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Intraspecific variation of *Haloxylon salicornicum* (Amaranthaceae) seed germination under salinity and simulated drought

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ABSTRACT

Haloxylon salicornicum (Moq.) Bunge ex Boiss. is a suitable species for desert and coastal restoration for its forage production and dune stabilization. Inter-population variation of seed parameters has previously received little attention. Variation in seed germination response to drought and salinity stress was evaluated for three Kuwaiti populations for use in restoration projects. Germination parameters varied significantly among populations. Seeds from Kabd were larger and germinated at a higher percentage than the other two populations, Mutla and Liya, under conditions of saline (62.8%, 40.0%, and 50.7% respectively) and moisture (58.2%, 32.6%, and 45.6%) stress. Increasing salinity and drought simulation progressively inhibited seed germination across all populations. Drought simulation by PEG 6000 inhibited germination from -0.3 MPa, while salinity affected the germination proportion from 400 mM NaCl for all the studied populations. All populations exhibited a high recovery from NaCl and PEG stress, indicating the species is broadly adapted to survival through drought and saline conditions. Our findings indicate that revegetation success with this species will be influenced by the population characteristics of the maternal seed source.

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Introduction

Deserts and coastal ecosystems present challenging conditions for plant survival, characterized by high temperature, low and unpredictable rainfall, high evaporation rates, high soil salinity and poor soil fertility (Shahid and Al-Shankiti 2013). Drylands of the Arabian Peninsula are highly vulnerable to climate change (FAO 2010), and recovery from anthropogenic stresses is very slow compared to other ecosystems (Richer 2008). Rehabilitation and restoration of Arabian deserts is necessary to prevent further loss of biodiversity and improve rangeland productivity (Heller and Zavaleta 2009; Bisaro et al. 2014). The most viable approach to restoration is to remove anthropogenic stresses. When this is impractical, impossible, or too slow, the next approach is to select appropriate germplasm for restorative intervention (Waller et al. 2015). Many desert and

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sand dune species exhibit high intraspecific variation. Thus, it is beneficial to select species, and populations within species, to maximize restoration success (Seglias et al. 2018). Native species are usually favored for restoration because they are expected to facilitate restoration of the broader ecosystem due to their innate adaptation and low damage to the environment (Elzenga, Bekker, and Pritchard 2019). Restoration is often restricted in Arabian deserts by poor availability of planting material and limited information on propagation and management (Shahin and Salem 2014; Bhatt, Pérez-García, et al. 2016; Bhatt and Santo 2017a).

Drought and salinity play an important role in determining the growth and survival of Arabian desert plant species (Abu Sukar, Almerri, and Almurekki 2007). Desert plants have evolved anatomical, morphological and physiological adaptations to respond to these abiotic stresses (Ward 2008; Lowry et al. 2009). Generally, salinity and water stress are spatiotemporally varied and are likely to cause selective pressures, which can lead to local adaptation. Thus, the maternal environmental conditions during seed development and maturation play an important role in determining seed dormancy and germination (Wulff 1995). Knowledge of inter-population variability in seed germination could be useful for selecting seeds from natural populations that optimize rehabilitation or restoration efforts.

Haloxylon salicornicum (Moq.) Bunge ex Boiss. (Amaranthaceae) is widely distributed in Egypt, Iraq, Jordan, Kuwait, Palestine, Pakistan, Qatar and the United Arab Emirates (Norton et al. 2009). Its high mineral content has made it a preferred fodder for domesticated livestock (Ashraf et al. 2012). The species is tolerant of temperature extremes, drought, salinity, poor nutrition and high light intensity (Casati, Andreo, and Edwards 1999; Huang et al. 2003). Large shrubs frequently accumulate a raised mound of sand, known locally as nebkhas (Zaman et al. 2006; El-Keblawy and Al-Shamsi 2008), the absence of which is a strong indicator of desertification (Belgacem and Louhaichi 2013). The species was one of several that were shortlisted for native urban landscapes in the region (Phondani et al. 2016).

Several studies have examined the effect of temperature, light and salinity on seed germination of *H. salicornicum* (Kaul and Shankar 1988; Brown and Al-Mazrooei 2001; El-Keblawy and Al-Shamsi 2008). Association of fruit dimorphism with seed germination, salinity tolerance, and longevity of seed viability has also been examined (Bhatt, Phartyal, and Nicholas 2016; Bhatt and Santo 2017b). All these studies relied on a single population for their seed source. They reported intrapopulation variation in seed mass, dormancy, and germination parameters that could be linked to adaptation strategy (Tavşanoğlu and Çatav 2012; Cochrane et al. 2015; El-Keblawy et al. 2017). Inter-population variation in seed dormancy and germination can be linked to the distribution of populations across habitats (Wagmann et al. 2012; Fernández-Pascual et al. 2013; Baskin and Baskin 2014). The presence of this variation indicates a high genetic diversity that facilitates survival across environmental spatiotemporal heterogeneity (Fernández-Pascual et al. 2013). However, studies that sample inter-population variability are especially rare in Arabian Desert plants (El-Keblawy, Gairola, and Bhatt 2016; El-Keblawy et al. 2017). In addition, the success of interventive restoration projects depends on a reliable seed source because it can directly influence seedling establishment (Zahawi and Holl 2014).

Table 1. Description of *H. salicornicum* seed sources used in the present study.

Location	GPS Co-ordinates	Altitude (m asl)	Habitat	Disturbance ^a	pH _{paste}	EC _{paste} (dS/m)	Associated species
Kabd	29° 5' 43.40''N; 47° 24' 38.59''E	100	Sandy plain	High	<u>7.8</u>	2.59	<i>Plantago boissieri</i> Hausskn. Bornm., <i>Panicum turgidum</i> Forssk., <i>Rhanterium epapposum</i> Oliv.
Mutla	29° 24' 14.78''N; 47° 41' 34.38''E	30	Shallow depression	Moderate	7.5	1.93	<i>Cornulaca monacantha</i> Del., <i>Panicum turgidum</i> Forssk., <i>Neurada procumbens</i> L.
Liyah	29° 32' 35.36''N; 47° 36' 14.11''E	100	Gravel desert	Low	7.6	2.03	<i>Fagonia bruguieri</i> DC., <i>Haplophyllum tuberculatum</i> (Forsk.) Ad. Juss., <i>Cornulaca monacantha</i> Del.

^aDisturbances were attributable to overgrazing by domestic camels, and human recreational activities, primarily camping. pH and EC were determined in water saturated soil paste.

Seeds of halophytic species are frequently exposed to salinity and water stresses under natural conditions, the response to which can be influenced by light (Elnaggar et al. 2019; Bhatt, Gairola, et al. 2020). Evaluation of drought and salinity tolerance during seed germination is thus informative of arid desert adaptability. Knowledge of how osmotic stress and salinity affect germination assists in developing rehabilitation protocols, since germination is a critical stage in the lifecycle of a species. Similarly, the knowledge of how these factors vary among wild populations may improve rehabilitation work through more effective seed sourcing. The aims of this study were to investigate if populations differed in (i) seed mass or germination parameters, (ii) germination response to drought and salinity gradient treatments, i.e., water stress, under 12 h light and darkness, and (iii) germination recovery after exposure to water stress. We hypothesized that seeds collected from different populations would exhibit significant differences in drought and salinity tolerance during germination. Variation in soil salinity and nutritional states among habitats was expected (Migahid and Elhaak 2001) though not tested directly in this study.

Materials and methods

Seed collection

Mature fruits of *H. salicornicum* were collected in December 2017 from three Kuwaiti locations with differing plant communities (Table 1 and Figure 1). The climate of Kuwait is characterized by a long, dry, hot summer with a sporadic annual precipitation of 114 mm occurring mostly between November and March (Omar, Al-Mutawa, and Zaman 2007). Temperature can exceed 50 °C in summer and fall to winter lows of 4 °C (Annual Statistical Report 2006).

Seeds were collected and pooled from 30 to 35 maternal plants at each location. Maternal plants were selected visibly to represent any intrapopulation genetic variation, by sampling across the location spatially and of plants with macro-morphological differences. Seeds were stored in brown paper bags at room temperature (20 ± 2 °C) until March 2018. Mean seed mass was determined by weighing three replicates of 100 seeds from each population. Five soil samples were collected randomly from each population at 0–10 cm soil depth then pooled together to form one composite sample. Soil pH and



Figure 1. Locations of sampled *Haloxylon salicornicum* (Moq.) Bunge ex Boiss. populations within Kuwait.

soil electrical conductivity (EC) were determined by the saturated paste method (AFNOR 1987).

Water stress

Eight water stress treatments were used, including four of salinity (100, 200, 400, and 600 mM NaCl in distilled water), three of simulated drought using polyethylene glycol 6000 (PEG6000, Michel and Kaufmann 1973; $\psi = -0.3, -0.6$ and -0.9 MPa), and a control of distilled water. The presence and the absence of light was also tested. Four replicates were used for each of the 48 combinations of population, treatment, and light exposure. Each replicate was a 9 cm Petri dish containing 25 seeds, with one Whatman No. 1 filter paper disk moistened according to the treatment, and sealed with parafilm to prevent evaporation. Dishes were placed in a germinator set at 12/12 hour cycles of 20/30 °C and either 0/0 (dark) or 0/12 (light) hours of light. Petri dishes subjected to the dark treatment were wrapped in aluminum foil. Germinated seeds in the light

treatments were counted daily; defined as the emergence of a radicle $>1\text{mm}$. Germinated seeds in dark treatments were counted at the end of the 25-day experiment.

Recovery from water stress

Non-germinated seeds from the previous light-exposed, water-stressed treatments were tested for germination in conditions free from water stress. The remaining seeds were rinsed with distilled water and placed in newly prepared Petri dishes, as described previously, but moistened with distilled water. These Petri dishes were placed in light at 20/30 °C, and germinated seeds were counted daily for 7 days.

Data analysis

All analyses were performed with R (R Core Team 2019). Effect of population on seed mass was tested with an analysis of variance with Tukey's multiple comparison of means. Assumptions of normality (Shapiro–Wilk test) and homogeneity of the residuals (Bartlett test) were validated prior to analysis.

Final germination was assessed using a Generalized Linear Mixed Model, and germination percentage using a Time-to-Event Analysis (also known as Survival Analysis). These analyses were chosen for their ability to account for random effects (for more details see Onofri, Gresta, and Tei 2010; Sileshi 2012). The final germination models for water stress and recovery were binomial error distributed with logit link function (“lme4” package [Bates et al. 2014]). The model selection accounted for significant interactions and the best AIC (Akaike Information Criterion) (Zuur et al. 2009). We tested the effects of population, water stress treatments, and light exposure on the final seed germination. For the salinity model (mM NaCl) we included all first-order interactions. For the simulated drought model (PEG6000), only the treatment \times light exposure interaction was included as the others were not significant. Replicates were included as components to the random intercept. Model coefficients (β) were analyzed by multiple pairwise Z-test comparison via least-square means (“multcomp” package [Hothorn et al. 2008] and “lsmeans” package [Lenth 2016]).

We used Time-to-Event Analysis for germination rate modeling (‘survival’ package [Therneau and Grambsch 2000]; Onofri, Gresta, and Tei 2010). Germination times of individual seeds were used to calculate the probability that one seed may germinate after a specific time t once the assay began. Parametric Accelerated Failure Time (AFT) modeling was then run with lognormal distribution, the best AIC score and the most appropriate in relation to the non-parametric Kaplan-Meier estimator. The model tested significance of treatment, population, and the interaction as fixed factors (Onofri, Gresta, and Tei 2010). From those models, we obtained the t_{50} estimation and presented as a germination time parameter. Final models were Z-tested for the effects on the germination curve coefficients and comparison via least-square means.

Results

Seeds from the Kabd population (108.3 ± 1.4 mg) were significantly heavier ($F_{2,9} = 9.39$, $p = 0.014$) than seeds from Mutla (90.1 ± 8.4 mg) and Liya (96.4 ± 3.8 mg). The latter

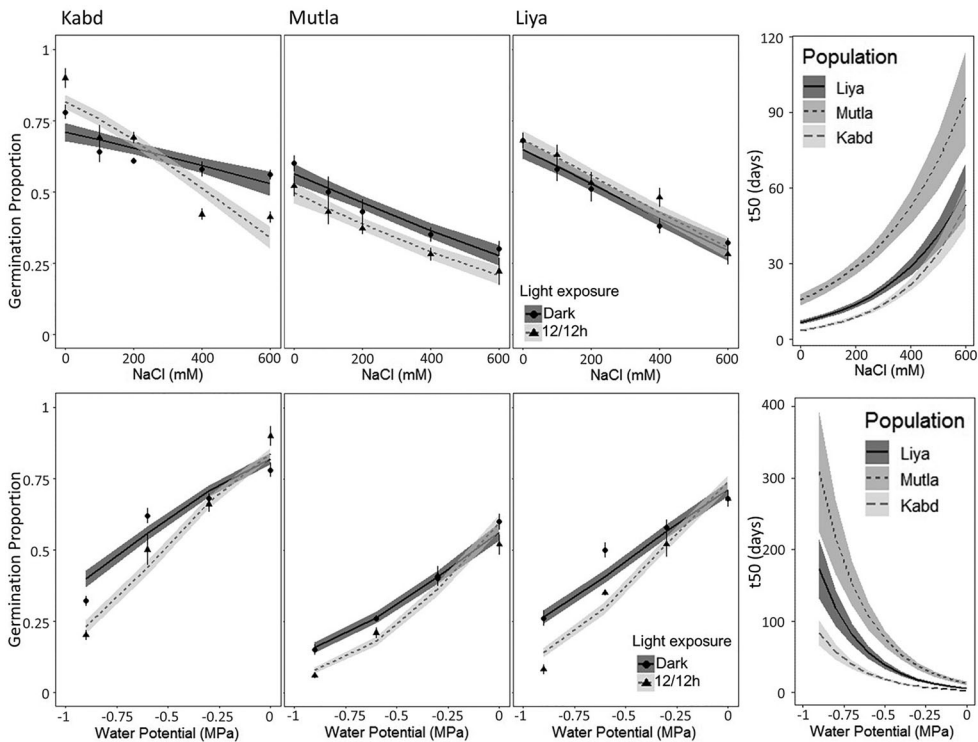


Figure 2. Models of germination response to salinity (A–D) and drought simulation (E–H), showing estimated germination response (lines) \pm SE (shading). Final germination proportions of the seed populations were modeled using a Binomial regression logit link (A–C, E–G). Estimated time to 50% germination was modeled by Accelerated Failure Time model (lognormal distribution; D, H). Points and whiskers represent mean \pm SE of replicates.

populations did not differ significantly. Kabd was a sandy, disturbed habitat with a high soil pH and EC (Table 1).

Germination proportion varied among populations from an average of 39% at Mutla to 64% at Kabd. Salinity significantly affected overall germination ($\beta_{\text{salinity}} = -0.001 \pm 0.0004$, $z = -3.008$, $p = 0.003$), with averages across populations ranging from 69.3% to 34.8% in 0 and 600 mM respectively (Figure 2(a–d)). Light exposure during germination was significant overall ($\beta_{\text{light exposure}} = -0.59 \pm 0.22$, $z = 2.65$, $p = 0.008$) but affected germination only slightly, from 50.2% to 52.1% in the light and dark treatments respectively. However, light exposure affected populations differently ($\beta_{\text{salinity} \times \text{light interaction}} = 0.002 \pm 0.0006$, $z = -3.623$, $p < 0.001$), influencing Mutla the most (36.4% germination in light; 43.6% in darkness). Light exposure increased germination across all salinity levels at Liya, lower than the dark treatment across all salinity levels at Mutla, and had a mixed effect at Kabd. Germination rate was greatly affected by salinity ($\beta_{\text{salinity}} = 0.0045 \pm 0.0004$, $z = 11.01$, $p < 0.001$, Figure 2(d)). The Kabd population germinated faster ($t_{50} = 11.6 \pm 1.01$ days) and Mutla slower ($t_{50} = 34.4 \pm 3.46$ days), but their response pattern was similar.

Drought simulation significantly affected overall germination ($\beta_{\text{drought}} = 2.14 \pm 0.19$, $z = 10.99$, $p < 0.001$), the control with 69.3% and the most simulated drought treatment

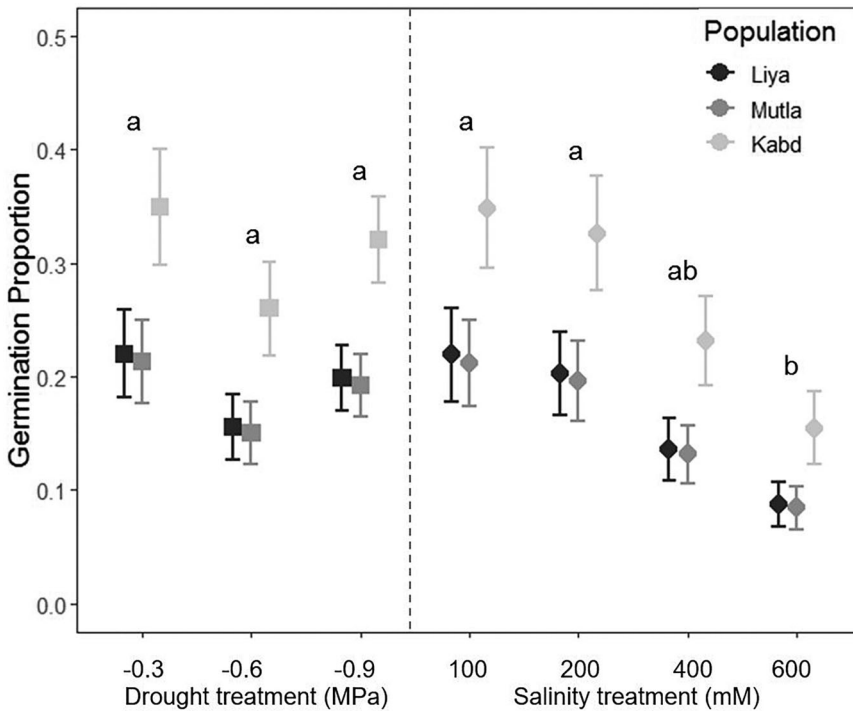


Figure 3. Germination (mean \pm SE) of seeds in distilled water after recovery from drought and salinity treatments, from three *Haloxylon salicornicum* populations in Kuwait. Seeds from the Kabd recovered more than seeds of the other populations ($p < 0.01$). Letters represent significant differences ($p < 0.05$) among treatments.

with 17.8%. Exposure to light during germination appeared to exacerbate the influence of simulated drought, however, the overall effect of light exposure was not significant ($\beta_{\text{light exposure}} = 0.13 \pm 0.15$, $z = 0.8599$, $p = 0.39$; Figure 2(e–g)). The effect of populations on germination rate was significant ($\beta_{\text{population}} = -3.76 \pm 0.34$, $z = -11.02$, $p < 0.001$), being fastest for the Kabd population ($t_{50} = 15.3 \pm 1.8$ days) and slowest for Mutla ($t_{50} = 63.2 \pm 9.2$), though Mutla did not differ significantly from Liya ($t_{50} = 31.8 \pm 4.1$ days)

Seeds from the Kabd population were significantly more able to recover from water stress than seeds from the other populations (Figure 3). In general, increasing water stress resulted in poorer recovery for both salinity and drought simulation. Recovery varied across the experiments with 17.5% to saline treatment and 21.9% to drought simulation. Recovery from the salt solution concentration of 600 mM was lower than other concentrations, indicating levels were toxic ($p < 0.05$). Simulated drought presented similar regeneration among treatments.

Discussion

Plant growth and survival in desert and coastal systems are mostly affected by water stress from drought, salinity, or both (Chen and Jiang 2010). Seed is the life stage that is most resistant to extreme environmental stresses. Population persistence in extreme

habitats is highly dependent on the rate of successful seed germination and seedling establishment (Gutterman 1993). Therefore, selection of germplasm that is tolerant to salinity and moisture stress improves the economic viability of restoration projects (Ahmad 1999). Drought and salinity reduce the water potential of the substrate and consequently restrict water and nutrient uptake, also the saline stress may lead to cytotoxic effects (Lobet et al. 2014; Pessarakli 2014). Assessment of the intraspecific variation in tolerance to moisture stress is therefore important for identifying seed sources for anthropogenic restoration of desert and coastal ecosystems.

Seed traits of size, dormancy, and germination response to abiotic conditions exhibit variation among populations. This variation benefits species persistence in habitats where the timing of conditions suitable for seedling survival are unpredictable (Tavşanoğlu and Çatav 2012; Cochrane et al. 2015; Bhatt, Gairola, et al. 2020; Bhatt, Bhat, et al. 2020). Usually, large seeds have a higher survival advantage from seedling establishment to reproduction due to a higher reserve of nutrients (Metz et al. 2010). Habitat disturbance causes plants to allocate proportionally more resources to reproduction (Grime 1993). The higher seed mass of *H. salicornicum* growing at Kabd, the most disturbed site, might, therefore, be a response to this disturbance, producing seedlings that are more resistant to drought and herbivory during this early stage of development (Leishman 2001; Moles and Westoby 2004). However, it might also be a response to sandy habitats that are characterized by low water-holding capacity and poor nutrient supply (Matar, Torrent, and Ryan 1992). In the present study, soil pH and EC appeared to influence seed mass. Generally, a non-optimal pH and high soil EC affect plant growth and reproductive performances by reducing their nutrient uptake ability and use efficiency (Ramírez-Rodríguez, López-Bucio, and Herrera-Estrella 2005; Fageria, Gheyi, and Moreira 2011). Therefore, we assumed that the plant growing at high stress habitat might allocate more resources to the reproduction and hence the seeds of Kabd population have a higher seed mass. In addition to the larger seed size, the Kabd population also exhibited greater germination percentage. The relationship between seed size and tolerance to drought and salinity during germination has been reported in other desert species (Whitmore 2000; El-Keblawy, Bhatt, and Gairola 2014; Bhatt and Santo 2016).

Variation in maternal environmental conditions such as climate, soil moisture, and soil nutrient concentrations influence seed mass (Quesada, Winsor, and Stephenson 1996; Tremayne and Richards 2000). Climate in the present study was similar for each population, but variation in moisture, soil type, and genetics of each population could influence seed mass (Aarssen and Burton 1990; Ortman et al. 2016). Therefore, significant variation in germination between three spatially close populations of *H. salicornicum* in response to light, salinity and drought tolerance could be due to the difference in edaphic selective pressures and disturbance, which over time lead to localized adaptations (McElroy et al., 2004; Oduor, Leimu, and Kleunen 2016).

Any variation in edaphic factors influences germination, growth and reproduction (Saisho, Takumi, and Matsuoka 2016). Competition and edaphic factors are more influential at smaller spatial scales, while climatic factors are more influential among regions (Snaydon and Davies 1982; Macel et al. 2007; Becker et al. 2008; Carta et al. 2016). Intraspecific variation in seed mass and germination in relatively close populations could be linked to the survival strategy (Gimenez-Benavides, Escudero, and

Perez-Garcia 2005). Further research is needed to identify whether genetic selection or maternal environment is more influential. Different populations of *H. salicornicum* responded differently in their sensitivity to light during germination. Kabd seeds that were not exposed to water stress germinated in higher proportion when exposed to light, but when exposed to 600 mM salinity the effect was reversed. Liya seed germination was similar across light treatments, whereas Mutla seeds germinated in higher proportion in darkness than in light. The variation in light requirement among different populations indicates that some care is needed in optimizing the use of each seed batch during restoration work. Previous studies of the species have also produced ambivalent results; seeds from Egypt and Kuwait germinated in higher proportion in darkness (Hammouda and Bakr 1969; Brown and Al-Mazrooei 2001), while seeds from the United Arab Emirates and Qatar germinated in higher proportion in light than in darkness (El-Keblawy and Al-Shamsi 2008; Bhatt, Phartyal, and Nicholas 2016). These results indicate that variations in maternal habitat conditions even at spatially close population can affect the light requirement during germination stage and, hence, broader study is needed to identify the source of variation and care should be taken before interpreting the germination requirements in wild species using single population.

Inter-population variability in salinity and drought tolerance of *H. salicornicum* seeds, and germination recovery after alleviating these stresses could have a survival advantage in desert habitats by reducing the risk of synchronizing germination. It might also explain the ability of *H. salicornicum* to grow in a wide range of arid habitats across the Arabian desert. The ability of *H. salicornicum* seeds to germinate at high salinity might be the adaptation strategy that provide them opportunities to ensure their population persistence under high-salt environments. Moreover, halophytic production and accumulation of osmoregulating substances (e.g. Na⁺, proline, betaine, polyols, soluble sugars, seed starch) may reduce the water potential of seeds and hence facilitate rapid germination under saline solutions (Song and Wang 2015; Zhao et al. 2018).

Some germination occurred at the highest studied salinity level of 600 mM NaCl in all the studied populations. This ranged from 27.7% for Mutla seeds to 52.9% for Kabd seeds. In the present study, heavier seeds of the Kabd population showed significantly higher germination at high salinity (600 mM NaCl) compared to the other populations ($p < 0.05$). Therefore, variation in salinity tolerance during germination between the population could be linked to the seed mass. Differences in salinity tolerance during germination were observed among populations of different species such as *Anabasis setifera*, *Rouya polygama*, *Spartina patens* and *Suaeda aegyptiaca* (Santo et al. 2014; El-Keblawy, Gairola, and Bhatt 2016; El-Keblawy et al. 2017). Increasing NaCl concentration progressively inhibited seed germination of *H. salicornicum* irrespective of the population. However, germination response to light regime in saline conditions seems to be population-dependent, because the seeds from Kabd showed germination inhibition in darkness at concentrations of NaCl up to 200 mM, but above 400 mM germination inhibition was higher in the light treatment. These differences among populations in the interaction of light and NaCl treatments on germination indicate that light requirement may be environmentally influenced (Gutterman, Kamenetsky, and Van Rooyen 1995).

Drought simulation (PEG treatments) reduced the germination percentage of *H. salicornicum* to a larger extent than salinity, particularly at lower water potentials (-0.9 MPa). Seeds from the Kabd population appear to be significantly more drought tolerant, which could be attributed to their heavier mass. In deserts, low soil moisture is one of the main constraints for germination and seedling establishment. Lighter seeds are more likely to be rendered inviable than heavier seeds due to desiccation. Therefore, higher germination percentage from heavier seeds may be beneficial in establishing plants under dry soil conditions (Mian and Nafziger 1994). Higher germination percentages were recorded for seeds incubated in continuous darkness in all populations. In previous studies, the osmotic treatment changed the involvement of phytochrome in the inhibition of germination (Thanos and Mitrakos 1979; Freitas and Takaki 2000). Previous studies concluded that the effect of salinity on germination is primarily osmotic stress, whereas other life stages are affected in higher proportion by specific ion toxicities (Ungar 1978; Zhang et al. 2015). Thus, PEG simulates the osmotic stress of salinity more closely at germination than at other life stages. The 400 mM solution water potential was approximately -1.82 MPa, twice that of the PEG solution, but the effects were milder. This may be related to the species adaptation to use sodium ions to increase water uptake (Sun 2002; Bakhshandeh et al. 2020).

Non-germinated seeds of *H. salicornicum* were able to recover their germinability after they were transferred from NaCl and PEG solutions to distilled water. Germination recovery gradually decreased with increasing NaCl concentration, but seeds retained germinability up to 400 mM NaCl concentration. However, higher concentration of NaCl (above 400 mM) can damage the seeds via a toxic effect of NaCl. A similar effect was observed for *Lachnoloma lehmannii* seeds at 600 mM (Mamut et al. 2019). The germination recovery in PEG was gradually increased with increasing PEG depending on the population. *Haloxylon salicornicum* seeds recovered germinability after high osmotic potentials in PEG, indicating adaptation to water stressed, moderately saline habitats of the Arabian desert. That different populations produce seeds with different germination and recovery responses after alleviating the osmotic stress may be important for species survival in this harsh habitat.

Haloxylon salicornicum seeds are well adapted to drought and saline conditions and may recover immediately after drought or salinity stress are alleviated via rainfall. In deserts, *H. salicornicum* seeds remain dormant during summer and germinate in winter (November and March) when the chances of rainfall are high (Omar, Al-Mutawa, and Zaman 2007). This fast germination response to fresh water might be useful for utilizing even the short period of water availability after rainfall that could ensure rapid seedling establishment.

Understanding of inter-population variability can strengthen our understanding of the mechanisms that regulate seed germination and how they relate to seed provenance. In the present study, the inter-population variability in seed mass, light requirement, salinity and drought tolerance during germination could be due to habitat variations, whether edaphic, maternal condition, or level of disturbance. Our findings indicate that revegetation success in the species will be influenced by the maternal seed source. Care should, therefore, be taken when studying germination of a species from a single population. Origin of plant material should be factored in to the handling of seeds during

desert restoration. Further research is needed to identify whether this is due to genetic variation or edaphic influences on the maternal plant. This interpopulation variability could be useful for screening the best seed sources for achieving maximum productivity in restoration programs and for conservation purposes. Therefore, we recommend that seeds with relatively high seed mass be targeted to improve restoration efficiency since large seeds have the highest ability to face drought and salinity stress.

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