2-month acclimatization period, seedlings underwent irrigation cycles of 7, 14, and 28 days, and morphological parameters were assessed at the end of the 28-day period. Then, irrigation in all treatments was suspended for 360 days, after the third morphological assessment conducted during the seedling growth period. After this period, the morphological and biochemical evaluation of the reducing sugars was carried out. The seedlings were irrigated and then the parameters were evaluated again. The GMI confirmed, for the first time, the presence of hydration memory in this species, even under optimal water conditions, suggesting an inherent adaptive capacity. Treatment with two HD cycles was most effective, enhancing early growth in terms of height, stem diameter, root length, and biomass. HD cycles trigger physiological mechanisms linked to hydration memory, improving drought resilience. Notably, all seedlings survived the year-long drought. These findings demonstrate that hydration memory remains functionally active beyond germination, throughout seedling development, and even after extended periods of water deficit.

KEYWORDS

ecophysiology, growth, HD cycles, irrigation cycles, seedlings

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1 | INTRODUCTION

The Caatinga is generally classified as a Seasonally Dry Tropical Forest (SDTF), characterized by prolonged dry periods, vegetation adapted to water deficit, and a semi-arid climate. Seeds produced and dispersed in the Caatinga naturally undergo hydration–dehydration cycles (HD cycles), which involve the interruption of water uptake during imbibition due to soil water loss caused by high temperatures and low relative humidity. As a result, water remains available in the soil for only a short period of time (Meiado, 2013; Pinheiro et al., 2016). This prevents seeds deposited in the upper soil layers from continuously progressing through the three phases of the imbibition process in the environment, naturally subjecting them to HD cycles (Alvarado-López et al., 2014; Dubrovsky, 1996, 1998). Dehydration during imbibition acts as a primary stress, triggering a range of molecular, biochemical, physiological, and even epigenetic responses that can lead to the acquisition of tolerance to abiotic stresses (Chen & Arora, 2013; Mauch-Mani et al., 2017). Some of these changes are temporary, while others may persist throughout the plant's life cycle and, in some cases, be passed on to subsequent generations (Hossain et al., 2018).

The ability of seeds to withstand initial exposure to stress, provided by HD cycles, represents a strategic adaptation for their development and establishment in arid and semi-arid ecosystems (Shivanna, 2016). Since species occurring in these dry regions constantly face low water availability due to environmental dynamics, drought-related stresses become inevitable (Seleiman et al., 2021). Therefore, the formation and expression of seed hydration memory play a fundamental role in their development and establishment in the field (Lima & Meiado, 2018a). Seeds can express this hydration memory during germination or early development, ensuring seedling establishment even under stressful conditions (Lima & Meiado, 2017, 2018a). Consequently, the different levels of memory expression may vary depending on the plant's life stage, the type of stress applied, or its intensity.

The Caatinga constitutes an ecosystem within the SDTF and has historically experienced extreme weather events (Nascimento et al., 2023). Projections associated with climate change suggest a significant expansion of semi-arid areas, with a high risk of desertification by 2100 (Moraes et al., 2023). Currently, the Northeast region of Brazil hosts six major desertification centers, driven by deforestation, fires, agriculture, and extensive cattle ranching. These activities promote habitat fragmentation and, consequently, biodiversity loss (Althoff et al., 2018; Antongiovanni et al., 2020; Perez-Marin et al., 2012). Deforestation alerts in the Caatinga have identified and quantified the loss of 322 847 hectares of vegetation (Costa et al., 2024). The scarcity of Full Protection Units, particularly Categories I, II, and III of the International Union for Conservation of Nature, further aggravates this issue. Currently, only 8% of the Caatinga benefits from legal protection under Brazil's national natural reserve legislation (Law no. 9.985, of July 18, 2000), and within this total, only 1.3% falls under reserves with full legal protection (Teixeira et al., 2021).

As a strategy to recover degraded areas in the Caatinga, planting in the field seedlings has proven to be the most efficient technique so far (Carvalho et al., 2022). However, obtaining seeds with high physiological and physical quality remains the greatest challenge, as these seeds produce vigorous seedlings capable of establishing themselves quickly and uniformly in the field, even under conditions of water scarcity. The seed hydropriming technique, which simulates HD cycles, appears to be a promising and low-cost approach, showing significant results for seeds from semi-arid regions (Nascimento & Meiado, 2021). Seedlings produced from seeds subjected to HD cycles consistently maintain their growth patterns during early development, even under water deficit conditions (Freitas & da Silva, 2024; Lima & Meiado, 2018a).

In the recovery of degraded areas in semi-arid environments, using species of Cactaceae represents an effective characteristic, particularly in areas prone to desertification, due to their ability to thrive under extreme drought conditions (Nefzaoui & El Mourid, 2007). For instance, seedlings of *Xiquexique gounellei* (F. A. C. Weber ex K. Schum) Lavor and Calvente subsp. *gounellei* successfully establish in these regions, forming a forage layer that facilitates the nucleation process and creates favorable conditions for the establishment of new species in the environment (E. A. V. Santos et al., 2020). The Natural Regeneration Acceleration Core Planting Method with Secondary Species involves dense planting, aiming to create a more favorable microclimate for seedling development within the core. This method employs tree species and columnar cacti to promote the regeneration of areas exhibiting signs of natural regeneration or some water availability (Socolowski et al., 2023).

Current research on this species primarily focuses on cladode planting, a propagation method that produces clones and results in low genetic variability among individuals within the same population (E. A. V. Santos et al., 2020). To enhance the recovery of degraded areas, our study proposes the production of *X. gounellei* subsp. *gounellei* seedlings from seeds subjected to HD cycles, aiming for their application in environmental restoration projects. We investigated the formation and expression of seed hydration memory at two stages of the plant's life

cycle, from germination to initial development. We formulated the following hypotheses: (i) seeds subjected to HD cycles can form hydration memory, even if this memory is not expressed during the germination phase. This hypothesis aligns with the findings of B. S. Santos et al. (2023), who reported a neutral germination response in this species' seeds, even after undergoing HD cycles. These results suggest that hydration memory may be stored and expressed at later developmental stages rather than during germination. Furthermore, we hypothesized that (ii) seedlings produced from seeds subjected to HD cycles will exhibit hydration memory-related responses during initial development, even under drought conditions; and (iii) seedlings originating from seeds subjected to HD cycles will demonstrate greater resilience after prolonged water deficit exposure for 360 days, contributing to the long-term sustainability of environmental restoration projects in semi-arid areas. Therefore, this study aimed to evaluate the effects of HD cycles on the germination and initial development of *X. gounellei* subsp. *gounellei* seedlings following prolonged exposure to water deficit.

2 | MATERIALS AND METHODS

2.1 | Study site and seed collection

Xiquexique Lavor, Calvente, and Versieux is a genus in the family Cactaceae that includes three species: *Xiquexique frewenii* (Zappi and Taylor) Lavor and Calvente, which occurs on limestone outcrops in central Minas Gerais; *Xiquexique tuberculatus* (Werderm.) Lavor and Calvente, restricted to sandy habitats, especially in ancient dune fields near the São Francisco River; and *Xiquexique gounellei* (F. A. C. Weber) Lavor and Calvente, together with its subspecies *Xiquexique gounellei* subsp. *zehntneri* (Britton and Rose) Lavor and Calvente and *X. gounellei* subsp. *gounellei*, which occur on rocky and stony soils and dominate Caatinga regions characterized by low and sparse vegetation across all northeastern Brazilian states (Lavor et al., 2020; Taylor & Zappi, 2004; Zappi & Taylor, 2011).

We collected seeds of *X. gounellei* subsp. *gounellei* in Brazil, South America (Figure 1a); in the state of Sergipe (Figure 1b); and in the municipality of Canindé de São Francisco (9°38′25.45″ S, 37°46′33.87″ W) (Figure 1c), in a dense hyperxerophilous Caatinga area on the banks of the São Francisco River. In this population (Figure 1d), we collected ripe fruits (Figure 1e); in addition, we observed young seedlings developing on a rock (Figure 1f). The ripe fruits were manually collected and processed, and the seeds were dried in plastic trays at room temperature until the funicular pulp was completely dehydrated. We then manually removed the dehydrated funicular pulp, washed the seeds under running water, and dried them again at room temperature. Afterwards, the seeds were stored in a cold chamber at 5°C for 2 months until the beginning of the experiments.

2.2 | Seed hydropriming technique for simulating HD cycles

We applied the seed hydropriming technique to simulate HD cycles, serving as a pre-germination treatment to evaluate the expression of the seed hydration memory. Initially, we determined the imbibition curve by consecutively weighing 400 seeds placed in Petri dishes with distilled water, divided into four replicates of 100 seeds, at 60-min intervals, until the weight stabilized. After establishing the imbibition curve, we defined a point on the curve as Interval X, corresponding to half of phase I of the imbibition process (Lima et al., 2018).

We also determined the dehydration curve using 400 seeds, divided into four replicates of 100 seeds. We hydrated the seeds until they reached Interval X, then removed them from contact with water and dried them in an oven with forced air circulation at 40°C in trays. We weighed the seeds on an analytical scale at 60-min intervals until they returned to their initial weight (Lima et al., 2018). After determining the imbibition and dehydration curves, we subjected the seeds to 0 (Control), 1, 2, and 3 HD cycles, with Interval X defined as 5 h of hydration and 3 h of dehydration for this species.

2.3 | Experimental setup

We conducted an experiment in a greenhouse covered with translucent tiles to prevent irrigation from natural rainfall. We subjected the seeds of *X. gounellei* subsp. *gounellei* to 0, 1, 2, and 3 HD cycles and then sowed them in plastic pots containing 500 g of soil collected from the same location as the seeds. We established 20 replicates of 50 seeds for each treatment, totaling 80 pots. During the first 30 days, we irrigated all pots regularly according to the soil's field capacity to ensure seed germination and seedling development. We monitored germination daily during this period. After 30 days, we randomly selected 20 seedlings per pot and used them for the acclimatization process, which involved once-weekly irrigation for 2 months for all treatments. Following acclimatization, we subdivided the replicates of each treatment to initiate the irrigation cycles, defined as 7 days (Control), 14 days (Deficit I), and 28 days (Deficit II), applied to the 0, 1,

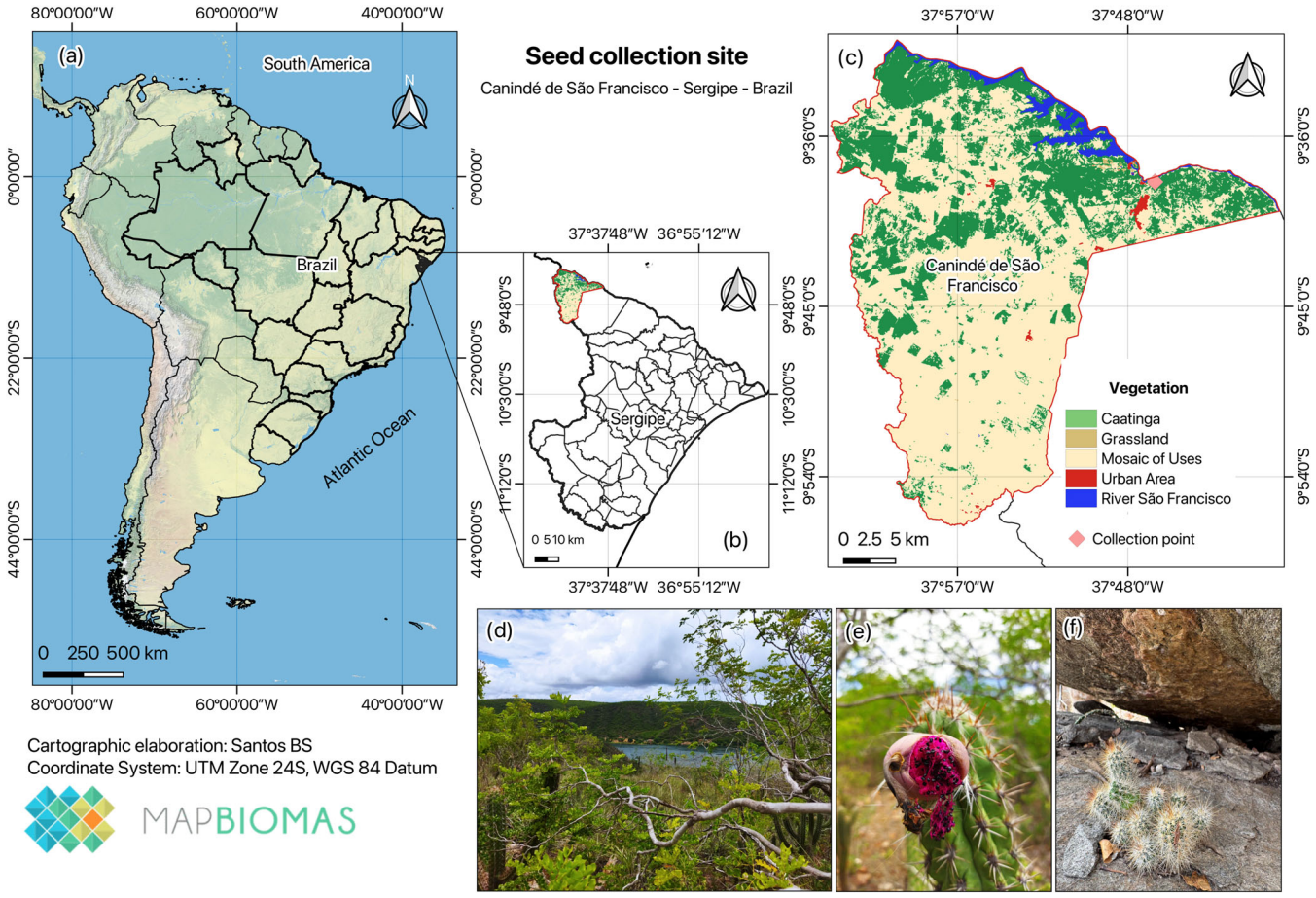


FIGURE 1 Seed collection site *Xiquexique gounellei* (F. A. C. Weber ex K. Schum) Lavor and Calvente subsp. *gounellei* (Cactaceae): (a) Brazil, in South America; (b) the state of Sergipe; (c) the municipality of Canindé de São Francisco (9°38′25.45″ S, 37°46′33.87″ W). (d) The studied population, (e) the collected fruits, and (f) a seedling developing on a rock. The map was generated in QGIS using data from the MapBiomas Brazil project (Souza Jr et al., 2020).

2, and 3 HD cycle treatments. Morphological assessments were conducted at the end of the 28-day cycle, by which time seedlings had received four (Control), two (Deficit I), and one (Deficit II) irrigation events, respectively.

2.4 | Morphological analyses

Seven days after applying the Deficit II irrigation cycle, we conducted morphological evaluations, including measurements of height (cm), basal diameter (mm), apical diameter (mm), root length (cm), and dry biomass weight (mg). We performed morphological evaluations at five time points (T_n): T_0, before the start of the irrigation cycles, following 2 months of acclimatization; T_1, 35 days after the start of the irrigation treatments; T_2, 65 days after the start, by which time seedlings in the control had received eight irrigations, those in the Deficit I had received four, and those in the Deficit II had received two. T_3 was carried out 360 days after the start of the irrigation cycles, following the suspension of irrigation after T_2; and T_4, 390 days after the start, following seedling rehydration and 30 additional days of irrigation.

2.5 | Biochemical analyses

During the T_3 and T_4 evaluations, we quantified the reducing sugar content to assess the metabolic adaptations of the plants during prolonged water deficit and their recovery capacity after rehydration. For this analysis, we macerated 200 mg of plant material in 5 mL of 100 mM potassium phosphate buffer solution (pH 7.8) and centrifuged the material at 4000 rpm for 40 min. After centrifugation, we discarded the pellet and collected the supernatant using an automatic pipette. We subdivided each replicate into aliquots and stored them in 1.5-mL *Eppendorf* tubes at −18°C until macromolecule quantification. For the analysis of reducing sugars, we used 350 μL aliquots and analyzed them using a

spectrophotometer at a wavelength of 460 nm, with 3,5-dinitrosalicylic acid as the reagent and a standard glucose solution as a reference (Miller, 1959).

2.6 | Statistical analysis

2.6.1 | Germination Memory Index

Using daily germination data, we calculated six germination metrics to characterize germinative behavior through the *germinationmetrics* package in the R software (Aravind et al., 2025; R Core Team, 2025). We applied these metrics to calculate the GMI following the methodology proposed by Lima et al. (2025).

We characterized seed germination through germinability (G; %) as a parameter of germination capacity, where $\sum_{ni}$ represents the number of germinated seeds and N is the total number of seeds, expressed by the equation:

$$G = \left(\frac{\sum_{ni}}{N}\right).100,\ 0 \le G \le 100.$$

We used ($t_{50\%}$; days) as a measure of germination time, represented in days to achieve 50% of the sampled germination, calculated by the equation:

$$t_{50\%} = t_i + \frac{\left(\frac{N}{2} - n_i\right)(t_j - t_i)}{n_j - n_i},\ 0 < t_{50\%} < k.$$

where N is the final number of germinated seeds, and n_i and n_j are the cumulative numbers of germinated seeds from adjacent counts at times t_i and t_j, respectively, with $n_i < (N/2) < n_j$ (Farooq et al., 2005).

We determined the Mean Germination Rate $\left(\bar{v}; \text{dias}^{-1}\right)$ as an indicator of the speed of the germination process, expressed by the equation:

$$\bar{v} = \frac{1}{\bar{t}},\ 0 < \bar{v} \le 1.$$

where $\bar{t}$ is the Mean Germination Time, calculated as $\bar{t} = \left(\sum_{i=1}^{k} n_i.t_i / \sum_{i=1}^{k} n_i\right)$, t_i is the period from the start of the first count to the n observation, n_i is the number of seeds germinated at time i (not a cumulative value), and k corresponds to the final germination time (Labouriau, 1983).

We assessed the Coefficient of Variation of Time (CV_t; %) to represent the uniformity of germination, expressed as:

$$CV_t = \left(\frac{S_t}{\bar{t}}\right)100,\ 0 < CV_t < \infty.$$

where S_t is the standard deviation of germination, calculated as $s_t = \sqrt{\sum_{i=1}^{k} n_i (t_i - \bar{t})^2 / \left(\sum_{i=1}^{k} n_i - 1\right)^{-1}}$, and $\bar{t}$ is the mean germination time (Ranal & Santana, 2006).

We evaluated the synchronization of the germination process using the synchrony index (Z), expressed by the equation:

$$Z = \frac{\sum C_{ni,2}}{N}, \text{with } C_{ni,2} = \frac{n_i(n_i - 1)}{2} \text{ and}$$
$$N = \frac{\sum n_i(\sum n_i - 1)}{2},$$
$$0 \le Z \le 1.$$

where $C_{ni,2}$ is the combination of seeds germinated at time i (Ranal & Santana, 2006).

Finally, we represented the uncertainty of germination through the uncertainty parameter (U; bit), an adaptation of the Shannon index that measures the degree of uncertainty in predicting informational entropy, given by the equation:

$$U = -\sum_{i=1}^{k} f_i \log_2 f_i, \text{with} f_i = \frac{n_i}{\sum_{i=1}^{k} n_i},\ 0 \le U \le \log_2 n.$$

where f_i is the relative frequency of germination at time i, n_i is the number of seeds germinated on day i and k is the last day of observation (Ranal & Santana, 2006).

Lima et al. (2025) developed a mathematical model based on these germination metrics to evaluate the expression of seed hydration memory. This model incorporates the gains in germination capacity induced by HD cycles, using the equation:

$$GMI = \frac{\frac{(G_{cycle} - G_{ref})}{G_{cycle}} + \frac{(t_{50\%ref} - t_{50\%cycle})}{t_{50\%ref}} + \frac{(\bar{v}_{cycle} - \bar{v}_{ref})}{\bar{v}_{cycle}} + \frac{(CV_{tref} - CV_{tcycle})}{CV_{tref}} + \frac{(\bar{Z}_{cycle} - \bar{Z}_{ref})}{\bar{Z}_{cycle}} + \frac{(U_{ref} - U_{cycle})}{U_{ref}}}{6}.$$

where cycle refers to the seeds that underwent the HD cycles and ref to the seeds that did not undergo them. At

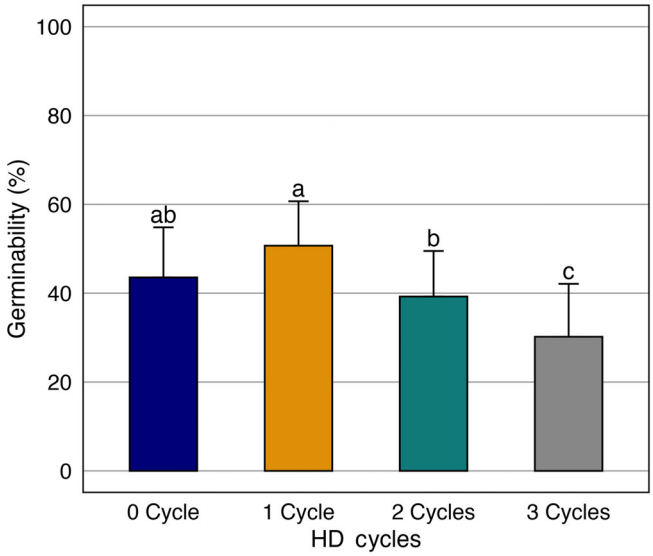


FIGURE 2 Germinability (%) of *Xiquexique gounellei* (F. A. C. Weber ex K. Schum) Lavor and Calvente subsp. *gounellei* (Cactaceae) seeds subjected to 0, 1, 2, and 3 hydration–dehydration cycles (HD cycles). Data are expressed as mean ± standard deviation, with a significance level of $p < 0.05$. Lowercase letters indicate significant differences among treatments.

the end of the calculation, the index is expressed in $0 \leq GMI \leq 1$.

2.6.2 | Initial development and biochemistry

We subjected all early development and biochemical parameters to normality and variance homogeneity tests using the Shapiro–Wilk and Levene tests. Subsequently, we performed a Factorial Analysis of Variance (HD Cycles, Irrigation Cycles, Time). We conducted all analyses in the R *software*, adopting a significance level of $p \leq 0.05$ (R Core Team, 2025).

3 | RESULTS

3.1 | Seed germination

The seeds of *X. gounellei* subsp. *gounellei* exhibited a low expression of hydration memory under conditions of constant water availability during the first 30 days, a period designed to ensure adequate soil moisture for germination. However, seeds subjected to 1 cycle showed the highest germinability (Figure 2) ($df = 3$; $F = 12.389$; $p < 0.0001$). Regardless of the HD cycle, the memory indices M_G, $M_{t_{50\%}}$, $M_{\bar{v}}$, M_{CV_t}, M_z, and M_U remained consistent across the different treatment levels (Figure 3). Consequently, the data did not fully support the first hypothesis, which predicted a neutral effect of HD cycles. However, we detected a small yet significant expression of hydration memory during germination, suggesting that despite its minimal manifestation, hydration memory is not entirely absent. This subtle response indicates that seeds subjected to HD cycles retain some adaptive capacity even under optimal water availability conditions.

3.2 | Initial development

Seedlings originating from seeds subjected to two HD cycles grew 26% more than the control group by the end of the experiment (Figure 4a and Table 1). This benefit of discontinuous hydration was observed across all evaluation intervals, regardless of the irrigation regime. Seedlings from seeds exposed to two HD cycles and subjected to deficit I and deficit II irrigation cycles grew 19.28% and 11.09% more, respectively, compared to the control. Under more restrictive irrigation conditions, the beneficial effects of HD cycles on seedling height became proportionally more evident, especially in the final evaluation conducted after 1 year of irrigation cycles (T_4) (Figure 4a).

Regarding basal diameter (Figure 4b), seedlings from seeds subjected to two HD cycles showed a 35.9% increase compared to the control, while apical diameter increased by 39.5% (Figure 4c and Table 1). The positive effects of HD cycles on these parameters persisted throughout all evaluation intervals and under all irrigation regimes (Table 1). However, at interval T_3, the basal diameter decreased by about 18% relative to the T_2, as did the apical diameter, likely due to the intense water deficit maintained for 360 days, which caused cell turgor loss and tissue dehydration, as discussed in the following section.

Root length also increased by 22.17% at the end of the experiment in seedlings derived from seeds subjected to two HD cycles (Figure 5a), paralleling the increase observed in dry biomass (Figure 5b and Table 1). This superior performance remained consistent over time, regardless of irrigation frequency. However, seedlings subjected to Deficit I and Deficit II irrigation cycles showed reductions of 16% and 25.3%, respectively, in root length and dry biomass compared to plants under control irrigation.

3.3 | Reducing sugars

Biochemical analysis revealed an increase in reducing sugar concentration in seedlings subjected to HD cycles and irrigated under the control regime. However,

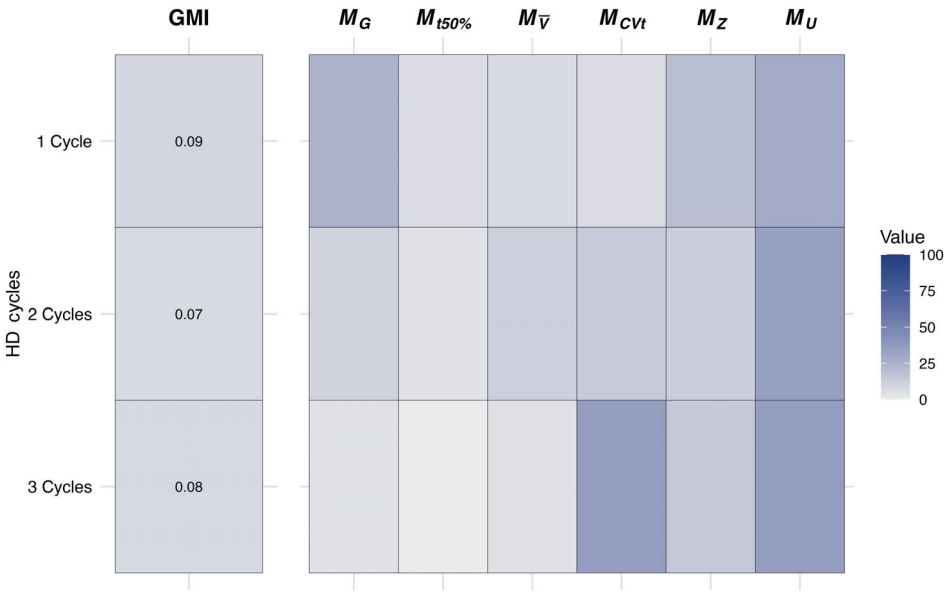


FIGURE 3 *Germination Memory Index* (GMI) and its contributions from each memory component of seeds of *Xiquexique gounellei* (F. A. C. Weber ex K. Schum) Lavor and Calvente subsp. *gounellei* (Cactaceae) subjected to 0, 1, 2, and 3 hydration–dehydration cycles (HD cycles). M_{CVt}, memory of germination uniformity; M_G, memory of germination capacity; $M_{t50\%}$, memory of germination time; M_U, memory of germination uncertainty; $M_{\bar{v}}$, memory of germination rate; M_z, memory of germination synchrony. Values from 0 to 100 represent the % contribution of each component.

seedlings from seeds exposed to three HD cycles and subjected to the deficit II regime showed a significant reduction in sugar concentration, with values approaching those observed during the recovery phase. Additionally, seedlings exposed to HD cycles combined with water deficit accumulated higher levels of reducing sugars overall (Figure 5c and Table 1), with the most pronounced accumulation observed at the T_3 evaluation. Following rehydration at T_4, however, sugar levels declined sharply all irrigation treatments.

4 | DISCUSSION

Seeds subjected to HD cycles improve their germination behavior even under water deficit conditions, increasing germination percentage and reducing the time required for this process, regardless of the population from which the seeds were produced or the seasonality (Lima & Meiado, 2017, 2023). However, seeds of *X. gounellei* subsp. *gounellei* subjected to HD cycles do not exhibit changes during the germination process, even when exposed to water deficit conditions, suggesting no expression of hydration memory during germination (B. S. Santos et al., 2023). However, our results contradict the findings of B. S. Santos et al. (2023), as we observed a small but significant expression of hydration memory. It is important to highlight that the authors considered only the parameters of Germinability (%), Mean Germination Time (days), Mean Germination Rate (days^{-1}), and Synchrony (Z). Our study evaluated six metrics characterizing germination behavior and employed a mathematical model that enabled more accurate detection of memory expression. The new mathematical tool proposed by Lima et al. (2025) played a crucial role in identifying even subtle expressions of hydration memory. This approach highlights the importance of considering multiple germination parameters for a more complete understanding of hydration memory mechanisms in seeds.

Our results provide new insights into the expression of hydration memory in this species, revealing that memory manifests during the initial development of seedlings, allowing them to grow even under water deficit conditions. This suggests that the levels of memory expression are directly associated with the intensity of applied stress and the plant's life stage, highlighting the species' plasticity in responding to different environmental conditions. These findings support the study's hypotheses and demonstrate that seedlings derived from seeds subjected to HD cycles exhibited responses associated with hydration memory, even under drought conditions. Furthermore, these seedlings displayed greater resistance following a prolonged dry period, underscoring the significant expression of hydration memory during early development.

The ability of cacti to leverage the irregularity of soil water availability for their initial development is crucial for species in semi-arid ecosystems (Lima & Meiado, 2017). Once seeds disperse in these environments, they settle in the most superficial soil layers and naturally undergo HD cycles due to rapid water evapotranspiration caused by high temperatures and low relative humidity. This results in brief soil water retention, preventing seeds from continuously reaching the three phases of the imbibition process (Dubrovsky, 1996, 1998). Experiencing these conditions is important not only during germination but also in the initial development phase, since it enhances competitive advantages,

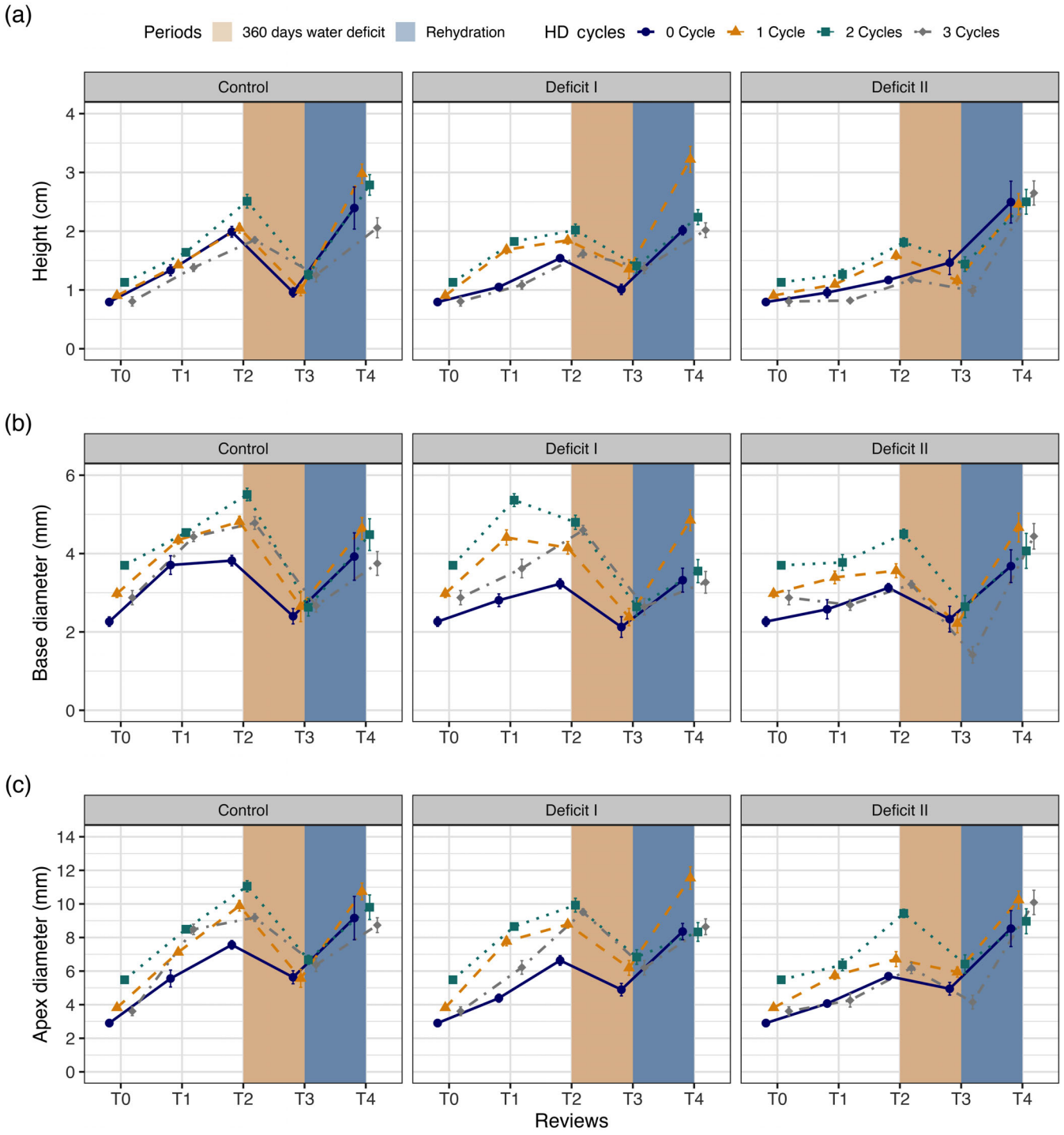


FIGURE 4 (a) Height (cm); (b) base diameter (mm) and (c) apex diameter (mm) of seedlings of *Xiquexique gounellei* (F. A. C. Weber ex K. Schum) Lavor and Calvente subsp. *gounellei* (Cactaceae) originated from seeds that went through 0, 1, 2, and 3 hydration–dehydration cycles (HD cycles) and were subjected to irrigation cycles of 7 (Control), 14 (Deficit I) and 28 days (Deficit II) of water suspension. T_0: Interval zero, before starting the irrigation cycles, after 2 months of acclimatization. T_1: 35 days after the start of the irrigation cycles. T_2: 65 days after the start of the irrigation cycles. T_3: 360 days after the start of irrigation cycles. T_4: 390 days after the start of irrigation cycles. We used $n = 20$, expressed as mean ± confidence interval with a significance level of $p < 0.05$.

promoting better development and greater resilience in the environment where they establish (López-Urrutia et al., 2014).

Studies evaluating the effects of HD cycles during early development combined with irrigation cycles show significant results. Morphological responses in seedling

TABLE 1 *F*-value (*F*), degree of freedom (df), and level of significance (*p*) obtained in the results of the analysis of factor analysis with the initial development parameter, for the factors: hydration–dehydration cycles (HD cycles), times (T_0, T_1, T_2, T_3, and T_4), and irrigation cycles (7, 14, and 28 days).

Factors	*F*	df	*p*
Height (cm)			
HD cycles	134.80	3	<0.0001
Times	1216.74	4	<0.0001
Irrigation cycles	50.33	2	<0.0001
Base diameter (mm)			
HD cycles	218.03	3	<0.0001
Times	508.84	4	<0.0001
Irrigation cycles	104.31	2	<0.0001
Apex diameter (mm)			
HD cycles	277.75	3	<0.0001
Times	1165.39	4	<0.0001
Irrigation cycles	135.09	2	<0.0001
Root length (cm)			
HD cycles	22.86	3	<0.0001
Times	791.04	4	<0.0001
Irrigation cycles	3.09	2	0.04597
Dry biomass (mg)			
HD cycles	283.66	3	<0.0001
Times	731.96	4	<0.0001
Irrigation cycles	78.73	2	<0.0001
Reducing sugars (μmol/g WF)			
HD cycles	10.994	3	<0.0001
Times	183.646	1	<0.0001
Irrigation cycles	3.824	2	<0.0001

development vary according to species. Lima and Meiado (2018b) observed that seedlings of *Mimosa tenuiflora* (Willd.) Poir. (Fabaceae) subjected to HD cycles exhibited higher values of leaf biomass, stem diameter, and root length. *M. tenuiflora* can thrive in environments with degraded soils due to its resilience, and HD cycles accelerate its growth, making it an important species for recovering degraded areas (Lima & Meiado, 2018b). Conversely, Silva et al. (2021) reported that *Triplaris gardneriana* Wedd. (Polygonaceae) seedlings grew less when subjected to HD cycles combined with irrigation cycles.

Considering the impact of recent climate change and the desertification process of the Caatinga caused by soil cover removal, water deficit has been linked to adverse effects on plant growth, development, and significant reductions in plant yield and biomass. However, this perspective focuses on productivity and global food insecurity (Seleiman et al., 2021). When examining non-cultivated species from drought-prone environments, general perceptions of these effects must change, as these phenomena enhance the plants' ability to tolerate low soil water availability by optimizing growth to maintain turgor pressure and plant physiology (C. S. Santos et al., 2024). Reduced growth serves as a beneficial mechanism for water deficit tolerance, as observed in the species studied. Seedlings subjected to three HD cycles combined with 28-day irrigation cycles developed smaller but resistant plants, withstanding a year without water. This perspective should be incorporated into discussions on seed hydration memory and recovery techniques for degraded areas. In recovering degraded environments, the most advantageous approach is to use seedlings capable of withstanding harsh conditions and establishing themselves rapidly. Combining these characteristics of endurance and fast growth remains a challenge. Our study demonstrated that *X. gounellei* subsp. *gounellei* unites these two characteristics, resisting drought conditions while continuing to grow under unfavorable conditions.

Seeds and seedlings experiencing water deficit during development tend to acquire higher drought tolerance, vital for survival in ecosystems where water is scarce and irregular (Yang et al., 2021). Studies show that this tolerance largely depends on parental genetic conditions and the seeds' ability to maintain biochemical changes induced by HD cycles (Lima & Meiado, 2023; Seleiman et al., 2021; Yang et al., 2021). These changes act as metabolic signals, modulating gene expression related to water deficit responses. Our regulation helps the plant adjust its metabolism, reducing growth rates and redirecting resources toward survival mechanisms (Matzrafi et al., 2021).

During drought, plants redistribute reducing sugars from leaves to roots to maintain root function and water uptake (Poonam et al. 2016). The accumulation of these sugars in different tissues prepares the plant for recovery after rehydration, as observed in this study at interval (T_3), with increased sugar levels, especially after undergoing HD cycles. Reducing sugars act as osmoprotectants, maintaining osmotic balance in plant cells. During drought, increased solute concentration can lead to cellular dehydration. The accumulation of reducing sugars helps retain water and maintain cell turgidity, essential for preserving cell function and growth (Kaur et al., 2021; Ozturk et al., 2021; Poonam et al., 2016). Additionally, drought induces the production of reactive oxygen species (ROS), which damage proteins, lipids, and DNA. Reducing sugars possesses antioxidant properties, neutralizing ROS and protect cells from oxidative damage. Also, reducing sugars stabilize proteins and cell membranes, preventing denaturation and maintaining cell integrity (Ozturk et al., 2021).

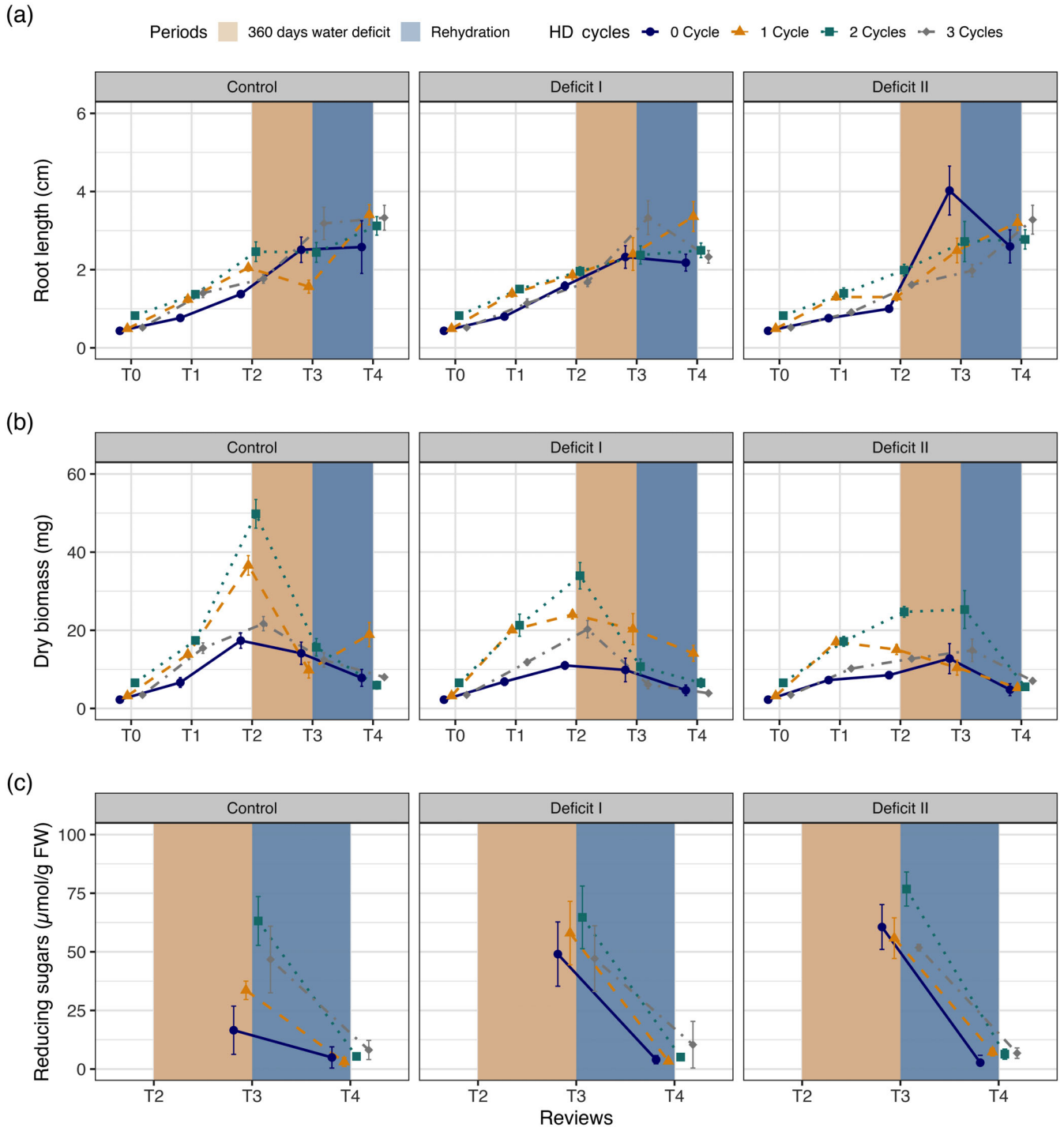


FIGURE 5 (a) Root length (cm); (b) dry biomass (mg) and (c) reducing sugars (μmol/g FW) of seedlings of *Xiquexique gounellei* (F. A. C. Weber ex K. Schum) Lavor and Calvente subsp. *gounellei* (Cactaceae) originated from seeds that went through 0, 1, 2, and 3 hydration–dehydration cycles (HD cycles) and were subjected to irrigation cycles of 7 (Control), 14 (Deficit I), and 28 days (Deficit II) of water suspension. T_0: interval zero, before starting the irrigation cycles, after 2 months of acclimatization. T_1: 35 days after the start of the irrigation cycles. T_2: 65 days after the start of the irrigation cycles. T_3: 360 days after the start of irrigation cycles. T_4: 390 days after the start of irrigation cycles. We used $n = 20$, expressed as mean ± confidence interval with a significance level of $p < 0.05$. FW, fresh weight.

Thus, our research highlights the benefits conferred by HD cycles during the early stages of development, demonstrating their potential as a tool for producing seedlings that are more resistant to water deficit conditions, an advantage that can be applied in degraded area restoration projects. The successful survival of seedlings

after a year of drought is closely linked to the intrinsic characteristics of cacti. Upon germination, young individuals face prolonged drought lasting several months by regulating water loss and maintaining low transpiration rates, even under conditions of high-water availability (Lina & Eloisa, 2018). Additionally, sensitivity to soil water deficit may be more strongly related to root distribution patterns and rooting depth than to stem morphology (Hultine et al., 2023). This supports our findings, in which, even under 360 days without water, root growth persisted while the aerial part decreased due to the loss of tissue turgor. The Crassulacean Acid Metabolism (CAM) pathway, combined with water storage in tissues and the presence of mucilage, allows individuals to remain dormant for weeks or even months in the face of drought (Eggli & Nyffeler, 2009; Lüttge, 2004).

5 | CONCLUSION

The HD cycles in seeds of *X. gounellei* subsp. *gounellei* promoted the expression of seed hydration memory, which enhanced the initial development of seedlings even under prolonged water deficit conditions. This finding demonstrates that the benefits of hydration memory extend beyond immediate germination, persisting throughout a year of drought. The persistence of this memory over several months indicates that the positive effects of HD cycles support seedling development, increasing their resilience to extended drought periods, such as those anticipated with climate change.

The dynamic influence of seed hydration memory on species development and survival underscores its ecological significance throughout the year. In seasonally dry tropical environments, the occurrence of discontinuous hydration allows seeds and seedlings to adjust their physiological characteristics in response to water availability, thereby ensuring population regeneration and long-term persistence even under prolonged water deficit conditions.

Therefore, this study highlights the crucial role of hydration memory in seeds in promoting seedling development under water deficit, demonstrating its potential application in ecological restoration projects in the Caatinga. By enhancing seedling resilience and adaptability, the use of seeds subjected to HD cycles could improve the success of restoration efforts in semi-arid ecosystems.

AUTHOR CONTRIBUTIONS

The authors develop the conception and design of the study. The preparation of the material, data collection and analysis were carried out by Bruno de Santana Santos, Cristianne Santana Santos, and Marcos Vinicius Meiado. The first draft of the manuscript was written by Bruno de Santana Santos and all authors comment on previous versions of the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

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