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Original research

Germination of *Cedrus atlantica* seeds following the breaking of induced dormancy under conditions of salinity and drought stress

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Abstract

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Cedrus atlantica is a forest tree species endemic to North Africa and widely used in reforestation and ecological restoration programmes across Mediterranean ecosystems because of its ecological and socio-economic importance. However, information on effective pre-treatments to overcome seed dormancy and on the impact of salinity and drought stress on germination remains limited. This study aimed to address this knowledge gap by evaluating various dormancy-breaking pre-treatments and examining the impact of salinity and drought stress on seed germination. The findings revealed that immersing seeds in hot water at 60°C for 5 minutes produced the most effective pre-treatment, achieving a germination rate of 70%. By comparison, soaking the seeds in either 2% hydrogen peroxide (H_2O_2) for 30 minutes or distilled water at 20°C for 24 hours resulted in lower germination rates of 45% and 25%, respectively. Both salinity and PEG-induced drought stress significantly reduced germination percentage and speed in a concentration-dependent manner. Compared with the control, germination was reduced by 73.34% under the highest salinity treatment (8 g L^{-1} NaCl) and by 78.04% under the most severe drought treatment (−6 bar PEG). Nevertheless, seeds remained capable of germinating at all tested stress levels. These findings improve our understanding of the germination ecology of *Cedrus atlantica* and provide useful information for seed propagation and nursery production in conservation and ecological restoration programmes.

Keywords: drought stress, polyethylene glycol, salinity stress, seed germination.

INTRODUCTION

Climate change is a major cause of forest ecosystem degradation worldwide. In the Mediterranean Basin, frequent droughts, unpredictable rainfall, and progressive soil salination are endangering forest biodiversity, ecosystem functioning, and the natural regeneration of woody species (Aurelle et al., 2022; Hidalgo-Triana et al., 2023). Soil salinisation is a significant environmental issue affecting many countries

worldwide (Karle et al., 2021). It is particularly severe in arid and semiarid regions, where high evapotranspiration rates, limited rainfall and poor land management practices lead to the build-up of soluble salts in the root zone (Feghhenabi et al., 2021; Sánchez et al., 2023). These environmental constraints are expected to intensify over the coming decades, further reducing the natural regeneration capacity of forest species and jeopardising the long-term sustainability of Mediterranean forest ecosystems.

Seed germination is one of the most sensitive stages of plant development to abiotic stresses because successful seedling establishment depends on rapid water uptake and the activation of numerous physiological and biochemical processes (Xiao et al., 2019). Germination begins with seed imbibition, followed by reactivation of cellular metabolism, mobilisation of stored reserves, and enzyme synthesis. Ultimately, radicle protrusion occurs. Disruption of any of these processes may delay or completely inhibit germination, resulting in poor seedling establishment and reduced regeneration capacity (Seleiman et al., 2021).

Salinity and drought are two of the most significant abiotic factors that limit seed germination and subsequent seedling establishment. Although both stresses reduce water availability to seeds, they operate through different physiological mechanisms. Drought primarily restricts water uptake by lowering soil water potential. In contrast, salinity combines osmotic stress with ion toxicity caused by excessive accumulation of sodium (Na^+) and chloride (Cl^-) ions (Dos Santos et al., 2022). These constraints impair seed imbibition, disrupt cellular metabolism and inhibit the activity of hydrolytic enzymes responsible for reserve mobilisation. They also promote oxidative stress, ultimately delaying or inhibiting germination. Consequently, numerous studies have reported a progressive decline in germination percentage, germination rate, and seedling vigour with increasing levels of salinity and drought stress. In Algeria, several studies have investigated seed germination responses to dormancy-breaking treatments and abiotic stresses in Mediterranean species. For instance, Zouidi et al. (2019) have examined the impact of pre-treatments on *Pinus halepensis* Mill. germination, and Aouadj et al. (2022) have assessed the germination responses of *Juniperus oxycedrus* L. and *Pistacia lentiscus* L. in response to environmental constraints. Similar investigations have examined Saharan psammohalophytes (Trabelsi & Kherazze, 2021), *Medicago sativa* L. (Kadri et al., 2021), *Zygophyllum album* L.f. (Hadjadj et al., 2022) and *Lygeum spartum* L. (Zouidi et al., 2023). These studies consistently show that appropriate seed pre-treatment can, to some extent, alleviate the adverse effects of salinity and drought by improving germination performance under stressful conditions. However, most existing studies have focused on herbaceous or agricultural species, whereas comparatively little information is available for endemic Mediterranean forest trees, particularly *Cedrus atlantica*. Furthermore, previous studies have generally evaluated dormancy-breaking techniques or abiotic stresses in isolation, providing limited insight into the interaction between seed pre-treatment and subsequent exposure to drought and salinity.

Cedrus atlantica is one of the most emblematic conifer species in North Africa and plays a vital role in Mediterranean mountain forest ecosystems. In addition to maintaining biodiversity, protecting watersheds, sequestering carbon and stabilising soils, the species provides substantial socio-economic benefits through timber production, ecosystem services, and its high landscape and cultural value. Because of its ecological significance and increasing vulnerability to climate change, the species has become a priority for conservation, ecological restoration and sustainable forest management throughout its natural distribution range.

Between 1980 and 2025, *Cedrus atlantica* forests experienced high mortality rates, primarily due to prolonged drought, rising temperatures, and recurrent climatic stress, which weakened tree vitality and increased vulnerability to environmental disturbances (Touchan et al., 2017; Hamida & Kouba, 2025). Studies conducted by Camarero et al. (2015), Abel-Schaad et al. (2018), Sarmoum et al. (2018), Navarro-Cerrillo et al. (2019), and Hamida & Kouba (2025) have highlighted the ongoing decline and mortality of cedar forests, predicting more severe scenarios in the future due to reduced cedar forest areas and a lack of natural seed regeneration.

This study therefore evaluated the effectiveness of different seed pre-treatments in overcoming dormancy and improving the germination performance of *Cedrus atlantica* under salinity and drought stress. Specifically, our objectives were to: (a) compare the efficiency of various methods of breaking dormancy; (b) evaluate the

impact of increased salinity and water deficit on seed germination; and (c) establish whether seed pre-treatment improves tolerance to these abiotic stresses. It was hypothesised that appropriate seed pre-treatment would significantly improve germination percentage, accelerate germination, and increase tolerance to osmotic and saline stress. This would provide useful information for the conservation, restoration and sustainable management of *Cedrus atlantica* forests.

MATERIALS AND METHODS

Study species

Cedrus atlantica is an endemic, relict forest tree species native to the Tellian and Saharan Atlas mountains in North Africa. In Algeria, it once covered about 2089 km² (Arar et al., 2020). However, it is currently declining rapidly, particularly along its southern range edge, due to increasing drought intensity and human activity (Hamida & Kouba, 2025). Specific environmental thresholds strictly constrain the reproductive and establishment dynamics of this species. Seed dormancy release requires low winter temperatures combined with annual precipitation exceeding 600 mm. In spring, snowmelt triggers germination, taking advantage of optimal moisture levels in deep, loose, well-drained soils (predominantly loamy sand or limestone). Although the dispersal of winged seeds is primarily anemochorous, it remains restricted to a narrow radius around the mother tree. Long-term seedling survival in natural conditions is the main obstacle to natural regeneration, especially in heavily disturbed areas, as young trees' root systems are vulnerable to summer drought stress, surface soil compaction, and livestock trampling.

Seed collection and preparation

Cedrus atlantica seeds were collected in January 2024 from mature cones harvested from healthy, dominant trees located on Mount Zaccar in the Ain Defla region (36.3311° N, 2.2133° E). To ensure the seeds were high-quality and homogeneous for the subsequent experiments, they underwent a strict multi-step selection process. First, a visual and tactile inspection was conducted to discard seeds showing mechanical damage, fungal contamination, or morphological abnormalities. Secondly, the water flotation method was used to eliminate empty or non-viable seeds; those that floated to the surface were discarded, while those that sank, indicating well-developed, filled endosperms and intact embryos, were retained for the study. Before the germination tests, the selected viable seeds were surface-sterilised by immersion in a 5% sodium hypochlorite solution (NaOCl) for five minutes to eliminate superficial pathogens. After sterilisation, the seeds were thoroughly rinsed several times with sterile distilled water to remove chemical residues, then air-dried under a laminar flow hood at room temperature.

The first step was to evaluate the effect of four seed pre-treatments on germination to identify the most effective treatment. This treatment was then used to assess the effects of salinity and drought stress. The following pre-treatments were tested: (1) soaking the seeds in hot distilled water at 60°C or 80°C for five minutes (Jaouadi et al., 2010); (2) soaking the seeds in distilled water at room temperature for 24 hours; and (3) soaking the seeds in 2% hydrogen peroxide (H_2O_2) for 30 minutes.

The second step involved evaluating the impact of increasing salinity and drought stress on seed germination using sodium chloride (NaCl) and polyethylene glycol (PEG 6000), respectively.

Salinity stress treatments used NaCl concentrations of 0 g/L, 1 g/L, 4 g/L, 6 g/L and 8 g/L, while drought stress was simulated using PEG 6000 solutions with osmotic potentials of 0, –1, –2, –4, –6 and –8 bar.

For each test in both experimental steps, optimal germination conditions were maintained. Twenty seeds were placed in each Petri dish, with three independent replicates per treatment.

The Petri dishes were randomly arranged in a thermostatically controlled incubator at 20 ± 1°C and incubated in darkness. Germination was monitored every two days for 30 days. Seeds were considered germinated when the radicle exceeded 1 mm in length, and germinated seeds were counted and removed from each Petri dish after each observation.

Statistical analysis

Before statistical analysis, the germination percentage data from each treatment were examined to ensure compliance with the assumptions of parametric analysis. Residual normality was assessed using the Shapiro-Wilk test, and the homogeneity of vari-

ances was evaluated using Levene's test. Because these assumptions were met, a one-way analysis of variance (ANOVA) was performed to evaluate the effects of salinity and drought stress treatments on seed germination. When significant differences were detected, treatment means were compared using Fisher's least significant difference (LSD) post-hoc test at a significance level of $p \leq 0.05$.

RESULTS

Effects of dormancy-breaking treatments on seed germination and germination rate

Seed pre-treatments significantly affected the germination of *Cedrus atlantica* seeds (Fig. 1). The highest germination percentage (approximately 70%) was obtained after soaking the seeds in hot distilled water at 60°C for five minutes (HDW 60). This treatment differed significantly from all other treatments and was assigned to group "a" according to Fisher's LSD test.

The second highest germination rate (45%) was observed for seeds treated with 2% hydrogen peroxide (HP), which formed a separate statistical group (b). In contrast, the lowest germination percentage (about 25%) was recorded for seeds soaked in distilled water at 20°C for 24 hours (T24), corresponding to group c.

Analysis of variance revealed a statistically significant effect of the pre-treatments on germination ($F = 610$, $p < 0.001$), indicating that the dormancy-breaking treatments substantially influenced the germination capacity of *Cedrus atlantica* seeds.

Dormancy-breaking treatments did not significantly affect the germination speed of *Cedrus atlantica* seeds (Fig. 2). Germination occurred within a narrow range of approximately 6.2 to 7.0 days across all treatments. Although seeds soaked in hot distilled water at 60°C (HDW 60) and those soaked in tap water for 24 h (T24) exhibited slightly longer germination times than the hydrogen peroxide treatment (HP), these differences were not statistically significant ($F = 0.403$, $p = 0.685$).

Effects of salinity stress on seed germination and germination speed

Salinity stress significantly affected both the germination percentage and germination speed of *Cedrus atlantica* seeds. As NaCl concentration increased, germination progressively declined, decreasing from 81.67% in the control treatment to 8.33% at 8 g L^{-1} NaCl. Analysis of variance revealed a statistically significant ($F = 24.67$, $p < 0.001$) effect of salinity on germination rate (Fig. 3).

Post-hoc comparisons indicated that the control treatment formed a distinct statistical group with the highest germination, while the highest salinity level (8 g L^{-1}) produced the lowest germination values. Intermediate concentrations (2–6 g L^{-1}) showed overlapping statistical groups, reflecting a gradual inhibitory effect of increasing salinity.

Salinity also significantly ($F = 6.15$, $p = 0.005$) influenced germination speed (Fig. 4). Seeds ex-

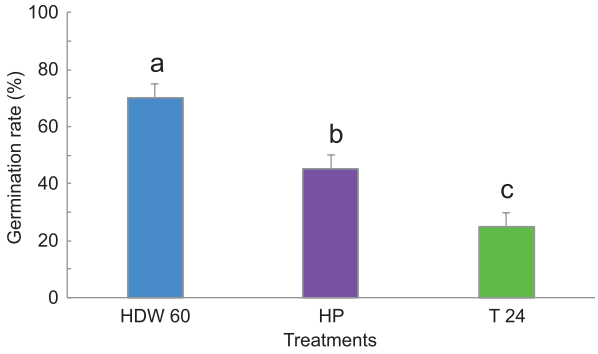


Fig. 1. Histogram of germination rate of different dormancy-breaking treatments. Treatments: HDW 60 – hot distilled water at 60°C; HP – hydrogen peroxide; T24 – tap water soaking for 24 h. Different lowercase letters above bars indicate Fisher's least significant difference (LSD) post-hoc test at a significance level of $p \leq 0.05$.

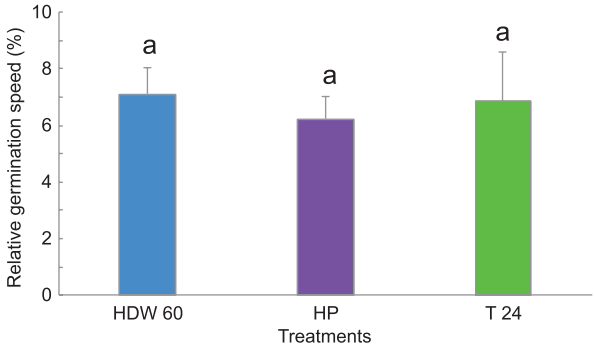


Fig. 2. Histogram of germination speed percentage of different dormancy-breaking treatments. Treatments: HDW 60 – hot distilled water at 60°C; HP – hydrogen peroxide; T24 – tap water soaking for 24 h. Different lowercase letters above bars indicate Fisher's least significant difference (LSD) post-hoc test at a significance level of $p \leq 0.05$.

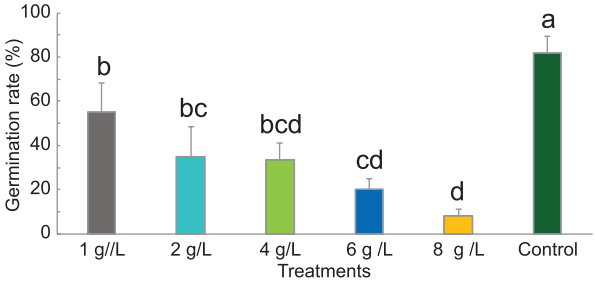


Fig. 3. Histogram of germination rate for different salinity treatments. Treatments: salt concentration. Different lowercase letters above bars indicate Fisher's least significant difference (LSD) post-hoc test at a significance level of $p \leq 0.05$.

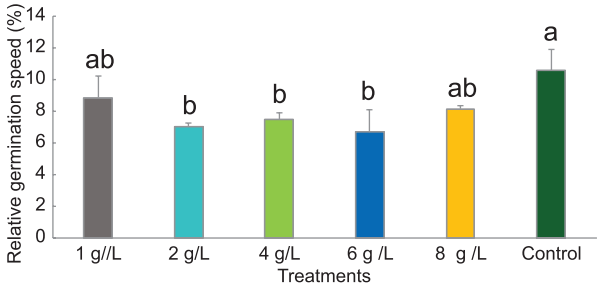


Fig. 4. Histogram of germination speed percentage for different salinity treatments. Treatments: salt concentration. Different lowercase letters above bars indicate Fisher's least significant difference (LSD) post-hoc test at a significance level of $p \leq 0.05$.

posed to NaCl treatments showed a delay of nearly three days compared with the control, indicating that saline conditions slow germination. Intermediate treatments showed moderate delays, confirming the progressive impact of salt stress.

These findings demonstrate that increasing salinity negatively affects the germination performance of *Cedrus atlantica*. The observed reduction in germination and germination speed at higher salt concentrations is likely related to osmotic stress and ion toxicity, which limit water uptake and disrupt metabolic processes during the early stages of germination. Although the species shows some tolerance to low salinity levels, high salt concentrations strongly inhibit seed germination, which may have important implications for cedar regeneration in environments affected by soil salinisation and climate change.

Effects of water stress on seed germination

The results indicate that increasing water stress significantly affected both the germination percentage and germination speed of *Cedrus atlantica* seeds. As osmotic potential decreased with increasing polyethylene glycol (PEG) concentrations, germination percentage declined progressively compared to the control treatment. The control showed the highest germination rate (about 68–70%). In contrast, PEG treatments (1–6 bar) resulted in markedly lower germination rates, with reductions exceeding 33%. Analysis of variance revealed a statistically significant effect of water stress on germination ($F = 21.37$, $p = 6.91e\text{-}05$) (Fig. 5). The control formed a distinct statistical group with the highest germination rate. In contrast, all PEG treatments exhibited significantly lower germination.

A similar trend was observed for germination speed. Statistical analysis revealed significant differences among treatments ($F = 7.28$, $p = 0.005$) (Fig. 6). The control and the 2-bar treatment showed the highest values and belonged to the same statistical group. In contrast, higher stress levels (4 and 6 bar) significantly reduced germination speed, delaying germination by more than four days. The one-bar treatment exhibited an intermediate response,

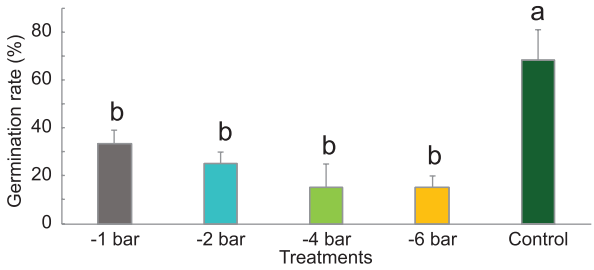


Fig. 5. Histogram of germination rate for different water stress treatments. Treatments: osmotic pressure. Different lowercase letters above bars indicate Fisher's least significant difference (LSD) post-hoc test at a significance level of $p \leq 0.05$.

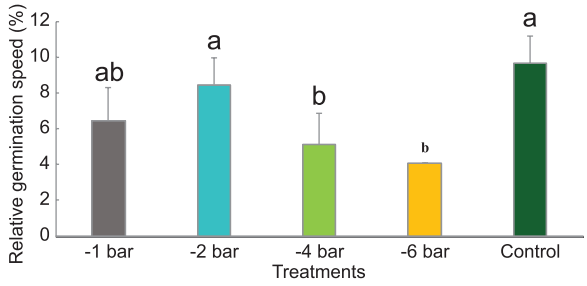


Fig. 6. Histogram of germination speed percentage for different water stress treatments. Treatments: osmotic pressure. Different lowercase letters above bars indicate Fisher's least significant difference (LSD) post-hoc test at a significance level of $p \leq 0.05$.

indicating a moderate effect of water stress on germination dynamics.

Overall, these results show that increasing water deficit markedly reduced both germination capacity and germination speed in *Cedrus atlantica*, likely due to reduced water uptake during seed imbibition phase.

DISCUSSION

The results showed that different seed pre-treatments positively affected seed coat dormancy. According to Bewley et al. (2013), seed soaking techniques generally alleviate certain dormancy constraints. The different pre-treatments produced significant differences in germination rates, corroborating Hafidou et al. (2021), who found that physical and chemical scarification affect seed germination behaviour. The same authors recorded the highest germination rate in the hot water treatment (77%). Similarly, soaking seeds in distilled water for 24 hours improves the germination rate (Topwal et al., 2024).

Chemical seed soaking has frequently been reported to improve both germination percentage and germination rate (Boukli et al., 2021; Hafidou et al., 2021). Previous studies have shown that seeds which initially failed to germinate under unfavourable substrate conditions may subsequently germinate when exposed to low water potentials or saline conditions (Mircea et al., 2023). In some cases, such pre-treatments not only stimulate germination but also increase both final germination percentage and germination rate (Mundada et al., 2022; Noori et al., 2022).

In general, seed pre-treatments that break dormancy promote germination and support rapid, uniform seedling establishment (Sharma et al., 2014). They may also improve tolerance to abiotic stress, supporting plant establishment and growth under adverse environmental conditions (Bewley et al., 2013).

Understanding the physiological effects of drought is essential for interpreting seed germination responses under water-limited conditions. Drought primarily reduces soil water availability while simultaneously increasing the concentration of dissolved salts in the soil solution, thereby intensifying osmotic stress and limiting water uptake by seeds (Miri & Mirjalili, 2013; Hadi et al., 2014; Arnold et al., 2014; Cavallaro et al., 2014; Shahrajabian et al., 2017). These combined effects adversely influence seed germination and subsequent seedling growth.

The mechanisms by which salinity and drought stress affect seed germination require further clarification. According to Farooq et al. (2015), Safdar et al. (2019), and Aljasmi et al. (2021), salinity not only increases the risk of ion penetration but also induces osmotic stress by lowering the external water potential. This restricts water uptake during seed imbibition and promotes the accumulation of toxic ions within the seed, which may damage the embryo and impair germination.

Several studies show that exposure to salinity stress reduces seed germination and inhibits rapid seedling growth in many species (El-Keblawy & Gairola, 2017; Al-Shamsi et al., 2020). However, its effect depends mainly on the salt concentration used and the species tested (Mbinda & Kimtai, 2019). For example, 100 mM NaCl severely reduces the germination rate of *Corchorus capsularis* L. (Bhuyan et al., 2018) and may even completely inhibit germination (Nedjimi & Guit, 2021).

Seed germination results also differ depending on the type of salt used. Nedjimi (2017) has reported that salinity stress negatively affects the germination rate of *Pinus halepensis* Mill seeds, with NaCl showing higher toxicity than $CaCl_2$, Na_2SO_4, and $MgCl_2$. For the same species, the germination rate decreases as salinity and drought stress increase (Zouidi et al., 2019). Similar results have been reported for *Tetraclinis articulata* (Vahl) Mast. (Zohra et al., 2021).

Nesrine et al. (2022) have reported that increasing drought stress progressively reduces seed germination. A similar trend has been reported for *Bidens subalternans* L. (Sousa et al., 2018) and *Thymus vulgaris* L. (Stefanello et al., 2018), where increasing water deficit significantly reduced germination performance.

When comparing salinity and drought stress, the results indicate that the impact of these two stresses depends mainly on the species. For example, salinity stress is more harmful than drought stress in species such as *Henophyton deserti* Coss. (Gorai et al., 2014), *Ceratonia siliqua* L. (Cavallaro et al., 2016), and *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth

(Aljasmi et al., 2021). In contrast, the opposite effect has been observed in other species such as *Haloxylon stocksii* (Boiss.) Hook.f. (Rasheed et al., 2019) and *Suaeda vermiculata* Forssk. ex J.F.Gmel. (Al-Shamsi et al., 2020; El-Keblawy et al., 2018).

Both salinity and drought stress ultimately produce similar effects at the seed level. Due to reduced water potential or specific ion toxicity, these stresses cause molecular damage (Rozentsvet et al., 2017), prevent the utilisation and hydrolysis of seed reserves (Ali & Elozeiri, 2017), and disrupt the normal functioning of the plasma membrane and protein synthesis (Ibrahim, 2016; Hasanuzzaman et al., 2018). This ultimately reduces germination percentage and germination speed (Hameed et al., 2021).

The present findings also have important practical implications for the conservation and restoration of *Cedrus atlantica* forests. Increasing degradation of Mediterranean forest ecosystems and growing demand for native seedlings have highlighted the need to develop reliable germination protocols for forest species (Rego et al., 2009). Since successful seedling production depends largely on seed germination, identifying effective dormancy-breaking methods is an essential prerequisite for nursery propagation and ecological restoration programmes.

The high germination obtained after hot-water treatment confirms previous observations reported by Hafidou et al. (2021), who have demonstrated that thermal scarification is one of the most effective methods for improving the germination capacity of *Cedrus atlantica.* According to Zhu et al. (2021), hot-water treatment induces small cracks in the seed coat without damaging the micropyle, thereby facilitating water uptake and initiating germination. Similarly, soaking seeds in distilled water may promote germination by removing inhibitory compounds, including phenolic substances present in the seed coat (Mehanni et al., 2021). Comparable beneficial effects of hot-water treatment have also been reported for *Cupressus atlantica* Gaussen (Arjouni et al., 2013), *Abelmoschus esculentus* L. (Mohammadi et al., 2012) and *Sesbania punicea* Cav. (Al-Hadedy et al., 2024), suggesting that thermal scarification is an effective and inexpensive technique for several forest and woody species.

Although increasing salinity and drought stress significantly reduced germination, *Cedrus atlantica* seeds germinated under all stress levels tested, suggesting that seed propagation remains feasible under moderately adverse environmental conditions. These findings may therefore improve nursery practices by facilitating the selection of suitable pre-treatments and by providing useful information for seed collection, propagation and restoration programmes in Mediterranean regions increasingly affected by climate change. Nevertheless, further studies under nursery and field conditions are required to determine whether this germination response translates into successful seedling establishment and long-term survival.

CONCLUSIONS

This study clarified the effect of various pre-treatments on dormancy breaking in *Cedrus atlantica* seeds, as well as their responses to salt and water stress. It highlighted the importance of pre-treatments in increasing germination rate and improving growth rate. Meanwhile, exposure of these seeds to high concentrations of NaCl and high osmotic pressure yielded encouraging results, as the seeds managed to grow despite the severe nature of both stresses. This study also highlights the importance of seed provenance, which plays a key role in the results and will serve as a local information source and a basis for comparison in national and international research.

Against the backdrop of climate change and the restoration of degraded habitats using native tree species with agroecological benefits, our results, obtained under controlled laboratory conditions, need to be supplemented by field studies to better assess the real germination potential with and without pre-treatment, to expose the seeds to a wider range of salinity and water stress conditions, and to test seeds sourced from different provenances.

Author contributions. ND and MZ conceptualised the study, designed the methodology, conducted the investigation, performed the formal analysis, curated the data, and wrote the original draft; AA contributed to the methodology, performed the formal analysis, validated the results, and reviewed and edited the manuscript; DS collected the seeds and conducted the investigation. All authors read and approved the final version of the manuscript.

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