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Seed germination response of the invasive *Haloxylon persicum* in Tunisia

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Abstract: Biological invasion represents a major worldwide threat to native biodiversity and environmental stability. *Haloxylon persicum* was introduced to Tunisia (North Africa) with Saharan bioclimate in 1969 to fix sandy dunes. Since then, it has gained significant interest for its potential to colonize, proliferate, and become naturalized in Tunisia. Hence, understanding the seed germination response of *H. persicum* to abiotic conditions, including temperature, water stress, and salt stress, is crucial for predicting its future spread and adopting effective control strategies. Our work investigated the germination behavior of this invasive plant species by incubation at temperatures from 10.0°C to 35.0°C and at various osmotic potentials (–2.00, –1.60, –1.00, –0.50, and 0.00 MPa) of polyethylene glycol-6000 (PEG_{6000}, indicating water stress) and sodium chloride (NaCl, indicating salt stress) solutions. Results showed remarkable correlations among the seed functional traits of *H. persicum*, indicating adaptive responses to local environmental constraints. The maximum germination rate was recorded at 25.0°C with a rate of 0.39/d. Using the thermal time model, the base temperature was recorded at 8.4°C, the optimal temperature was 25.5°C, and the ceiling temperature was found at 58.3°C. Besides, based on the hydrotime model, the base water potential showed lower values of –7.74 and –10.90 MPa at the optimal temperatures of 25.0°C and 30.0°C, respectively. Also, the species was found to have excellent tolerance to drought (water stress) compared to salt stress, which has implications for its potential growth into new habitats under climate change. Combining ecological and physiological approaches, this work elucidates the invasive potential of *H. persicum* and contributes to the protection of species distribution in Tunisian ecosystems.

Keywords: *Haloxylon persicum*; seed germination; osmotic potentials; seed functional traits; hydrotime model; thermal time model; Tunisian Saharan bioclimate

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1 Introduction

Seed germination is a crucial physiological process in developing a new plant, particularly in arid and semi-arid areas (Krichen et al., 2014, 2017). A seedling initiates and grows by activating biological and metabolic events (Poudel et al., 2019; Farooq et al., 2022). From a physiological perspective, seed germination is a complicated process that involves several signals. It is controlled by internal factors, such as seed dormancy and available food reserves, and external factors, such as water, light, oxygen, and temperature (Alvarado and Bradford, 2002; Wolny et al.,

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2018). However, the two key factors influencing seed germination are temperature and water stress (Yuan and Wen, 2018).

Temperature is critical in regulating germination rate (GR) and germination percentage (GP) of plant species. The study of this parameter is based on the thermal time model (Alvarado and Bradford, 2002), which represents the prediction of the species' response to temperature variations. The plant life cycle undergoes three critical cardinal temperatures: base temperature (T_b), below which seed germination is prevented; optimum temperature (T_o), at which seed germination proceeds most quickly; and ceiling temperature (T_c), above which seed germination does not occur (Bakhshandeh et al., 2013). According to Bakhshandeh and Jamali (2020), these cardinal temperatures differ based on the species and environmental factors in which they are produced. Likewise, GR typically rises linearly with temperature between T_b and T_o and decreases linearly or curvilinearly at $T_c > T_o$ (Alvarado and Bradford, 2002; Abdellaoui et al., 2019). Moreover, water availability significantly impacts seed germination and plant establishment success (Haj Sghaier et al., 2022). According to Bakhshandeh et al. (2020), GP and GR typically rise with water availability and fall at higher negative water potential (Ψ). In addition, salinity represents a limit factor to seed germination through both osmotic and ion-specific effects. The impact of Ψ on seed germination at a particular temperature has been measured using the hydrotime model created by Bradford (1990). According to the model, the inverse percentage of the time to seed germination is determined by the difference between the physiological threshold for radicle emergence (base water potential (Ψ_b)) and the Ψ of the seed environment, which varies for every seed in the population (Patanè et al., 2016).

Haloxylon persicum (white saksaoul) is an Irano-Turanian desert plant (Le Houerou, 2000) that originated in Central Asia (Alghanem, 2018). It belongs to the Amaranthaceae family (Kafi and Salehi, 2019) and is an annual evergreen shrub-like C_4 species. It is a super-xerophytic and typical psammophyte shrub that only grows in saline sandy deserts (Song et al., 2005). This species can reach 4.00–6.00 m in height (Zhaglovskaya et al., 2015), with a prolific rhizospheric system (Casati et al., 1999), retrogressed leaves like succulent branches (Thayale Purayil et al., 2020), and winged bisexual flowers (Zhaglovskaya et al., 2015). *H. persicum* was introduced to the Saharan bioclimatic zones of Tunisia during 1960–1970 to fix and stabilize sand dunes (Le Floc'h et al., 2010). Currently, it is in the process of invasive expansion and has spread all over the country (Le Floc'h et al., 2010). *H. persicum* can produce a high canopy density (Thayale Purayil et al., 2020). Despite its biological and ecological characteristics, *H. persicum* was classified as endangered in 2019 by the International Union for Conservation of Nature (IUCN) in the Red List of Threatened Species (Oldfield, 2020). This classification could be due to the overexploitation of rangelands, which caused the extinction of *H. persicum* species. This extinction results in the dominance of inedible plants in most regions where *H. persicum* is widespread, especially in its native habitat in Central Asia (Alghanem, 2018). For this concern, understanding the factors influencing the germination success of *H. persicum* is crucial for researchers, conservationists, and land managers pursuing the revitalization and conservation of Saharan ecosystems (Breman et al., 2021). Thus, understanding the invasive potential of *H. persicum* has been a part of green belt development activities for a long time (Soltani, 2011). In fact, *H. persicum* possesses remarkable germination abilities and flexibility in arid environments, especially at extreme temperatures and low moisture accessibility (Abdi et al., 2019). Its endurance to environmental circumstances led us to study its seed germination response to temperature and osmotic factors using the thermal time and hydrotime models.

To the best of our knowledge, the seed germination of *H. persicum* has previously been studied in China long ago (Song et al., 2005), and the results revealed that GP decreased with the increasing of salinity, and the inhibitory effect of polyethylene glycol-6000 (PEG_{6000}) treatments on seed germination was significantly stronger than that of sodium chloride (NaCl) treatments. Soltani (2011) studied the seed germination of this plant species in Iran and discovered that a water deficit below –1.00 MPa greatly affected the GR of *H. persicum*. However, these studies have not examined how the seeds of *H. persicum* cope with the Mediterranean environment, particularly the Tunisian Saharan bioclimatic zones. In addition to being influenced by the parental environment, genotypic variability can also impact seed germinability (Bakker, 2001). Our work intends to fill this gap by investigating the seed germination response of *H. persicum* under Tunisian Saharan bioclimate using a range of temperatures and osmotic potentials. To evaluate the germination mechanisms and ecological amplitude of *H. persicum* and understand the factors that promote its invasiveness, this study analyzed the seed functional traits of *H. persicum*, examined the effects of temperature, water stress, and salt stress on its seed germination characteristics, and estimated the cardinal temperatures of seed germination using the thermal time and hydrotime models.

2 Materials and methods

2.1 Seed collection

The seeds of *H. persicum* were manually harvested from a Saharan bioclimatic zone in Tunisia, i.e., Kebili (33°40′N, 08°59′E; 60 m a.s.l.). As described by Emberger (1971), this region is characterized by an arid climate, with hot and dry summers (temperatures exceeding 40.0°C), an average annual rainfall of 100 mm, a very high evapotranspiration of 1700 mm, an annual average temperature of >20.0°C, and an extreme aridity index of 8.40 (Ferchichi, 1996).

In January 2023, ten healthy *H. persicum* species with the height of 2.00–4.00 m were selected in Kebili, and seeds with an approximate diameter of 2.00 mm were then randomly chosen. Finally, 9430 freshly matured seeds were collected. After removing debris, these seeds were air dried and stored at 2.0°C until further use.

2.2 Seed functional traits

To determine the proportion of embryoless seeds, we evenly divided 100 seeds into 4 groups (25 seeds per group) and viewed them using a Zoom Trinocular Stereoscope (Optech Optical Technology, München, Germany) as described by Zanetti et al. (2020). Following the International Rules for Seed Testing (ISTA, 2013), we measured embryo viability in the experiments by counting viable and non-viable seeds after a 6-d incubation period (Krichen et al., 2023). The percentage of seeds with developing embryos or growing cotyledons was used to calculate embryo viability. Seeds with degradation or brown/black stains were deemed unviable. The tests were repeated 4 times with 50 seeds each (Ma et al., 2016). Three replicates of 1000 seeds were weighed digitally to specify thousand seed weight.

Additionally, a sample of 30 seeds was randomly picked and analyzed using image analysis software ImageJ (National Institutes of Health, Bethesda, the United States) to determine seed area and seed diameter (Chen et al., 2022). Three replicates of 100 fresh seeds were weighed and then oven-dried at 70.0°C for 3 d before being reweighed. Seed water content (SWC; %) was calculated using the equation listed below (Krichen et al., 2023).

$$\text{SWC}=((\text{FW}-\text{DW})\div\text{DW})\times 100\%, \tag{1}$$

where FW is the fresh weight (g); and DW is the dry weight (g).

2.3 Pretreatment and seed contamination prevention

To prevent fungal infection, the seeds were surface sterilized for 2 min in a 5.00% sodium hypochlorite solution. Then, they were rinsed three times with distilled water (Nosrati et al., 2014).

2.4 Effects of abiotic stresses on seed germination

2.4.1 Effect of temperature on seed germination

Totally 1800 seeds were utilized to find the T_o conditions for the seed germination of *H. persicum*, with 6 replications for each temperature test and 50 seeds placed on a filter paper within a 9 cm Petri plate for each replication. Depending on the temperature, 2 Whatman No. 1 filter paper layers were moistened with variable volumes of sterilized distilled water (Zagoub et al., 2022). The Petri plates were sealed with parafilm sheets to avoid evaporation and incubated in complete darkness in an LMS Cooled Incubator (Bioblock Scientific, Cedex, France) with a temperature range of 10.0°C–35.0°C and an incubation period of 21 d. We chose these temperature values (10.0°C, 15.0°C, 20.0°C, 25.0°C, 30.0°C, and 35.0°C) according to specific environmental conditions in Tunisian Saharan bioclimatic zones. According to Dhaouadi et al. (2021), this habitat, mainly the sandy desert, is characterized by significant temperature fluctuations, where the temperature can reach 55.0°C in summer (July) and fall to below 5.0°C in winter. The low moisture availability is also a characteristic of the study area, with an average annual rainfall below 100 mm and an average annual potential evapotranspiration around 1700 mm (Ouled Belgacem et al., 2019; Dhaouadi et al., 2021; Dhief et al., 2022). Yahaghi et al. (2019) defined seed germination as the appearance of a radicle reaching a length of approximately 2.00 mm. Over 21 d, the germinated seeds in each Petri plate were counted daily. The formula of GP (%) is as follows:

$$\text{GP} = (\text{The number of germinted seeds / The number of incubated seeds}) \times 100\%. \quad (2)$$

2.4.2 Effect of osmotic potentials on seed germination

For this test, 3000 seeds were utilized to investigate the effect of water stress and salt stress on the seed germination performance of *H. persicum*. Experiments were carried out in the dark, with 6 replicates per treatment and 50 seeds per replicate under water stress and salt stress conditions. Following the formula provided by Michel and Kaufmann (1973), we controlled osmotic potentials (–2.00, –1.60, –1.00, –0.50, and 0.00 MPa) using various concentrations of PEG_{6000} (indicating water stress) and NaCl (indicating salt stress) solutions.

$$\psi = -(1.18\times10^{-2})C - (1.18\times10^{-4})C^2 + (2.67\times10^{-4})CT + (8.39\times10^{7})C^2T, \quad (3)$$

where Ψ is the water potential (MPa); C is the PEG_{6000} concentration (g/L) or NaCl concentration (mmol/L); and T is the incubation temperature (°C).

The generated osmotic potentials in PEG_{6000} or NaCl solutions were validated by measuring molality using a VAPRO Pressure Osmometer 5520 (Wescor Co., Logan, Utah, USA) (Zagoub et al., 2022). Seeds were placed on 2 Whatman No. 1 filter paper layers moistened with 7 mL of PEG_{6000} or NaCl solution and incubated at temperatures of 15.0°C, 20.0°C, 25.0°C, and 30.0°C. Germination progress was monitored daily for 21 d. Mean germination time and GR were calculated and analyzed to assess the germination behavior under different stress conditions.

2.5 Mathematical model

2.5.1 Thermal time model

The thermal time or "heat sums" model, described by Alvarado and Bradford (2002), predicts necessary time and temperature for seed germination. The characteristics of seed germination response to temperature were referred to as "cardinal temperatures", which were classified into three categories: T_b, base temperature (below which seed germination is prevented); T_c, ceiling temperature (above which seed germination does not occur); T_o, optimal temperature, which can produce the most rapid seed germination (Bakhshandeh et al., 2013).

The formula for thermal time to GR ($\theta_{T(g)}$; °C/d) is as follows:

$$\theta_{T(g)} = (T_g - T_b)t_g, \quad (4)$$

where T_g is the germination temperature (°C); and t_g is the germination time (d).

The formula for GR is as follows:

$$\text{GR} = 1/t_g = (T_g - T_b)/\theta_{T(g)}, \quad (5)$$

where GR (or $1/t_g$) is the germination rate, which is a linear function of temperature between T_b and T_c. Specifically, GR increases linearly with temperature above T_b with a slope of $1/\theta_{T(g)}$.

2.5.2 Hydrotime model

Bradford (1990) proposed a hydrotime model to characterize the germination response to decreasing Ψ.

Given that θ_H is the hydrotime constant (MPa·d), it can be calculated as follows:

$$\theta_H = (\psi_a - \psi_{b(g)}) \times t_g, \tag{6}$$

where Ψ_a is the actual water potential of seed germination (MPa); and $\Psi_{b(g)}$ is the base water potential defined for a specific GP (MPa).

Since the fluctuation in $\Psi_{b(g)}$ conforms with a normal distribution, the probit analysis was used to compute the variables in the hydrotime model for the seed germination:

$$\text{Probit}_{(g)} = \left[\psi_a - (\theta_H / t_g) - \psi_{b(50)}\right] / \sigma\psi_{b(g)}, \tag{7}$$

where Probit$_{(g)}$ is the probit germination; $\Psi_{b(50)}$ is the base water potential when GP is 50.00% (MPa); and $\sigma\Psi_{b(g)}$ is the standard deviation of the base water potential defined for a specific GP (MPa).

2.6 Statistical analysis

All statistical analyses were accomplished using the *R* statistical package (version 4.2.1). Nonparametric two-way analysis of variance (ANOVA) was used to analyze the variation between groups utilizing the "nparLD" package in *R* (Noguchi et al., 2012). Bonferroni post-hoc test at $P<0.05$ level was applied to check the differences between temperature and osmotic potential. The thermal time model and hydrotime model methods were conducted using the "seedr" package in *R*. The asymmetric correlation matrix assessed the relationship between the seed functional traits and seed parameters using the "heatmap with pheatmap" package in *R*.

3 Results

3.1 Seed functional traits

For the investigated *H. persicum* population, 1000 seeds had an average weight of approximately 3.15 g, with a remarkably low coefficient of variation (0.95%), showing a consistent weight distribution throughout all seed samples (Table 1). These seeds had spherical shape, brownish-grey shade, spirally twisted embryos, and an average diameter of around 2.00 mm. The coefficient of variation for seed diameter was only 0.20%, indicating that the diameter is consistent throughout all examined seeds. Additionally, 22.51% of the seeds lacked embryos, while embryo viability was around 74.33%. Furthermore, SWC was around 14.76% and seed area was approximately 3.14 mm^2.

Table 1 Seed functional traits of *Haloxylon persicum*

Seed functional trait	Mean±SE	Coefficient of variation (%)
Thousand seed weight (g)	3.15±0.00	0.95
Percentage of embryoless seeds (%)	22.51±1.68	45.50
Embryo viability (%)	74.33±0.00	15.71
Seed diameter (mm)	2.00±0.00	0.20
Seed area (mm^2)	3.14±0.07	0.02
Seed water content (%)	14.76±0.06	0.03
Seed shape	Round	
Seed color	Brownish grey	
Embryo form	Spirally twisted	

3.2 Effect of temperature on germination behavior

The results of the germination kinetics are expressed as germination curves (Fig. 1), which represent the evolution of the cumulative percentage of germinated seeds as a function of time. The seed germination of *H. persicum* was significantly ($P<0.05$) affected by temperature. The seeds could germinate at a temperature range between 10.0°C and 35.0°C. The maximum GP was recorded at 25.0°C with a value of 80.00% (Fig. 1), followed by 72.00% at 20.0°C. The medium GP was recorded at 15.0°C, 30.0°C, and 35.0°C by a value of around 50.00%. The lowest GP was noticed at 10.00°C with a final value of about 33.00%.

The maximum GR was observed at 25.0°C (0.39/d), enlightening a full rapid germination ability at this temperature, followed by 20.0°C (0.37/d), 30.0°C (0.30/d), and 35.0°C (0.30/d). Further, the GR declined at 15.0°C and 10.0°C, with the values of 0.12/d and 0.07/d, respectively.

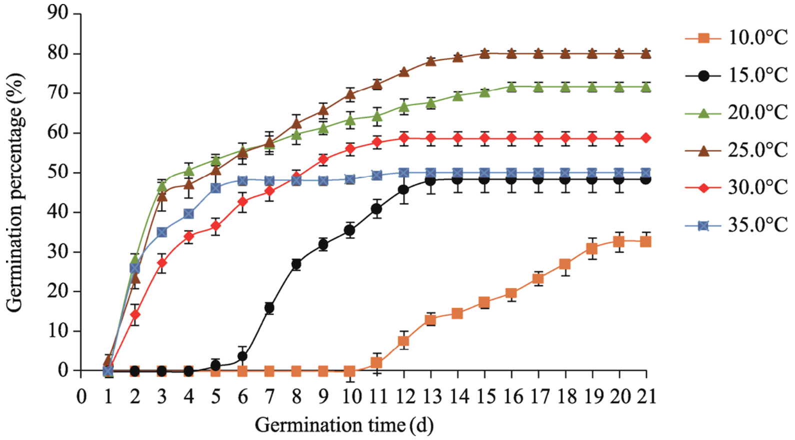

Fig. 1 Germination percentage of *Haloxylon persicum* at different temperatures. Each point represents the mean of replicates of 50 seeds. Bars mean standard deviations.

The mean germination time varied significantly among all temperatures, from 9.36 to 13.18 d ($P<0.05$; Table 2). The initial germination time at 10.0°C and 15.0°C was 12.00 and 6.00 d, respectively, revealing a medium germination speed. However, at 25.0°C, the initial germination time was only 1.50 d, and at 20.0°C, 30.0°C, and 35.0°C, it was 2.00 d. The final germination time varied between 13.00 and 15.00 d at the optimal temperature range (15.0°C–25.0°C), while it was 10.00 and 11.00 d at the highest temperatures (30°C and 35.0°C, respectively). The most extended germination period was observed at 10.0°C with a final germination time of 20.00 d. This variability reflects that environmental factors greatly influence the germinative capacity of *H. persicum*'s seeds, underlining the significance of knowing the ecophysiological needs for effective germination at regulated temperatures.

Table 2 Seed germination parameters of *H. persicum* at different temperatures

Temperature (°C)	Final germination percentage (%)	Initial germination time (d)	Final germination time (d)	Mean germination time (d)
10.0	33.00±2.42^{b}	12.00±0.41^{a}	20.00±0.41^{c}	9.36±0.85^{a}
15.0	48.00±3.04^{c}	6.00±1.26^{c}	13.00±0.41^{b}	13.18±0.56^{b}
20.0	72.00±1.17^{a}	2.00±0.00^{a}	15.00±1.51^{b}	10.25±0.24^{a}
25.0	80.00±0.09^{a}	1.50±0.54^{a}	14.00±0.99^{a}	10.14±0.55^{a}
30.0	51.00±1.63^{b}	2.00±0.00^{b}	10.00±1.22^{b}	10.35±0.56^{a}
35.0	50.00±1.26^{b}	2.00 ±0.00^{b}	11.00±0.75^{c}	10.73±0.22^{b}

Note: Mean±SD. Different lowercase letters in the same column indicate significant differences among different temperatures at $P<0.05$ level.

3.3 Effect of osmotic potentials on germination behavior

When seeds were exposed to PEG_{6000} or NaCl solutions with different concentrations, the impact of temperature on seed germination decreased significantly ($P<0.05$; Fig. 2). The final GP of *H. persicum* was also affected considerably by osmotic potentials. It was more sensitive to osmotic stress caused by PEG_{6000} (or NaCl) than by temperature. Specifically, it decreased significantly with the decreasing osmotic potential ($P<0.05$) at all temperatures (15.0°C, 20.0°C, 25.0°C, and 30.0°C). With the decrease of osmotic potential, the seeds of *H. persicum* could germinate at all temperatures.

Meanwhile, under the PEG_{6000} and NaCl treatments, all the seeds could germinate at all temperatures. For example, at the optimal temperature (25.0°C), the final GP decreased from 80.00% at the osmotic potential of 0.00 MPa under the control treatment to 42.00% at the osmotic potential of –2.00 MPa under the PEG_{6000} treatment, followed by 20.0°C (decreasing from 71.00% to 24.00%), 30.0°C (decreasing from 58.00% to 9.00%), and 15.0°C (decreasing from 48.00% to 5.00%) (Fig. 2a). At the highest NaCl concentration (osmotic potential of –2.00 MPa), the best final GP was recorded at 25.0°C to reach a value of 27.33%, followed by 20.0°C with a value of about 23.00%, 30.0°C with a value of 10.67%, and 15.0°C with a value of 7.33% (Fig. 2b). These results enlightened the idea that the seeds could germinate under different osmotic potential conditions, thus confirming its invasive potential.

Temperature, water stress, and salt stress are all factors that significantly influence the seed germination pattern of *H. persicum* (P<0.0001; Table 3). The two-way ANOVA results exhibited significant differences among these factors. Their interaction also greatly affected the final GP (P<0.0001).

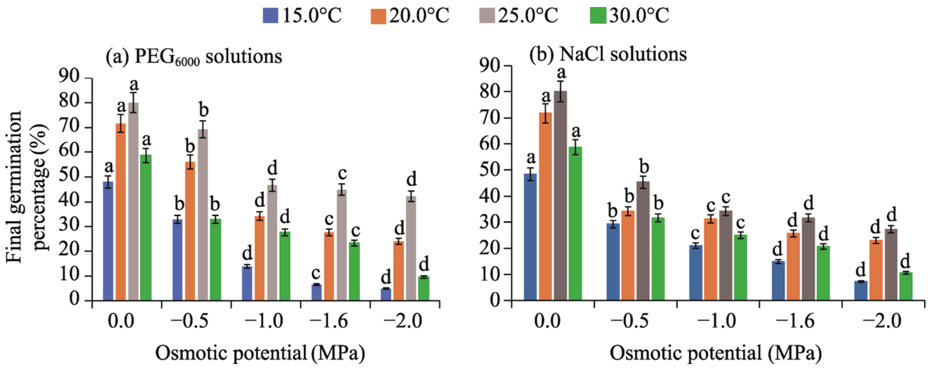

Fig. 2 Effect of osmotic potentials of PEG_{6000} (polyethylene glycol-6000; a) and NaCl (sodium chloride; b) on the seed germination of *H. persicum*. Different lowercase letters indicate significant differences of final germination percentage at P<0.05 level. Bars mean standard deviations.

Table 3 Effects of PEG_{6000} (polyethylene glycol-6000) and NaCl (sodium chloride) and their interactions with temperature on the final germination percentage of *H. persicum* based on the two-way analysis of variance (ANOVA)

	Salt stress			Water stress		
	Temperature	NaCl	Temperature×NaCl	Temperature	PEG_{6000}	Temperature×PEG_{6000}
df	1.39	2.24	2.68	2.15	1.16	3.96
F statistic	1571.77	153.93	44.62	909.27	255.09	26.58
P-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Note: *df*, degrees of freedom.

3.4 Thermal model and cardinal temperatures

Based on the predicted thermal time model, T_b was about 8.4°C, T_o was estimated as 25.5°C with a suboptimal $\theta_{T(50)(g)}$ (the median $\theta_{T(g)}$) of about 37.23 MPa, and T_c was around 58.3°C with a supraoptimal estimated $\theta_{T(50)(g)}$ of about 75.06 MPa at the osmotic potential of 0.00 MPa under the control treatment. In addition, the suboptimal model had a thermal time constant of 37.23 MPa with a standard deviation of 97.58 MPa and a coefficient of determination (R^2) of 0.55. In contrast, the supraoptimal model showed a thermal time constant of 75.06 MPa with a standard deviation of 110.58 MPa and a higher R^2 of 0.72.

3.5 Hydrotime model and probit germination

Table 4 and Figure 3 illustrate a successful relationship between the germination behavior of *H. persicum* and osmotic potentials of all PEG_{6000} and NaCl solutions at different temperatures

(15.0°C, 20.0°C, 25.0°C, and 30.0°C).

This relationship was assessed using a hydrotime model with R^2 ranging from 0.48 to 0.76. The $\Psi_{b(50)}$ increased with the decreasing temperature (Table 4). Under the water stress treatments, the $\Psi_{b(50)}$ values revealed a minimum fluctuation varying from –7.74 to –4.14 MPa at the suboptimal temperatures (15.0°C, 20.0°C, and 25.0°C). In contrast, the θ_H values decreased as increasing temperature. At 30.0°C, the predicted $\Psi_{b(50)}$ recorded the lowest value while the θ_H reached its highest value.

Table 4 Estimated hydrotime model parameters describing the seed germination of *H. persicum* at different temperatures under the water stress (PEG_{6000} solutions) and salt stress (NaCl solutions) treatments

Temperature (°C)	Water stress				Salt stress			
	$\Psi_{b(50)}$ (MPa)	θ_H (MPa•d)	$\sigma\Psi_{b(g)}$ (MPa)	R^2	$\Psi_{b(50)}$ (MPa)	θ_H (MPa•d)	$\sigma\Psi_{b(g)}$ (MPa)	R^2
15.0	–4.14	37.71	1.26	0.76	–3.61	14.50	2.07	0.71
20.0	–7.08	29.60	3.97	0.61	–7.03	25.84	4.02	0.61
25.0	–7.74	22.86	4.75	0.57	–4.66	21.09	2.48	0.48
30.0	–10.90	47.06	5.63	0.63	–6.66	20.30	3.47	0.60

Note: $\Psi_{b(50)}$, base water potential when the germination percentage is 50.00%; θ_H, hydrotime constant; $\sigma\Psi_{b(g)}$, standard deviation of the base water potential at a specific germination percentage; R^2, coefficient of determination.

Under the salt stress, the predicted $\Psi_{b(50)}$ was from –7.03 to –4.66 MPa at the temperature range of 20.0°C–30.0°C (Table 4). In addition, the θ_H highlighted the lowest values of 14.50 and 20.30 MPa•d at 15.0°C and 30.0°C, respectively. The highest θ_H was recorded at 20.0°C, with the value of 25.84 MPa•d. The predicted $\sigma\Psi_{b(g)}$ varied considerably between 1.26 and 5.63 MPa under all water and salt stress treatments. The lowest $\sigma\Psi_{b(g)}$ was recorded at 15.0°C, with the values of 1.26 and 2.07 MPa, respectively, under the water and salt stress treatments. These results proved that the invasive *H. persicum* can tolerate water stress better than salt stress.

Figure 3 elucidates the relationship between the probit germination model and $\Psi_{b(g)}$ via the "seedr" package. Probit germination, representing the cumulative probability of seed germination, showed a distinct positive correlation with $\Psi_{b(g)}$. The probability of germination declined with increasing $\Psi_{b(g)}$ at all measured temperatures, demonstrating that a decrease in water availability has a negative impact on germination success under both water stress (PEG_{6000}) and salt stress (NaCl) treatments.

3.6 Correlation matrix between seed germination parameters and seed functional traits of *H. persicum*

Figure 4 represents a heat map correlation between seed germination parameters and seed functional traits of *H. persicum* at 25.0°C. A strong negative correlation was highlighted between GR and thousand seed weight (r= –0.96) and between mean germination time and thousand seed weight (r= –0.96). In contrast, a strong positive correlation between GP and thousand seed weight (r=0.96) suggested that heavier seeds may have higher GP. Moreover, a strong positive correlation existed between GR and embryo viability (r=0.87) and between mean germination time and embryo viability (r=0.87). Furthermore, a negative correlation was found between GP and embryo viability (r= –0.87).

Conversely, the negative correlation between GP and percentage of embryoless seeds (r= –0.96) showed that the higher the percentage of embryoless seeds, the lower the GR. In addition, the negative correlation between GP and seed area (r= –0.87) indicated that seeds with larger extensive surface areas had lower GP. The positive relationship between mean germination time and seed area (r= –0.87) indicated that seeds with larger extensive surface areas have longer mean germination time. At last, the negative correlation between mean germination time and SWC (r= –0.94) indicated that seeds with higher water content can germinate faster. On the contrary, the positive correlation between GP and SWC (r=0.94) showed that seeds with higher water content have significant high final GP.

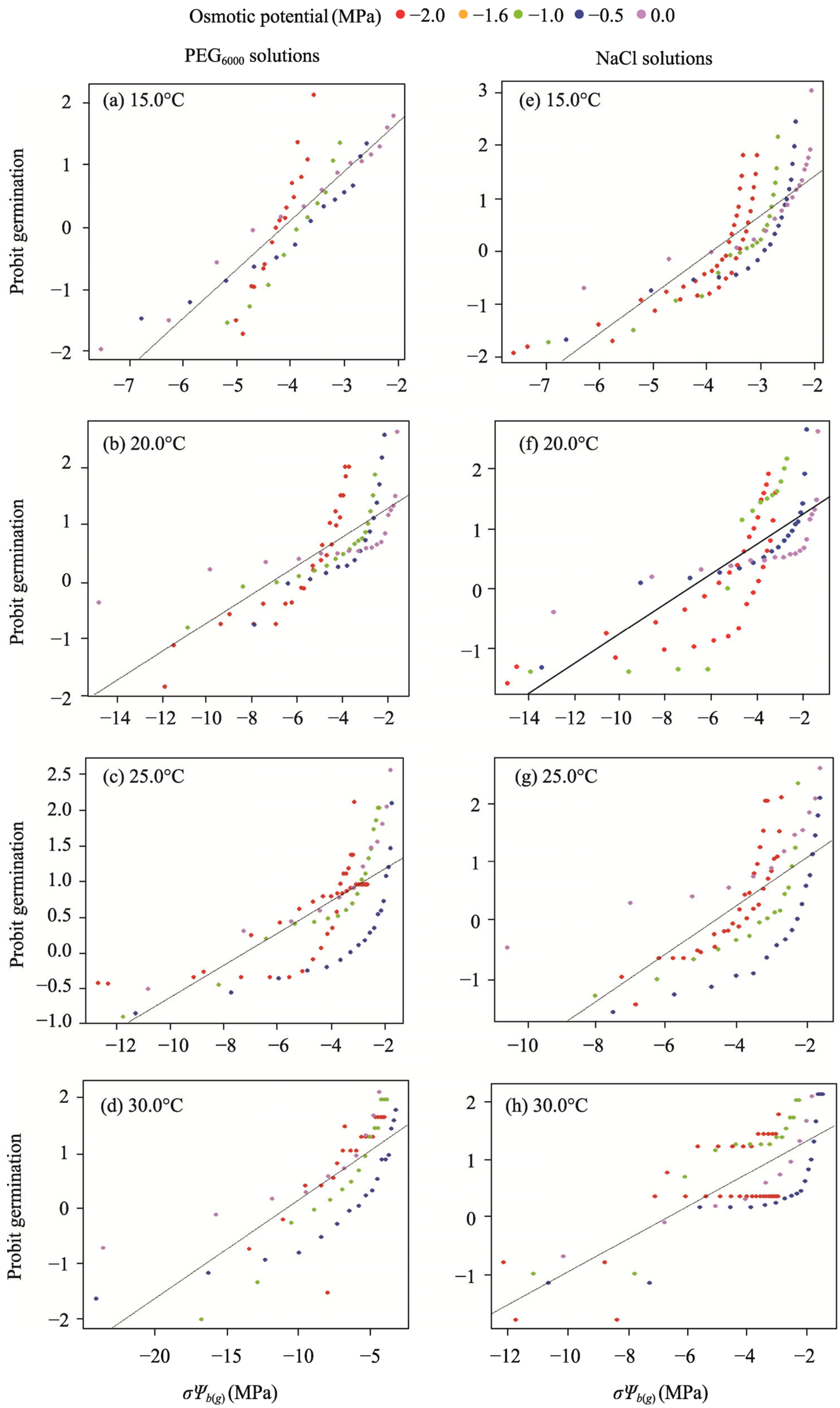

Fig. 3 Relationship between the probit germination model of *H. persicum* and $\sigma\Psi_{b(g)}$ at different osmotic potentials of PEG_{6000} (a–d) and NaCl (e–h) solutions at different temperatures (15.0°C, 20.0°C, 25.0°C and 30.0°C). $\sigma\Psi_{b(g)}$, standard deviation of the base water potential defined at a specific germination percentage.

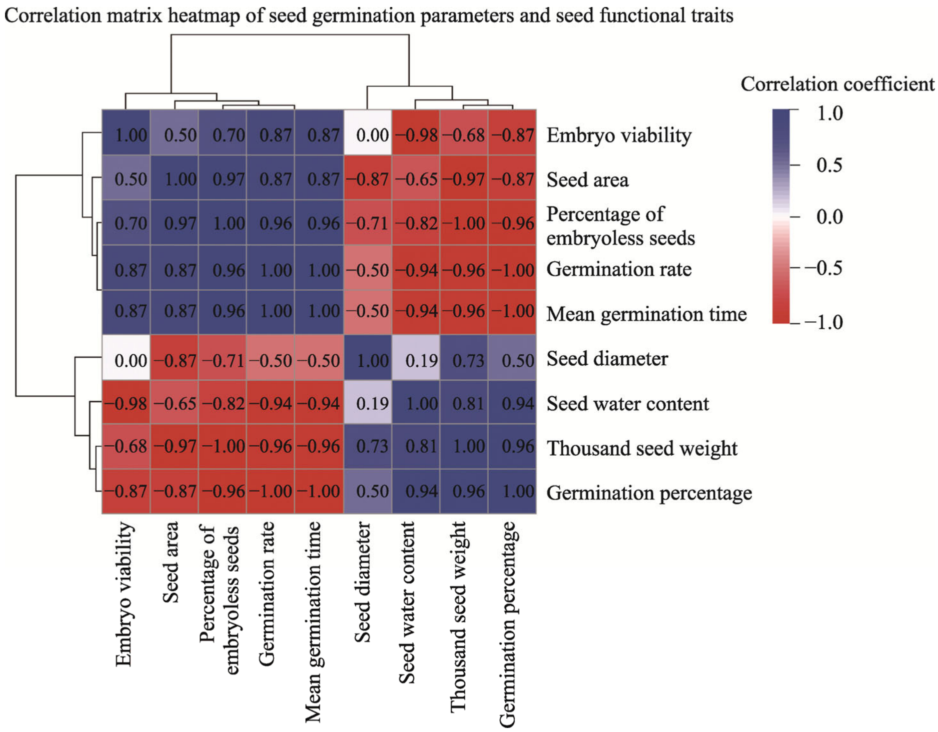

Fig. 4 Heat map correlation between seed germination parameters and seed functional traits of *H. persicum* at 25.0°C

4 Discussion

4.1 Seed functional traits of *H. persicum*

Under harsh environmental conditions in the arid bioclimate zones of North Africa, seed germination appears to be key to the establishment of plant populations, especially for invasive species whose seed germination may significantly affect native species. The invasive species use germinated seeds as a viable method for successful colonization and settlement (Guido et al., 2017), specifically in desertic regions. When investigating the seed functional traits of *H. persicum*, we noticed that SWC was around 14.76%. According to Tangney et al. (2019), this low content suggested that this species could survive at higher temperatures. Moreover, thousand seed weight of *H. persicum* was around 3.15 g with a low coefficient of variation being 0.95%, confirming the uniformity within the treated populations. This result was in line with the findings of Chen et al. (2022) for the seeds of *Salsola* species. The spirally twisted embryo shape and color of seeds are characteristics of the Chenopodiaceae family (Shepherd et al., 2005). *Sarcocornia blackiana* belongs to Salicornioideae, a sub-family of Chenopodiaceae; its seed has a peripheral embryo with the outer edge aligned with the inner surface of the bitegmic seed coat, limiting evaporative losses (Shepherd et al., 2005). Besides, understanding ecological processes in plants and the coexistence among species relies heavily on the link between seed functional characteristics. Functional traits are essential indicators of the metabolism and life cycle of plant species (Visser et al., 2016), especially for seeds, to study their source, usage, storage, and improvement strategies, resulting in lower costs and higher seedling establishing success (Zanetti et al., 2020).

4.2 Effect of temperature on the seed germination of *H. persicum*

Temperature represents a significant germination inhibitor (Notarnicola et al., 2023). An important abiotic stressor negatively impacts seed germination for several plant species (Bakhshandeh and Jamali, 2020). Our results suggested that the seeds of *H. persicum* can germinate at temperatures from 10.0°C to 35.0°C with different speeds (Table 2). Such a flexibility may offer *H. persicum* competitive benefits across crop-growing seasons in varied environments. The maximum GP was recorded at 25.0°C (P<0.0001; Fig. 1), with a high germination speed (1.00 d) and the highest GP (0.39/d) under the control treatment (osmotic potential of 0.00 MPa), knowing that the species of Chenopodiaceae are characterized by a high germination speed, which could vary from several hours to a few days (Baskin et al., 2014). Similar results were reported previously for *Dioscorea dregeana* (Kulkarni et al., 2007) and *Stachys mouretii* (Ismaili et al., 2023). Seed form influences germination speed based on the environment, life cycle strategy, and climate (Vandelook et al., 2012). Besides, several studies have demonstrated that invasive plants may germinate earlier or more quickly under different conditions (Ozaslan et al., 2017; Gioria et al., 2018; Nešić et al., 2022). Additionally, Tobe et al. (2000) affirmed that the T_o of *H. persicum* growing in a non-saline area in China was 20.0°C. This variation of T_o may result from different climatic zones (Vázquez et al., 2017). The Mediterranean climate characterizes Tunisia with hot and dry summers and mild and humid winters (Bouatrous et al., 2022). China, on the other hand, has a climate with moderate temperatures and obvious seasonal variations (Wang et al., 2019). Seeds germinating optimally at 20.0°C in China may benefit from cold conditions (Li et al., 2006). In comparison, those *H. persicum* plants that grow in Tunisia (with T_o of 25.0°C) have to adapt to hotter and drier climate conditions, which can pose challenges under climate change scenarios (Rejili et al., 2010). In this concern, several studies on the seed germination of plant species in the Saharan bioclimatic zones found the same temperature range (Derbel and Chaieb, 2007; Hayder et al., 2024).

4.3 Effect of osmotic potentials on the seed germination of *H. persicum*

Temperature, osmotic potentials, and their combinations significantly impact the seed germination of the invasive *H. persicum.* Their interactions showed the potential invasive character of this species in the Saharan bioclimatic zones of Tunisia. Our results proved that *H. persicum* could germinate at different osmotic potentials of PEG_{6000} and NaCl solutions, as it could grow even at the osmotic potential of –2.00 MPa for both PEG_{6000} and NaCl solutions to attend the minimum final GP of 5.00% and 7.00%, respectively, at 15.0°C. On the other hand, at the optimal temperature (25.0°C), the minimum GP was recorded at the osmotic potential of –2.00 MPa (274 mmol/L for NaCl concentration), with the values of 27.33% and 42.33% for PEG_{6000} and NaCl solutions, respectively (Fig. 3). The maximum salt concentration necessary for seed germination and recovery after NaCl exposure indicates a species' resistance to high salinity levels (Hinojosa et al., 2018). Also, according to the results found in our research, the seeds of *H. persicum* showed better tolerance to PEG_{6000} solutions than NaCl solutions (Fig. 3). It is proven that *H. persicum* has more flexibility to water stress than salt stress under different concentrations. Our results corroborated the findings of Duan et al. (2004), who proved that the seed germination of *Chenopodium glaucum* (Chenopodiaceae) was lower in NaCl solutions than in iso-osmotic PEG_{6000} solutions with an osmotic potential less than –0.50 MPa. Conversely, our findings opposed those of Song et al. (2005), who showed that PEG_{6000} treatments had a more potent inhibitory impact on the seed germination of *H. persicum* than iso-osmotic NaCl treatments. Indeed, Song et al. (2005) emphasized that seedlings that underwent PEG_{6000} treatments did not experience ion toxicity. The final GP values were 43.00%, 48.00%, and 76.00% lower at the osmotic potentials of –1.34, –2.24, and –3.13 MPa under the PEG_{6000} treatments, respectively, compared to iso-osmotic NaCl treatments (Song et al., 2005). Moreover, Tobe et al. (2000) asserted that the GR of *H. persicum* decreased with increasing NaCl concentrations, with a final GR of 64.00% at the osmotic potential of –3.00 MPa (667 mmol/L for NaCl concentration). In addition, the leaves of *H. persicum* are tiny, allowing them to retain and preserve water. This capacity results from tremendous photosynthetic efficiency and high resistance to drought (Alsahli et al., 2015). However, the capacity for the seeds of *H. persicum* to germinate at high salinity levels may represent an adaptive strategy that allows this species to maintain its populations under extreme salt conditions. Thereby, it was emphasized by Ruan et al. (2006) that during drought period, the cells of *H. persicum* quickly accumulate solutes, such as proline, to prevent water loss and restore cell turgescence, which is maintained by osmotic adjustment. Hence, this mechanism can improve the drought tolerance of *H. persicum*. Indeed, Ozturk et al. (2021) further affirmed that this is the most effective stress-coping mechanism of all. The synthesis and accumulation of the osmoregulating chemicals (proline, betaine, polyols, soluble sugars, and seed starch) promote the rapid seed germination of halophytic species under salt conditions (Kumari et al., 2015).

4.4 Thermal model and cardinal temperatures for the seed germination of *H. persicum*

The effect of temperature on the seed germination of *H. persicum* was confirmed by the thermal time model, which showed that T_o was predicted to be 25.5°C, T_b was 8.4°C, and T_c was 58.3°C. The same T_c value was found previously for *Chenopodium quinoa* (quinoa), i.e., 54.0°C (Oveisi, 2017). It was reported previously that T_c value varies across seeds in the population and depends on the stress level (Alvarado and Bradford, 2002; Bakhshandeh et al., 2017; Abdellaoui et al., 2019). Also, our results opposed the findings of Peng et al. (2018), who found that the Chenopodiaceae family exhibits a lower T_b. This spectrum in the T_b of seed germination may be an adaptative trait in plants, as species growing in low temperatures have relatively low T_b. This behavior could be explained by the fact that C_4 species adapt highly to the ecological conditions in arid environments characterized by high temperatures. This adaptation is a common survival strategy of Mediterranean plants with T_o ranging from 15.0°C to 30.0°C (Baskin et al., 2000). Baskin et al. (2000) mentioned that the successful seed germination observed at high temperatures enables the seeds to avoid the risk of rapid dryness in the soil during the germination period. Furthermore, temperatures around 25.0°C are optimal for C_4 photosynthetic species (Khaeim et al., 2022; Zhu et al., 2022). Our results revealed a significant variability in the germination pattern of *H. persicum* species compared to previous findings (Tobe et al., 2000; Soltani, 2011). Although prior research indicated an optimal germination at lower temperatures (Song et al., 2005; Soltani, 2011), our data showed that the seeds of *H. persicum* can germinate better at moderate temperatures, which is one of the characteristics of Tunisian Saharan bioclimate. This environmental-dependent strategy allows *H. persicum* to survive, adapt, and quickly germinate under harsh habitat conditions for natural regeneration (Soltani, 2011). Indeed, Le Houerou (2000) stated that the average temperature throughout the spring and autumn seasons in the Tunisian Saharan bioclimatic zones is around 20.0°C, which is the beginning temperature point for seed germination for most species. Cardinal temperatures for seed germination are frequently linked to a species' climatic range of adaption, and they link germination time with favorable conditions for seedling emergence development and growth (Krichen et al., 2023). Consequently, a time-temperature relationship could be appropriate for woodland management projection via the *H. persicum* populations. Likewise, according to enthalpy methods, when the temperature increases, the energy in the water rises, causing an increase in diffusion pressure. This pressure boosts simultaneously metabolic and enzymatic activity while decreasing a seed's internal potential, which enhances water absorption (Haj Sghaier et al., 2022).

4.5 Hydrotime model and probit germination of *H. persicum*

The effect of low osmotic potentials on seed germination was investigated using the hydrotime model parameters estimated by the probit regression analysis with the $\sigma\Psi_{b(g)}$ as an indicator of seed germination uniformity in a seed lot (Table 4; Fig. 3) (Bradford and Still, 2004). Generally, seeds require a specific moisture level to germinate, suggesting that seeds with the Ψ_b higher than the Ψ_a cannot germinate. Thus, Ψ_b shows the water stress endurance of the seed population; the more significant (less negative) the Ψ_b, the lower the seeds' resistance to water stress (Patanè et al., 2016). In line with this, our results revealed that the seeds of *H. persicum* are more tolerant to water stress than salt stress, exhibiting the lowest Ψ_b (–10.90 MPa) at 30.0°C, which requires a greater cumulative soil water content. This finding is supported by the probit germination fit, indicating that the variation in GR is related to the species' adaptation to its native Saharan bioclimate. Consequently, these seeds required a longer time to germinate, which could attend

13.18 d. The hydrotime model posited that GR depends on the difference between the Ψ_a and Ψ_b (Cardoso and Bianconi, 2013). It has been emphasized in a recent study by Yang and Lv (2023) that as an adaptation strategy to water stress, *H. persicum* enhances the content of organic acids and their derivatives, and reduces the content of lignans and their related compounds. *H. persicum* has a high osmoregulatory capability, reactive oxygen species detoxification, and cell membrane stability by controlling vital metabolic pathways and anabolism of related metabolites. In this regard, *H. persicum* can adapt to long-term dry conditions by controlling required metabolism and metabolite production pathways.

4.6 Correlation between seed germination parameters and seed functional traits of *H. persicum*

The high correlation between thousand seed weight and seed diameter (r=0.73; Fig. 4), as emphasized by Tuthill et al. (2023), facilitates the wind dispersity, such as invasive species, to expand their populations, knowing that the seeds of *H. persicum* are winged. Indeed, winged seeds have a boosted dispersity, especially those of the Amaranthaceae family (Baskin et al., 2014). In addition, the smaller seeds are also likely better suited for long-distance wind dispersal because they require less energy.

Our study demonstrated that *H. persicum* has a strong invasive potential in Tunisia. However, it has been listed as endangered species in the Red List of Threatened Species in its native habitat, where it could face several environmental issues, such as habitat degradation. Indeed, its rapid germination and reproductive advantage threatens local biodiversity. The invasive potential of this species is linked to its introduction into Tunisia, where it experiences less ecological pressures, with favorable Mediterranean climate conditions.

5 Conclusions

Understanding the stress tolerance limitations of invasive C_4 species is crucial for predicting their reactions in changing environments. The seed functional traits of *H. persicum*, such as thousand seed weight, seed area, and SWC, influence germination success and time. The T_o for seed germination is 25.5°C, which can be explained by the annual average temperature of >20.0°C in the Tunisian Saharan bioclimatic zones. *H. persicum* showed high resistance to water stress and salt stress. These findings highlight the role of seed functional traits and environmental conditions in improving the tolerance of this species to environmental stressors. It confirms that *H. persicum*, which has a successful invasive potential, can adapt to various soil conditions in most arid and semi-arid habitats. Its distribution may spread due to its strong ability to adapt to harsh climatic environment caused by global warming in many areas.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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