Seed Science Research

cambridge.org/ssr

Seed mass, dormancy and germinability variation among maternal plants of four Arabian halophytes

Arvind Bhatt[1]*, David J Gallacher[2], Alfredo Jarma-Orozco[3] and Marcelo F. Pompelli[3]*

[1]Lushan Botanical Garden, Chinese Academy of Science, Jiujiang, China; [2]Drought Resilience Adoption & Innovation Hub, Charles Darwin University, Casuarina, NT 0810, Australia and [3]Facultad de Ciencias Agricolas, Universidad de Córdoba, Montería, Córdoba, Colombia

Research Paper

Cite this article: Bhatt A, Gallacher DJ, Jarma-Orozco A, Pompelli MF (2022). Seed mass, dormancy and germinability variation among maternal plants of four Arabian halophytes. *Seed Science Research* **32**, 53–61. https://doi.org/10.1017/S0960258522000083

Received: 30 October 2020
Accepted: 18 January 2022

Keywords:
germination parameters; mean germination time; principal component analysis; rehabilitation; seed weight; synchrony

***Authors for Correspondence**:
Marcelo F. Pompelli,
E-mail: marcelo@fca.edu.br;
Arvind Bhatt,
E-mail: drbhatt79@gmail.com

Abstract

Coastal desert vegetation of the Arabian Peninsula is almost entirely dominated by halophytes. Natural populations provide a genetic resource for ecological remediation and may also have direct economic value. High intrapopulation variation of seed traits is presumed to increase population persistence in the unpredictable climatic conditions of this hyper-arid desert. We investigated whether intrapopulation variation of seed mass, dormancy and germinability of four species was attributable to maternal individuals. *Arthrocnemum macrostachyum*, *Halothamnus iraquensis*, *Haloxylon salicornicum* and *Seidlitzia rosmarinus* are commonly distributed Arabian halophytes with differing seed weight variation. All species exhibited a higher germination when exposed daily to 12 h light, compared to seeds in darkness. A higher germination was correlated with a shorter germination time. For *H. iraquensis* and *S. rosmarinus*, a shorter germination time was negatively correlated with germination synchrony. *H. salicornicum* showed the highest intrapopulation variation of seed traits, followed by *A. macrostachyum*, *S. rosmarinus* and *H. iraqensis*. We found that individuals within populations of all the studied species showed variability in germination but the extent of variation was species-specific. The variation in seed mass and germination among the individuals of the studied species may facilitate a temporal distribution of germination, which may reduce the risk of seed bank exhaustion. The results of this study could assist conservation and management by improving the efficiency of seed collection from wild populations of these species.

Introduction

Seed traits such as mass, dormancy and germination are crucial to plant fitness (Baskin and Baskin, 2014; Gremer and Venable, 2014). Interpopulation variability in seed traits is common and related to differences in climate, geography and habitat (Tautenhahn et al., 2008; Bu et al., 2009; Saatkamp et al., 2019). Variability of seed traits also exists at the intrapopulation level where it is considered a bet-hedging strategy for enabling the species to produce numerous seeds optimized for different climatic conditions (Mitchell et al., 2017). This intrapopulation variation increases the probability of generational survival in an unpredictable or changing environment (Slatkin, 1974; Zhao et al., 2016). Coastal deserts frequently exhibit spatio-temporal variation in salinity and soil moisture (Castillo et al., 2000), hence environmental conditions for germination and seedling establishment are highly variable in time and space (Gremer and Venable, 2014; El-Keblawy et al., 2017). However, intrapopulation variation in germination of Arabian desert halophytes has received little attention. Studying intrapopulation variability of seed germination could improve our understanding of how desert halophyte species cope with high salinity and drought during seed germination.

Seed germination varies (1) within maternal individuals (Gutterman, 2000), (2) within populations (Narbona et al., 2006; Pérez-García, 2009; Santelices et al., 2017) and (3) among populations (Nordborg and Bergelson, 1999). Latitude, altitude, temperature, light, moisture, soil nutrients and habitat disturbance have been linked to interpopulation variation of seed dormancy and germination (Baskin and Baskin, 2014; El-Keblawy et al., 2017). Intrapopulation variation of seed dormancy enables temporal distribution of germination, which is critical for population persistence in the unpredictable climates of arid zones.

Most plant species of the Arabian desert germinate during winter, when temperature is lower and rainfall events more likely (Böer, 1997). Germination timing is strongly influenced by abiotic factors of light, temperature, plant-available moisture and salinity (El-Keblawy and Bhatt, 2015; Bhatt and Santo, 2016). Periods of sufficient moisture for germination are uncommon in arid systems. They are unpredictable in their occurrence and in whether the moisture will persist long enough for seedling establishment. Therefore, germination in these

Table 1. Seed collection and location details of selected species

Species	Location	GPS Coordinates	Associated species
Arthrocnemum macrostachyum	Julia	28°54′15.1″N 48°13′12.3″E	*Suaeda vermiculata, Aeluropus lagopoides, Tamarix species*
Halothamnus iraqensis	Julia	28°54′15.1″N 48°13′12.3″E	*Salsola imbricata, Pennisetum divisum, Deverra triradiata*
Haloxylon salicornicum	Mutla	29°24′21.8″N 47°41′42.8″E	*Cyperus conglomeratus, Zygophyllum qatarense, Tribulus species*
Seidlitzia rosmarinus	Julia	28°52′57.2″N 48°15′44.6″E	*Suaeda vermiculata, Aeluropus lagopoides, Tamarix species*

arid systems is regulated to respond to multiple abiotic factors (Ashraf and Foolad, 2005; Bewley et al., 2013; Bhatt et al., 2019a,c, 2020b).

Halophytic species can be used in phytoremediation of saline-sodic or salt-affected land, thus extracting salt to biomass, establishing plant cover and lowering a saline water table (Panta et al., 2014). The ability of halophytes to accumulate salt in shoot systems is dependent on each species' adaptive strategies (Graifenberg et al., 2003; Tester and Davenport, 2003; Rabhi et al., 2010). In field and glasshouse trials, several halophytic species absorbed the equivalent of 2 to 6 tonnes salt ha^{-1} yr^{-1} (Panta et al., 2014). Approximately 140 halophytic taxa from 31 plant families have been recorded on the Arabian Peninsula, which constitutes about 4% of the total flora (Ghazanfar et al., 2014). Halophytes are used for medicine, fodder, phytoremediation, biofuel and ornamentals (El Shaer, 2010; Qasim et al., 2010; Rabhi et al., 2010; Abideen et al., 2011; Manousaki and Kalogerakis, 2011; Ali et al., 2012; Gairola et al., 2015; Bañuelos et al., 2018). Describing and conserving this genetic resource should be a priority. Abiotic factors such as temperature, light, salinity and their interactions have been shown to have an effect of germination in many halophytic species, including *Anabasis setifera*, *Atriplex canescens*, *Halocnmum strobilaceum*, *Halothamnus iraqensis*, *Haloxylon salicornicum*, *Halopeplis perfoliata*, *Limonium stocksii*, *Salsola vermiculata*, *Salsola schweinfurthii*, *Suaeda aegyptiaca* and *Seidlitzia rosmarinus* (Zia and Khan, 2004; El-Keblawy and Bhatt, 2015; Bhatt and Santo, 2016). Interpopulation differences in seed dormancy and germination has been identified in *Anabasis setifera* (El-Keblawy et al., 2016a,b), *Limonium avei* (Santo et al., 2017), *Salsola drummondii* (Elnaggar et al., 2019), *Suaeda aegyptiaca* (El-Keblawy et al., 2017) and *Suaeda vermiculata* (El-Keblawy et al., 2018). Interpopulation variation has been attributed to differences in both population genetics and maternal environment (Baloch et al., 2001; Donohue et al., 2005; Narbona et al., 2006), although these studies have not used genotype by environment trial designs, instead relying on studies of maternal plants grown in similar microclimates and seeds produced during similar periods.

Successful seedling establishment is dependent of rainfalll in a rain event, and on the occurrence of later rain events that extend plant-available moisture levels through the growing season. Intrapopulation variation of dormancy and germination enables the population to spread germination across multiple rain events in the season if they occur. Temporal distribution of germination can also reduce competition among seedlings, both inter- and intraspecific, for limited resources (Brändle et al., 2003; Donohue et al., 2010). In contrast to the many studies of interpopulation variation, the authors know of no studies on germination and dormancy variation of Arabian halophyte seeds obtained from different maternal plants within a population. This information may have practical use in knowing whether it is beneficial to select seeds from maternal individuals, or whether population selection is sufficient. Thus, the aim of the present study was to identify if maternal seed source within a population influences (1) seed weight, dormancy and germination, (2) light and temperature requirement for germination and (3) if the extent of intrapopulation variation differs among species.

Materials and methods

Species

Arthrocnemum macrostachyum, *H. iraqensis*, *H. salicornicum* and *S. rosmarinus* each have potential for rehabilitating degraded desert rangelands and salt-affected soils. All are perennial branched shrubs belonging to Amaranthaceae. They are commonly found in Arabian coastal deserts (Ghazanfar, 2006; Freitag et al., 2009), are highly resistant to salinity and contribute to soil stabilization (Huang et al., 2003; Omar et al., 2007; Amiraslani and Dragovich, 2011; Mahmoodi et al., 2013). The species are also used for fodder, medicine, fuel wood and as windbreaks (Ashraf et al., 2012; Bidak et al., 2015). *Haloxylon salicornicum* was shortlisted as having potential for desert landscaping, along with other native species (Phondani et al., 2016), and *A. macrostachyum* was identified as a suitable species for phytoremediation (Redondo-Gómez et al., 2010).

Seed collection

Mature seeds were collected from ten maternal plants per species, December 2018 in Kuwait (Table 1). Maternal plants were at least 5 m apart but otherwise selected randomly along a 180 to 200 m line transect. Seeds were cleaned immediately after collection and germinated within one week. Seed mass was determined by weighing three 25-seed replicates from each maternal plant of each species using an analytical balance (Sartorius Analytical Balance mod. ENTRIS224-1S, Bradford, MA, USA; accurate to 0.1 mg).

Germination

Four 25-seed replicates were germinated for each combination of 4 species, 10 plants and 2 photoperiod regimes. Seeds for each replicate were placed in 9 cm diameter Petri dishes containing two sheets of filter paper (Whatman No. 1). Replicates were placed in incubators set at night/day 12/12 h temperature of 15/20°C for photoperiods of either 0 (dark) or 12 (light) hours light per day from a 50 W white fluorescent lamp (Sylvania Led T5 Tubes, Sylvania Portugal Lda, Lisboa, Portugal). This temperature regime has previously been found suitable for germination of this species in natural conditions. Petri dishes of dark replicates were wrapped in two layers of aluminium foil. Germination was defined as the protrusion of a radicle by ≥2 mm through the external integument (Allen and Alvarez, 2020). Germinated seeds of the light treatments were counted daily, and dark treatments were assessed at the end of the experiment.

Data analysis

A nested analysis of variance (ANOVA) with species as a fixed factor and maternal plants as random and nested within species was performed to assess whether seed weight and germination traits differed among species. A one-way ANOVA was then also performed for each species, with maternal plant as the fixed factor, to determine the species-specific influence of maternal plant for germination in light, germination in darkness, mean germination time, SYN uncertainty and seed weight. Correlation among seed weight and germination traits was determined using Pearson correlations. Analyses were performed using SPSS 26 (IBM Corporation, Armonk, NY, USA) and a Bonferroni correction was applied to avoid increased risk of Type I error.

A nested analysis of variance (ANOVA) was performed to assess the influence of the maternal plant and species on seed weight and germination, with species as a fixed factor and maternal plant as random and nested within species. A one-way ANOVA was then performed for each species to determine the species-specific influence of maternal plant on germination in light, germination in darkness, mean germination time, synchrony, uncertainty and seed weight. Rand Index was used to measure the similarity between data groupings and Euclidian distance for principal components analysis using Minitab 18.1.0.0 (Minitab LLC, Pennsylvania State University, PA, USA). Results were considered significant when $P \leq 0.01$. Principal component analysis was conducted on all germination features using Minitab. The summary function of principal components analysis was used to calculate the proportion of the variance of each parameter explained by each principal component. For hierarchical clustering, Pearson's correlations were used to compare the similarities between the studied species using the 'cor' function on the Sigmaplot v. 14.0 (Systat Software Inc., Chicago, USA) and its Excel package with the complete linkage method and the Euclidean distance measure were used for hierarchical clustering with the R index in the Minitab.

Results

All species produced a higher germination percentage in light than in darkness, with the difference ranging from 7.2% in *S. rosmarinus* to 9.2% in *H. salicornicum* (Table 2). Seed germination varied strongly among maternal plants of *H. salicornicum* in both light and dark treatments ($P < 0.0001$). Seed germination among maternal plants of *A. macrostachyum* was not significant after application of the Bonferroni correction ($P = 0.0189$) and was not significant for the other two species (Table 2).

Table 2. Influence of the maternal plant and species on seed weight and germination

	Germination in light (%)				Germination in darkness (%)				Mean germination time (days)			
	Mean	SE	P_2		Mean	SE	P_2		Mean	SE	P_2	
Species												
Arthrocnemum macrostachyum	90.1	0.9	0.0189	**	83.7	0.8	0.0144	*	2.71	0.03	0.0058	**
Halothamnus iraquensis	96.1	0.9	0.5098		88.4	0.8	0.3123		1.31	0.03	3.1×10^{-14}	***
Haloxylon salicornicum	86.3	0.9	1.7×10^{-12}	***	79.3	0.8	1.3×10^{-13}	***	1.89	0.03	1.6×10^{-6}	***
Seidlitzia rosmarinus	89.9	0.9	0.1487		83.9	0.8	0.1298		2.45	0.03	2.0×10^{-4}	***
P_1												
Species			0.0300	*			0.0542				8.8×10^{-15}	***
Maternal plant within species			3.9×10^{-15}	***			1.1×10^{-17}	***			6.6×10^{-15}	***

	Seed weight (g)				Synchrony				Uncertainty (bits)			
	Mean	SE	P_2		Mean	SE	P_2		Mean	SE	P_2	
Species												
Arthrocnemum macrostachyum	0.012	0.001	0.0120	*	0.340	0.01	0.1686		1.641	0.03	0.2021	
Halothamnus iraquensis	0.164	0.001	1.8×10^{-9}	***	0.651	0.01	3.8×10^{-9}	***	0.792	0.03	1.1×10^{-7}	***
Haloxylon salicornicum	0.116	0.001	2.7×10^{-9}	***	0.584	0.01	9.6×10^{-10}	***	0.959	0.03	7.7×10^{-12}	***
Seidlitzia rosmarinus	0.072	0.001	1.4×10^{-11}	***	0.330	0.01	2.0×10^{-4}	***	1.838	0.03	5.4×10^{-6}	***
P_1												
Species			8.2×10^{-20}	***			1.4×10^{-7}	***			2.3×10^{-9}	***
Maternal plant within species			3.1×10^{-33}	***			3.7×10^{-25}	***			2.5×10^{-20}	***

Analyses were a nested ANOVA with species as fixed, and maternal plant as random and nested within species (P_1), and a one-way ANOVA of maternal plants within each species (P_2). The Bonferroni correction makes values of $\alpha < 1.67 \times 10^{-3}$ non-significant.
$P > 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***).

Mean germination time (MGT) varied strongly among maternal plants of *H. iraquensis* ($P < 0.0001$), *H. salicornicum* ($P < 0.0001$) and *S. rosmarinus* ($P < 0.0001$), and significantly affected *A. macrosctachyum* ($P = 0.0058$). A maternal effect on seed weight, synchrony and uncertainty was also highly significant in all species except *S. rosmarinus* (Table 2).

Germination percentage in light and dark treatments were strongly correlated for *H. salicornicum*, *S. rosmarinus* and *A. macrostachym* ($r = 0.965$, 0.881, 0.873, respectively), but not significant for *H. iraquensis* (Table 3). MGT was negatively correlated with germination in light for *H. salicornicum* ($r = −0.720$) and for germination in both light ($r = −0.650$) and darkness ($r = −0.710$) for *A. macrostachym* (Table 3). However, these correlations were not significant after application of the Bonferroni correction. Likewise, seed weight was negatively correlated with germination under darkness (−0.655) in *H. iraquensis,* only if the Bonferroni correction was not used. MGT was strongly correlated with both synchrony and uncertainty for *H. iraquensis* (−0.906, and 0.914, respectively) and *S. rosmarinus* (−0.891, and 0.943, respectively) but not for the other species (Table 3).

Maternal plants of *H. salicornicum* were placed in a distinctly uniform cluster by PCA, separated from plants of other species (Fig. 1). Maternal plants of *H. iraquensis* also formed a distinct cluster with 70% similarity, which overlapped with a cluster of >71% similarity formed by maternal plants of *A. macrostachyum* and *S. rosmarinus*. The sum of PC1 and PC2 comprised 77.6% of the observed variation. Factors separating plant species in the PCA are demonstrated in Fig. 1B,C. Germination in darkness (0.659) and in light (0.644) had a strong positive effect on clustering, while synchrony had a strong negative effect (−0.560). Uncertainty (0.557), and MGT (0.513), had a similar positive influence on species separation. The strength with which each feature promoted clustering is distinct, while germination (both 12/12 h of light/dark cycles or complete darkness), seed weight and synchrony promoted germination (Fig. 1B,C).

Discussion

Usually, seeds collected from different individuals from any particular population are mixed together to test their germination response, which provides an average response at the population level. However, intrapopulation variability in the germination response is well known (Martin et al., 1995; Schütz and Milberg, 1997; Pérez-García, 2009). Intrapopulation variability in seed germination could be mechanism to overcome the risk of failed recruitment against unpredictable environmental conditions such as drought and salinity. This variability enables a species to deal with uncertainty via asynchronized germination. The different species showed differences in intrapopulation variability, indicating that each species has a different strategy for coping with the extreme coastal desert conditions of high salinity and drought.

Seeds of all the studied species matured at a similar time, hence microclimatic variation of collection sites was minimized. Intrapopulation variation of germination response among individuals could be due to genetic or maternal plant effects (Baloch et al., 2001; Donohue et al., 2005). The existence of variability in germination within the population of selected species could be helpful in spreading their germination in time and space because the favourable conditions for germination and seedling establishment are spatiotemporally highly variable in arid deserts (Gremer and Venable, 2014; El-Keblawy et al., 2017). This variability would ensure that seeds of these species will germinate during different times of the growing season between December to March when the temperature is low and the chances of rainfall are higher during this time of year under Arabian desert conditions (Böer, 1997), that can leach out the salinity.

Variability in seed germinability improves overall reproductive success in unpredictable desert conditions. Intrapopulation seed size variation affects seed dispersal, germination, seedling emergence and establishment (Hawke and Maun, 1989; Baskin and Baskin, 2014). The studied species exhibited differences in the amount of seed mass variation within maternal individuals. Factors such as maternal condition, microenvironment and genotype might be responsible for variability of seed size (weight), dormancy and germination within individuals of the same population (Platenkamp and Shaw, 1993; Benech-Arnold et al., 2000; Galloway, 2002). High inter-annual climatic variability and inherent water-limitations are usually a strong determiner of seed germination and seedling survival in arid conditions (Chesson et al., 2004; Torres-Martinez et al., 2016). Maintaining variation in seed mass and germination distributes germination throughout the winter season (October to March) when chances of rainfall are high. This benefits population persistence and reduces the risk of a local extinction event (Levy et al., 2012; Mitchell et al., 2017) in this environment of harsh and spatiotemporally unpredictable conditions for life. In other words, we can speculate that the higher the MGT and the lower the SYN, the greater the reproductive chance of the species, exceptionally in hostile environments such as deserts (Pompelli et al., 2010; Miranda et al., 2011; Moncaleano-Escandon et al., 2013; Lozano-Isla et al., 2018; Bhatt et al., 2019c, 2020a). Among the studied species, *H. salicornicum* showed the highest variation in seed germinability within the individuals of the same population followed by *A. macrostachyum*, *S. rosmarinus* and *H. iraqensis*. This highest variation in seed germinability within the individuals is due to high uncertainty in germination and high synchrony. For the sake of clarity, the existence of such variation in seed germination could be related to their reproductive strategy to survive under harsh condition by spreading their germination throughout the winter season. However, the interspecific variation in germination among the studied species might be helpful in allowing their coexistence in same community.

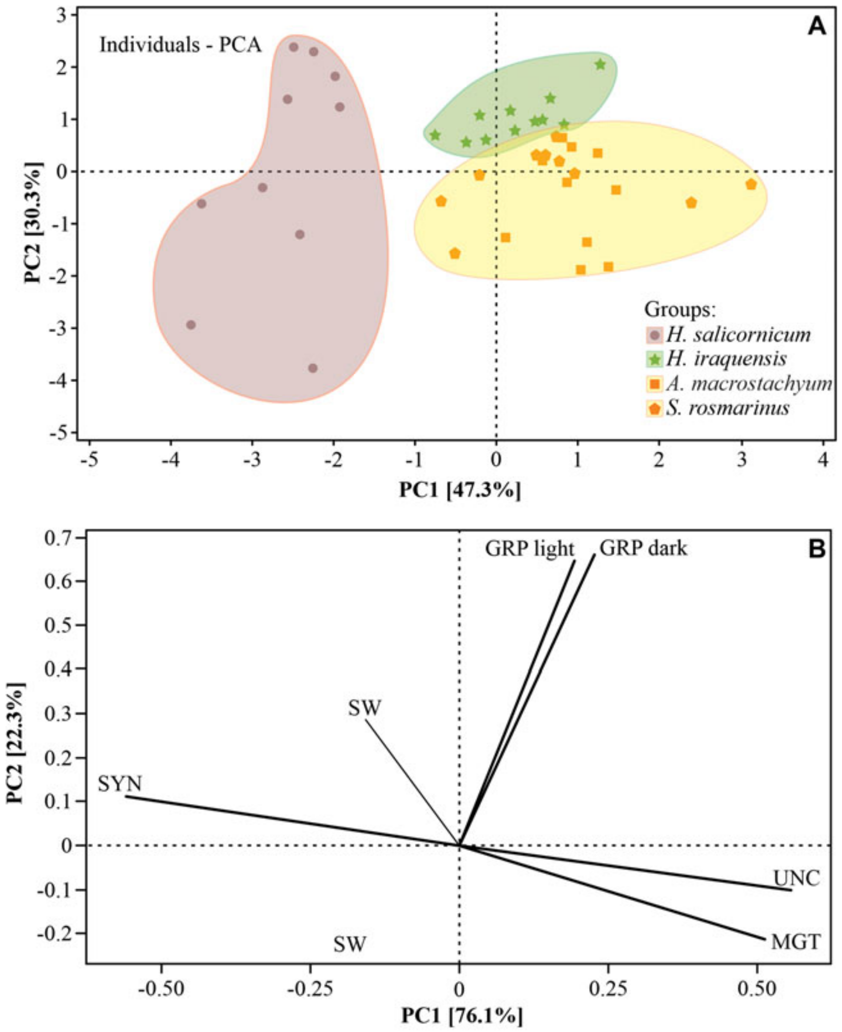
Overall, freshly collected seeds of all the selected species showed high germination percentages and showed similar germination patterns. Higher germination response of freshly collected seeds have been reported previously for these species, believed to be an adaptation strategy that coincides with the rainfall patterns in the Arabian desert (Bhatt et al., 2019a,b,c). In the Arabian desert, most halophytes mature during November–December when temperature is low, and the chances of rainfall are high. This might be how these species have evolved to prevent seedling recruitment in summer under such extreme conditions.

Seed weight did not influence seed germination in light or darkness of any species. *H. iraquensis* exhibited a significant correlation between seed weight and germination in darkness ($P = 0.0399$) but this was non-significant after application of the Bonferroni correction (Table 3). Seed size ranged from 2.8 mg in *A. macrostachyum* to 48.0 mg in *H. iraquensis*. Small seeds may require light to germinate, since endosperm reserves are sufficient for only a short epicotyl elongation to the soil surface (Milberg et al., 2000). However, intrapopulation variation in seed weight did not influence light requirement for germination in this or a similar study (Rojas-Aréchiga et al., 2013). All species exhibited higher germination in light but nevertheless germinated well in darkness,

Table 3. Pearson correlations (r) and their significance ($\alpha = 0.05$) of traits measured on ten plants per species

Germination in light	Germination in darkness	Mean germ. time	Synchrony	Uncertainty	Seed weight	*Arthrocnemum macrostachyum*			*Halothamnus iraquensis*			*Haloxylon salicornicum*			*Seidlitzia rosmarinus*		
						r	P		r	P		r	P		r	P	
x	x					0.873	0.0010	***	0.570	0.0852		0.965	6.3×10^{-6}	***	0.881	7.5×10^{-4}	***
x		x				−0.650	0.0418	*	−0.446	0.1967		−0.720	0.0189	*	0.220	0.5418	
x			x			0.025	0.9445		0.523	0.1205		0.260	0.4682		−0.447	0.1954	
x				x		−0.088	0.8098		−0.562	0.0910		−0.367	0.2974		0.445	0.1972	
x					x	0.286	0.4228		−0.467	0.1738		0.397	0.2557		−0.027	0.9417	
	x	x				−0.710	0.0215	*	−0.298	0.4029		−0.597	0.0683		0.352	0.3187	
	x		x			0.464	0.1767		0.566	0.0878		0.137	0.7051		−0.611	0.0604	
	x			x		−0.509	0.1328		−0.560	0.0922		−0.231	0.5210		0.589	0.0735	
	x				x	0.279	0.4347		−0.655	0.0399	*	0.487	0.1531		0.132	0.7170	
		x	x			−0.319	0.3688		−0.906	3.0×10^{-4}	***	−0.308	0.3874		−0.891	5.3×10^{-4}	***
		x		x		0.396	0.2572		0.914	2.2×10^{-4}	***	0.455	0.1860		0.943	4.3×10^{-5}	***
		x			x	−0.619	0.0562		−0.108	0.7670		0.168	0.6419		0.022	0.9518	
			x	x		−0.984	2.8×10^{-7}	***	−0.994	7.4×10^{-9}	***	−0.986	1.6×10^{-7}	***	−0.979	8.4×10^{-7}	***
			x		x	0.285	0.4248		−0.071	0.8458		−0.080	0.8251		−0.035	0.9225	
				x	x	−0.395	0.2591		0.082	0.8212		0.104	0.7752		0.008	0.9822	

The Bonferroni correction makes values of $\alpha < 8.3 \times 10^{-4}$ non-significant.
$P > 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***).



C

	Autovectors					
Variable	PC1	PC2	PC3	PC4	PC5	PC6
GRP light	0.193	0.644	0.297	0.004	-0.674	0.069
GRP dark	0.228	0.659	0.050	0.034	0.709	-0.085
MGT	0.513	-0.217	0.108	0.815	0.004	0.122
SYN	-0.560	0.111	0.186	0.456	-0.037	-0.656
UNC	0.557	-0.102	-0.285	-0.231	-0.140	-0.725
SW	-0.157	0.284	-0.884	0.273	-0.149	0.129

Fig. 1. (A) Principal component analysis to *A. macrostachyum* (square), *H. iraquensis* (star), *H. salicornicum* (circles) and *S. rosmarinus* (pentagon) showing the spatial distribution of each plant species. The large circles represent the three clusters formed by the Euclidean distance method considering ~70% of similarity. (B) Loading plot graph showing the direction and length of the lines are directly proportional to variables importance in separating groups. PC1, principal component 1; PC2, principal component 2. Abbreviations: GRP, germination percentage; MGT, mean germination time; SYN, synchrony; UNC, uncertainty; SW, seed weight.

indicating a preference for non-burial but ability to cope with it (Milberg et al., 2000). The high germination percentages indicate an absence of dormancy at the time of seed maturation, as has been reported for other Arabian halophytes (Bhatt et al., 2016; El-Keblawy et al., 2017; Ghazanfar et al., 2019). Seeds are ready to germinate immediately if there is sufficient moisture present.

Low germination synchrony is common in xeric plant species and has been linked to desert population persistence (Song et al., 2012; Lozano-Isla et al., 2018; Nimac et al., 2018; Bhatt et al., 2020a). In the present study, individuals within the population showed significant variation in MGT, depending on the species. The variation in mean germination timing within the individuals of the same population of selected species might be advantageous because it can limit the synchronous germination and ultimately reduce the risk of germination failure. This strategy may benefit the species through preventing local extinction when conditions suitable for seedling survival do not persist (Tielbörger et al., 2012). Our results are in accordance with the results obtained for other species such as *Ceratonia siliqua*, *Euphorbia nicaeensis*, *Nothofagus glauca* and *Tuberaria macrosepala* (Narbona et al., 2006; Pérez-García, 2009; Zaidi et al., 2010; Santelices et al., 2017).

Among the studied species, seeds of *H. iraqensis* germinated quickly (within 3 d) followed by *H. salicornicum* (5 d), *S. rosmarinus* (7 d) and *A. macrostachyum* (8 d). The fast germination of *H. iraqensis* and *H. salicornicum* indicates that seeds of these species might cope with low and unpredictable rainfall. A similar pattern was observed in other Arabian halophytes, including *Salsola rubescens* (El-Keblawy et al., 2013), *Halocnemum strobilaceum* and *Halopeplis perfoliate* (El-Keblawy and Bhatt, 2015), *Atriplex canescens* (Bhatt and Santo, 2016), *Salsola schweinfurthii* (Bhatt et al., 2016), *Salsola vermiculata* (Bhatt et al., 2017b) and *Haloxylon salicornicum* (Bhatt et al., 2017a). In the present study, intrapopulation variation of MGT from a day to a week after rainfall could be a complementary adaptive strategy with ecological significance.

A high seed germination after a light rainfall event is risky, since germinated seeds might not have sufficient moisture to ensure seedling survival. In this study, MGT variation was low in *H. iraquensis* (1.3–1.9 d) and *S. rosmarinus* (2.1–3.9 d).

Seeds of *H. iraqensis*, *H. salicornicum* and *S. rosmarinus* have winged perianths that assist their dispersal by wind (Burtt and Lewis, 1954) as well as regulate their dormancy status and soil seed bank dynamics (Bhatt et al., 2019c). The presence of these dispersal structures (winged perianths) provides a greater probability that some seeds will germinate in a suitable microhabitat, and thus improve population persistence under these extreme environmental conditions. Dispersal far from mother plants can also reduce intraspecific competition among seedlings. *A. macrostachyum* seeds lack dispersal structures and thus seedling density is greatest near maternal plants. Seeds are small and thus more easily buried, which might assist survival in habitats where surface salinity can vary greatly among periods between rainfall events. Uniformity of germination timing may be higher because seeds are too small to contain many mechanisms that disperse germination timing. However, *S. rosmarinus* and *H. iraquensis* also exhibited uniformity in germination timing despite being larger and containing wings for wind dispersal. *H. iraquensis* exhibited more intrapopulation variation than *S. rosmarinus*, since this species can form a semi-cluster, with characteristics that shade among these species. However, this finding occurs only when the analysis is made with a 75% cut base. If the cutting base is 70%, the two species form very distinct groups; a value that should be considered as important, especially if considered the high degree of disturbance of the environment where they occur. *H. salicornicum*, with an intermediate seed weight, was strongly represented as a distinct cluster and produced high germination percentages regardless of light exposure.

Using PCA enabled us to determine the main factors contributing to discrimination of genotypes. If there is high correlation between the measured and derived variables, then PCA may simplify evaluation indexes (Berner, 2011). In this study, species were organized into three large clusters, one of which encompassed two species. Thus *H. salicornicum* and *H. iraquensis* share characteristics that distinguish them from *A. macrostachyum* and *S. rosmarinum*, while the latter two are similar. The geospatial arrangement of *H. salicornicum* plants within the PCA indicates that this species has a very high amplitude among maternal plants within species. In contrast, *H. iraquensis* formed a single group but had less diversity among plants within species. The PCA also confirms that the high germination ability of *H. iraquensis* is the primary characteristic distinguishing it from other species, while synchrony, without acronym calculated in *H. salicornicum* is the primary characteristic for the separation of this species from the others. Some scholars recently used PCA as an auxiliary tool to improve the discussion about clustering of species and treatments, involving both seed germination (Bhatt et al., 2019c; Calone et al., 2020; Liu et al., 2020; Wang et al., 2020) and morphophysiological characteristics (dos Santos et al., 2019; Pompelli et al., 2019; Adar et al., 2020; Corte-Real et al., 2020; Prabu et al., 2020).

Conclusion

Intrapopulation variability in seed mass and germinability exist among the studied species, although the extent of variability depends on species. Seed weight (mass) showed no correlation with light requirement during germination. Seeds of all species germinated better in light but also could germinate in darkness at a lower percentage, indicating a preference for non-burial but ability to cope with it. Among the studied species, *A. macrostachyum* showed the lowest and *H. salicornicum* the greatest intrapopulation variability. The presence of intrapopulation variability can be considered as an adaptation strategy that can increase the reproductive success of these species in coastal Arabian deserts.

Acknowledgements. This work was made possible through financial support by Kuwait Institute for Scientific Research (KISR). We also thank the scholarships granted by the National Council for Scientific and Technological Development (CNPq Grants 163524/2017-3) to MFP. The first author thanks Flavio Lozano-Isla, PhD Student at the University of Hohenheim, Stuttgart, Germany for his valuable contributions to statistical analysis.

Author contributions. A.B. conceived and designed the experiments. A.B. and M.F.P. performed the experiments. A.B., D.J.G., A.J.O. and M.F.P. analysed the data. A.B., D.J.G., A.J.O. and M.F.P. wrote the manuscript. All authors contributed substantially and approved the final submission.

Conflicts of interest. All authors declare that they have no conflict of interest.

References

Abideen Z, Ansari R and Khan MA (2011) Halophytes: potential source of ligno-cellulosic biomass for ethanol production. *Biomass and Bioenergy* **35**, 1818–1822.

Adar M, Najih Y, Gouskir M, Chebak A, Mabrouki M and Bennouna A (2020) Three PV plants performance analysis using the principal component analysis method. *Energy* **207**, 118315.

Ali A, Iqbal N, Ali F and Afzal B (2012) *Alternanthera bettzickiana* (Regel) G. Nicholson, a potential halophytic ornamental plant: growth and physiological adaptations. *Flora – Morphology, Distribution, Functional Ecology of Plants* **207**, 318–321.

Allen E and Alvarez S (2020) *International rules for seed testing 2020*. Zürichstr, Bassersdorf, Switzerland, The International Seed Testing Association.

Amiraslani F and Dragovich D (2011) Combating desertification in Iran over the last 50 years: an overview of changing approaches. *Journal of Environmental Management* **92**, 1–13.

Ashraf M and Foolad MR (2005) Pre-sowing seed treatment: a shotgun approach to improve germination growth and crop yield under saline and none saline conditions. *Advances in Agronomy* **88**, 223–271.

Ashraf MA, Awan AR and Mahmood K (2012) Rehabilitation of saline ecosystems through cultivation of salt tolerant plants. *Pakistan Journal of Botany* **44**, 69–75.

Baloch HA, DiTommaso A and Watson AK (2001) Intrapopulation variation in *Abutilon theophrasti* seed mass and its relationship to seed germinability. *Seed Science Research* **11**, 335–343.

Bañuelos JA, Velázquez-Hernández I, Guerra-Balcázar M and Arjona N (2018) Production, characterization and evaluation of the energetic capability of bioethanol from Salicornia Bigelovii as a renewable energy source. *Renewable Energy* **123**, 125–134.

Baskin CC and Baskin JM (2014) *Seeds: ecology, biogeography and evolution of dormancy and germination* (2nd edn). London, Academic Press.

Benech-Arnold RL, Sanchez RA, Forcella F, Kruk B and Ghersa CM (2000) Environmental control of dormancy in weed seed soil banks. *Field and Crop Research* **67**, 105–122.

Berner D (2011) Size correction in biology: how reliable are approaches based on (common) principal component analysis? *Oecologia* **166**, 961–971.

Bewley JD, Bradford KJ, Hilhorst HWM and Nonogaki H (2013) *Seeds: physiology of development, germination and dormancy* (3rd edn). New York, Springer-Verlag.

Bhatt A and Santo A (2016) Germination and recovery of heteromorphic seeds of *Atriplex canescens* (Amaranthaceae) under increasing salinity. *Plant Ecology* **217**, 1069–1079.

Bhatt A, Pérez-García F, Carón MM and Gallacher D (2016) Germination response of *Salsola schweinfurthii* (Chenopodiaceae) to salinity and winged perianth removal. *Seed Science & Technology* **44**, 428–434.

Bhatt A, Phartyal SS and Nicholas A (2017a) Ecological role of distinct fruit-wing perianth color in synchronization of seed germination in *Haloxylon salicornicum*. *Plant Species Biology* **32**, 121–133.

Bhatt A, Phartyal SS, Phondani PC and Gallacher D (2017b) Perianth colour dimorphism is related to germination properties and salinity tolerance in *Salsola vermiculata* in the Arabian deserts. *Nordic Journal of Botany* **35**, 609–617.

Bhatt A, Bhat NR and Thomas MT (2019a) Germination behavior of *Seidlitzia rosmarinus* Boiss., a perennial halophyte of Arabian deserts. *Agricultural and Natural Resources* **53**, 348–354.

Bhatt A, Bhat NR, Murru V and Santo A (2019b) Eco-physiological studies on desert plants: germination of *Halothamnus iraqensis* Botsch. seeds under different conditions. *Journal of Arid Land* **11**, 75–85.

Bhatt A, Bhat NR, Lozano-Isla F, Gallacher D, Santo A, Batista-Silva W, Fernandes D and Pompelli MF (2019c) Germination asynchrony is increased by dual seed bank presence in two desert perennial halophytes. *Botany* **97**, 639–649.

Bhatt A, Batista-Silva W, Gallacher DJ and Pompelli MF (2020a) Germination of *Cenchrus ciliaris*, *Pennisetum divisum*, and *Panicum turgidum* are seasonally dependent. *Botany* **98**, 10.

Bhatt A, Bhat NR, Al-Nasser A, Caron MM and Santo A (2020b) Inter-population variabilities in seed mass and germination of *Panicum turgidum* and *Pennisetum divisum* on the desert of Kuwait. *Journal of Arid Land* **12**, 144–153.

Bidak LM, Kamal SA, Halmy MWA and Heneidy SZ (2015) Goods and services provided by native plants in desert ecosystems: examples from the northwestern coastal desert of Egypt. *Global Ecology and Conservation* **3**, 433–447.

Böer B (1997) An introduction to the climate of the United Arab Emirates. *Journal of Arid Environments* **35**, 3–16.

Brändle M, Stadler J, Klotz S and Brand R (2003) Distributional range size of weedy plant species correlated to germination patterns. *Ecology* **84**, 136–144.

Bu H, Du G, Chen X, Wang Y, Xu X and Liu K (2009) The evolutionary significance of seed germinability in an alpine meadow on the eastern Qinghai-Tibet Plateau. *Arctic, Antarctic, and Alpine Research* **41**, 97–102.

Burtt BL and Lewis P (1954) On the flora of Kuweit: III. *Kew Bulletin* **9**, 377–410.

Calone R, Sanoubar R, Noli E and Barbanti L (2020) Assessing *Salicornia europaea* tolerance to salinity at seed germination stage. *Agriculture* **10**, 29.

Castillo JM, Fernández-Baco L, Castellanos EM, Luque CJ, Figueroa ME and Davy AJ (2000) Lower limits of *Spartina densiflora* and *S. maritima* in a Mediterranean salt marsh determined by differential ecophysiological tolerances. *Journal of Ecology* **88**, 801–812.

Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplansky A and Weltzin JF (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Ecologia* **141**, 236–256.

Corte-Real N, Oliveira MS, Jarma-Orozco A, Fernandes D, dos Santos MA, Endres L, Calsa Jr T and Pompelli MF (2020) Comparative analysis of salt-induced changes in the leaves proteome of two contrasting *Jatropha curcas* genotypes. *Brazilian Journal of Development* **6**, 39845–39872.

Donohue K, Dorn LA, Griffith C, Schmitt J, Kim ES and Aguilera A (2005) Environmental and genetic influences on the germination of *Arabidopsis thaliana* in the field. *Evolution* **59**, 740–757.

Donohue K, Casas RRD, Burghardt L, Kovach K and Willis CG (2010) Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics* **41**, 293–319.

dos Santos OO, Mendes KR, Martins SVC, Batista-Silva W, dos Santos MA, Figueirôa JM, Souza ER, Fernandes D, Araújo WL and Pompelli MF (2019) Physiological parameters and plasticity as key factors to understand pioneer and late successional species in the Atlantic Rainforest. *Acta Physiologia Plantarum* **41**, 145.

El-Keblawy A and Bhatt A (2015) Aerial seed bank affects germination in two small-seeded halophytes in Arab Gulf desert. *Journal of Arid Environments* **117**, 10–17.

El-Keblawy A, Bhatt A and Gairola S (2013) Perianth colour affects germination behavior in the wind pollinated *Salsola rubescens* in the Arabian Deserts. *Botany* **92**, 69–75.

El-Keblawy A, Gairola S and Bhatt A (2016a) Maternal habitat affects germination requirements of *Anabasis setifera*, a succulent shrub of the Arabian deserts. *Acta Botanica Brasilica* **30**, 35–40.

El-Keblawy A, Gairola S and Bhatt A (2016b) Maternal salinity environment affects salt tolerance during germination in *Anabasis setifera*: a facultative desert halophyte. *Journal of Arid Land* **8**, 254–263.

El-Keblawy A, Gairola S, Bhatt A and Mahmoud T (2017) Effects of maternal salinity on salt tolerance during germination of *Suaedaa egyptiaca*: a facultative halophyte in the Arab Gulf desert. *Plant Species Biology* **32**, 45–53.

El-Keblawy A, Al-Shamsi N and Mosa KA (2018) Effect of maternal habitat, temperature and light on germination and salt tolerance of *Suaeda vermiculata*, a habitat-indifferent halophyte of arid Arabian deserts. *Seed Science Research* **28**, 140–147.

El Shaer HM (2010) Halophytes and salt-tolerant plants as potential forage for ruminants in the Near East region. *Small Ruminant Research* **91**, 3–12.

Elnaggar A, El-Keblawy A, Mosa KA and Navarro T (2019) Adaptive drought tolerance during germination of *Salsola drummondii* seeds from saline and nonsaline habitats of the arid Arabian deserts. *Botany* **97**, 123–133.

Freitag H, Atamov V, Çetin E and Aslan M (2009) The genus *Halothamnus* Jaub. & Spach (Chenopodiaceae) in Turkey. *Turkish Journal of Botany* **33**, 325–334.

Gairola S, Bhatt A and El-Keblawy A (2015) A perspective on potential use of halophytes for reclamation of salt-affected lands. *Wulfenia* **22**, 88–97.

Galloway LF (2002) The effect of maternal phenology on offspring characters in the herbaceous plant *Campanula americana*. *Journal of Ecology* **90**, 851–858.

Ghazanfar SA (2006) Saline and alkaline vegetation of NE Africa and the Arabian Peninsula: an overview, pp. 101–108 *in* Oztürk M; Waisel Y; Khan MA and Görk G (Eds) *Biosaline agriculture and salinity tolerance in plants*. Basel, Switzerland, Birkhaeuser Verlag.

Ghazanfar SA, Altundag E, Yaprak AE, Osborne J, Tug GN and Vural M (2014) Halophytes of Southwest Asia, pp. 105–133 *in* Khan MA; Böer B; Öztürk M; Al Abdessalaam TZ; Clüsener-Godt M and Gul B (Eds) *Sabkha ecosystems: volume IV: cash crop halophyte and biodiversity conservation*. Dordrecht, Springer Science Business Media.

Ghazanfar SA, Böer B, Khulaidi AWA, El-Keblawy A and Alateeqi S (2019) Plants of Sabkha ecosystems of the Arabian Peninsula, pp. 55–80 *in* Gul B; Böer B; Khan MA; Clüsener-Godt M and Hameed A (Eds) *Sabkha ecosystems*. Benji, Nature Switzerland.

Graifenberg A, Botrini L, Giustiniani L, Filippi F and Curadi M (2003) Tomato growing in saline conditions with biodesalinating plants: *Salsola soda* L., and *Portulaca oleracea* L. *Acta Horticultarae* **609**, 301–305.

Gremer JR and Venable DL (2014) Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. *Ecology Letters* **17**, 380–387.

Gutterman Y (2000) Maternal effects on seeds during development, pp. 59–84 *in* Fenner M (Ed) *Seeds: the ecology of regeneration in plant communities* (2nd edn). Wallingford, England, CABI Publishing.

Hawke MA and Maun MA (1989) Intrapopulation variation in reproduction and seed mass of a beach annual; *Cakile edentula* var. *lacustris*. *Journal of Coastal Research* **5**, 103–112.

Huang Z, Zhang X, Zheng G and Gutterman Y (2003) Influence of light, temperature, salinity and storage on seed germination of *Haloxylon ammodendron*. *Journal of Arid Environments* **55**, 453–464.

Levy SF, Ziv N and Siegal ML (2012) Bet hedging in yeast by heterogeneous, age-correlated expression of a stress protectant. *PLoS Biology* **10**, e1001325.

Liu B, Zhao D, Zhang P, Liu F, Jia M and Liang J (2020) Seedling evaluation of six walnut rootstock species originated in China based on principal component analysis and cluster analysis. *Scientia Horticulturae* **265**, 109212.

Lozano-Isla F, Campos MLO, Endres L and Pompelli MF (2018) Effects of seed storage time and salt stress on the germination of *Jatropha curcas* L. *Industrial Crops and Products* **118**, 214–224.

Mahmoodi T, Khoshhal J, Mousavi SH and Pourkhosravani M (2013) A comparative evaluation of adaptation of Nebkas to stabilize sand dunes of the desert in Sirjan using AHP model. *Iran Journal of Environmental and Erosion Research* **2**, 24–38.

Manousaki E and Kalogerakis N (2011) Halophytes present new opportunities in phytoremediation of heavy metals and saline soils. *Industrial & Engineering Chemistry Research* **50**, 656–660.

Martin A, Grzeskowiak V and Puech S (1995) Germination variability in three species in disturbed Mediterranean environments. *Acta Oecologica* **16**, 479–490.

Milberg P, Andersson L and Thompson K (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Science Research* **10**, 99–104.

Miranda RQ, Oliveira MTP, Correia RM, Almeida-Cortez JS and Pompelli MF (2011) Germination of *Prosopis juliflora* (Sw) DC seeds after scarification treatments. *Plant Species Biology* **26**, 186–192.

Mitchell J, Johnston IG and Bassel GW (2017) Variability in seeds: biological, ecological, and agricultural implications. *Journal of Experimental Botany* **68**, 809–817.

Moncaleano-Escandon J, Silva BCF, Silva SRS, Granja JA, Alves MCJL and Pompelli MF (2013) Germination responses of *Jatropha curcas* L. seeds to storage and aging. *Industrial Crops and Products* **44**, 684–690.

Narbona E, Ortiz PL and Arista M (2006) Germination variability and the effect of various pre-treatment on germination in the perennial spurge *Euphorbia nicaeensis* All. *Flora* **201**, 633–641.

Nimac A, Lazarević B, Petek M, Vidak M, Šatović Z and Carović-Stanko K (2018) Effects of salinity and seed priming on germination of sea fennel (*Crithmum maritimum* L.). *Agriculturae Conspectus Scientificus* **83**, 181–185.

Nordborg M and Bergelson J (1999) The effect of seed and rosette cold treatment on germination and flowering time in some *Arabidopsis thaliana* (Brassicaceae) ecotypes. *American Journal of Botany* **86**, 470–475.

Omar SAS, Al-Mutawa Y and Zaman S (2007) *Vegetation of Kuwait*. Kuwait, Kuwait Institute for Scientific Research.

Panta S, Flowers T, Lane P, Doyle R, Haros G and Shabala S (2014) Halophyte agriculture: success stories. *Environmental and Experimental Botany* **107**, 71–83.

Pérez-García F (2009) Germination characteristics and intrapopulation variation in carob (*Ceratonia siliqua* L) seeds. *Spanish Journal of Agricultural Research* **7**, 398–406.

Phondani PC, Bhatt A, Elsarrag E and Horr YA (2016) Ethnobotanical magnitude towards sustainable utilization of wild foliage in Arabian Desert. *Journal of Traditional and Complementary Medicine* **6**, 209–218.

Platenkamp GAJ and Shaw RG (1993) Environmental and genetic maternal effects on seed characters in *Nemophila menziesii*. *Evolution* **47**, 540–555.

Pompelli MF, Ferreira DTRG, Cavalcante PPGS, Salvador TL, Hsie BS and Endres L (2010) Environmental influence on the physico-chemical and physiological properties of *Jatropha curcas* L. seeds. *Australian Journal of Botany* **58**, 421–427.

Pompelli MF, Mendes KR, Ramos MV, Santos JNB, Youssef DTA, Pereira JD, Endres L, Jarma-Orozco A, Solano-Gomes R, Jarma-Arroyo B, Silva ALJ, Santos MA and Antunes WC (2019) Mesophyll thickness and sclerophylly among *Calotropis procera* morphotypes reveal water-saved adaptation to environments. *Journal of Arid Lands* **11**, 795–810.

Prabu R, Vanniarajan C, Vetrivanthan M, Gnanamalar RP, Shanmughasundaram R and Ramalingam J (2020) Diversity study using principal component analysis in barnyard millet (*Echinochloa frumentacea* (Roxb.) Link). *Electronic Journal of Plant Breeding* **11**, 606–609.

Qasim M, Gulzar S, Shinwari ZK, Aziz I and Khan MA (2010) Traditional ethnobotanical uses of halophytes from Hub, Balochistan. *Pakistan Journal of Botany* **42**, 1543–1551.

Rabhi M, Ferchichi S, Jouini J, Hamrouni MH, Koyro HW, Ranieri A, Abdelly C and Smaoui A (2010) Phytodesalination of a salt-affected soil with the halophyte *Sesuvium portulacastrum* L. to arrange in advance the requirements for the successful growth of a glycophytic crop. *Bioresource Technology* **101**, 6822–6828.

Redondo-Gómez S, Mateos-Naranjo E and Andrades-Moreno L (2010) Accumulation and tolerance characteristics of cadmium in a halophytic Cd-hyperaccumulator, *Arthrocnemum macrostachyum. Journal of Hazardous Materials* **184**, 299–307.

Rojas-Aréchiga M, Mandujano MC and Golubov J (2013) Seed size and photoblastism in species belonging to tribe Cacteae (Cactaceae). *Journal of Plant Research* **126**, 376–386.

Saatkamp A, Cochrane A, Commander L, Guja LK, Jimenez-Alfaro B, Larson J, Nicotra A, Poschlod P, Silveira FAO, Cross AT, Dalziell EL, Dickie J, Erickson TE, Fidelis A, Fuchs A, Golos PJ, Hope M, Lewandrowski W, Merritt DJ, Miller BP, Miller RG, Offord CA, Ooi MKJ, Satyanti A, Sommerville KD, Tangney R, Tomlinson S, Turner S and Walck JL (2019) A research agenda for seed-trait functional ecology. *New Phytology* **221**, 1764–1775.

Santelices R, Espinoza S, Magni C, Cabrera A, Donoso S and Peña K (2017) Variability in seed germination and seedling growth at the intra- and inter-provenance levels of *Nothofagus glauca* (*Lophozonia glauca*), an endemic species of Central Chile. *New Zealand Journal of Forestry Science* **47**, 10.

Santo A, Mattana E, Grillo O, Sciandrello S, Peccenini S and Bacchetta G (2017) Variability on morphological and ecological seed traits of *Limonium avei* (De Not.) Brullo & Erben (Plumbaginaceae). *Plant Species Biology* **32**, 368–337.

Schütz W and Milberg P (1997) Seed dormancy in *Carex canescens*: regional differences and ecological consequences. *Oikos* **78**, 420–428.

Slatkin M (1974) Competition and regional coexistence. *Ecology* **55**, 128–134.

Song R, Kelman D, Johns KL and Wright AD (2012) Correlation between leaf age, shade levels, and characteristics beneficial natural constituents of tea (*Camelia sinensis*) grown in Hawaii. *Food Chemistry* **133**, 707–714.

Tautenhahn S, Heilmeier H, Götzenberger L, Klotz S, Wirth C and Kühn I (2008) On the biogeography of seed mass in Germany-distribution patterns and environmental correlates. *Ecography* **31**, 457–468.

Tester M and Davenport R (2003) Na^+ tolerance and Na^+ transport in higher plants. *Annals of Botany* **91**, 503–527.

Tielbörger K, Petruů M and Lampei C (2012) Bet-hedging germination in annual plants: a sound empirical test of the theoretical foundations. *Oikos* **121**, 1860–1868.

Torres-Martinez L, Weldy P, Levy M and Emery NC (2016) Spatiotemporal heterogeneity in precipitation patterns explain population-level germination strategies in an edaphic specialist. *Annals of Botany* **119**, 253–265.

Wang L, Wu Y, Tian Y, Dai T, Xie G, Xu Y and Chen F (2020) Overexpressing *Jatropha curcas* CBF2 in *Nicotiana benthamiana* improved plant tolerance to drought stress. *Gene* **742**, 144588.

Zaidi CHA, González-Benito ME and Pérez-García F (2010) Morphological and physiological seed heterogeneity in the Mediterranean annual plant *Tuberaria macrosepala* (Cistaceae). *Plant Species Biology* **25**, 149–157.

Zhao NX, Zhang LH, Zhao TT, Mo LD, Zhang JL, Gao YB and Wang JL (2016) Trait differentiation among *Stipa krylovii* populations in the Inner Mongolia Steppe region. *Flora* **223**, 90–98.

Zia S and Khan MA (2004) Effect of light, salinity, and temperature on seed germination of *Limonium stocksii*. *Canadian Journal of Botany* **82**, 151–157.