

Maternal salinity environment affects salt tolerance during germination in *Anabasis setifera*: A facultative desert halophyte

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Abstract: The effects of maternal salinity and light incubation on the salinity tolerance of the facultative halophyte *Anabasis setifera* during their germination stages were assessed. Seeds were collected from non-saline habitats in Egypt and saline habitats in the United Arab Emirates (UAE). The seeds of the two populations were germinated in 0, 100, 200, 400, 600 and 800 mM NaCl, and incubated at 25°C/15°C in both 12-h light and 12-h darkness regimes and continuous darkness. Significantly more seeds germinated in the Egyptian population than in the UAE population. Salinity tolerance was significantly greater with the Egyptian population than with the UAE population, especially under the conditions of higher salinities. The difference in salinity tolerance between the seeds of two populations was attributed to their seed mass. In addition, germination was significantly faster for the Egyptian population than for the UAE population. Most of the saline treated seeds were able to recover their germination when transferred to distilled water, but this depended on their maternal salinity and light incubation. Recovery from higher salinities was significantly better for the seeds under darkness than for those under light in the UAE population, but the reverse was true for the seeds in the Egyptian population. The higher salinity tolerance for the *A. setifera* seeds from the non-saline Egyptian population and the lower salinity tolerance for the seeds from the saline UAE population cannot explain their natural distribution. Further studies about other possible roles, such as levels of different promoting and inhibiting phytohormones, are needed to understand the importance of salinity as an environmentally induced maternal effect.

Keywords: *Anabasis setifera*; facultative halophyte; germination; maternal salinity; seed mass

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Plants growing under natural stresses such as salinity, drought and heat have evolved strategies to cope with these stresses and ensure their own survival and the prosperity of the offspring (Hayashi et al., 1998; McNeil et al., 1999). Under the unpredictable heterogeneous environments such as those of arid deserts and disturbed sites, plants develop multiple strategies through producing offspring which differ in time and place of germination (Baskin and Baskin, 1998; El-Keblawy, 2003) and tolerance to environmental stresses (Sultan, 2003; Reed et al., 2010).

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Plants with phenotypic plasticity are more likely to survive in such changing environmental conditions (Donohue and Schmitt, 1998; Suter and Widmer, 2013). In addition, plants under maternal environment could produce progeny that fit well with the unpredictable heterogeneous habitats (Roach and Wulff, 1987). It has been reported that environmental maternal effects might be evolved as sources of adaptive plasticity between generations (Galloway, 2005). This capacity could enhance offspring fitness in different environments.

Maternal environmental effects may be adaptive when they confer a fitness advantage to offspring through increased recruitment and survival (Donohue and Schmitt, 1998; Van Zandt and Mopper, 2004). Several studies have reported that maternal habitats can determine subsequent dormancy and responses of seeds germination to environmental conditions and consequently, the fate of the next generation (Roach and Wulff, 1987; El-Keblawy et al., 1996; Baskin, 1998; El-Keblawy and Al-Rawai, 2006). As an example, early germination is a potentially adaptive trait that would affect adult fitness as the early recruited seedling should grow faster in the absence of competitors (Kalisz, 1986).

Exposure to environmental stress over several generations in plants may enhance trans-generational effects (Case et al., 1996; Rahavi et al., 2011). Plants exposed to an environmental stress may pass some information about that stress to successive generations and could lead to an increased stress tolerance among offspring (Boyko and Kovalchuk, 2011). Some researchers have indicated that the response of offspring to environmental stress is a product of some stress-inducible genes (Thomashow, 1999) and maternal environmental effects (Roach and Wulff, 1987). The progeny of heat-stressed *Arabidopsis* spp. plants has shown an enhanced stress tolerance when parents were exposed to the same stress (Migicovsky et al., 2014). Similarly, Suter and Widmer (2013) reported that exposure of *Arabidopsis thaliana* to salt stress increased salt tolerance in the next generation. These authors concluded that the trans-generational effects were maternally and paternally inherited.

Variation in germination of seeds produced under different environmental conditions has an important ecological advantage, especially under extreme saline habitats of arid deserts (Fenner, 1991; Gutterman, 2000). The time and amount of the first rain of a season is usually unpredictable in the deserts. Germination of seeds that is mainly triggered by the first rain would affect the emergence of plants and ultimately the future survival and fitness (Gutterman, 1996). Under saline habitats, emergence of germination is mainly controlled by the amount of rainfall that dilutes salts. Facultative halophytes which could grow in both saline and non-saline habitats produce seeds that differ in salt tolerance. Seeds with different dormancy and germination behavior enable facultative halophytes to spread their germination over time based on the amount of received rain. If little rain is received, only salt tolerant seeds would germinate. Otherwise, most of the seeds would be able to germinate after heavy rainfall.

Previous studies on the impact of maternal salinity on salinity tolerance of seeds during germination reported contradicted results. Some studies reported higher salinity tolerance during germination for the seeds developed and matured in saline sites in comparison to seeds of the same species from lower salinity sites (Krauss et al., 1998; Van Zandt and Mopper, 2004). However, plants of *Elymnus cinereus* from saline and non-saline habitats did not differ in their response to salinity during germination (Choudhuri, 1968). In addition, seeds of *Suaeda aegyptiaca* matured in non-saline habitats germinated better and tolerated higher salinities in comparison to seeds matured in saline habitats of the arid desert of the United Arab Emirates (UAE).

Anabasis setifera Moq. (Amaranthaceae) is a perennial dwarf succulent facultative halophytic shrub. It is widely distributed in Egypt, Arabia, Iran, Afghanistan, Pakistan and India (Ali, 1977). The ability of *A. setifera* to grow in both saline and non-saline environments provides good opportunity to understand the salinity tolerance for seeds of the same species developed and matured under contrasting salinity conditions. *A. setifera* produces winged fruits (hereafter referred to as seeds) that are dispersed by wind (Lev-Yadun et al., 2009). However, the wings are not persisted and disintegrate within a few months after dispersal. The ability of *A. setifera* seeds

to disperse enables them to germinate and grow in a habitat that differs from the one in which they developed and matured. Consequently, it would be expected to find little maternal salinity effect on the fate of the subsequent generation. The aim of the present study, therefore, was to assess the impact of maternal salinity on the germination behavior of *A. setifera* seeds (expressed as germination percentage and speed). The study also aimed to assess the interactive effects of maternal salinity and other environmental conditions such as salinity and light. The germination recovery when seeds were transferred from saline solutions to distilled water was also assessed at the above-mentioned environmental conditions.

1 Materials and methods

1.1 Study area

The impact of the maternal habitat on seed germination of *Anabasis setifera* was studied for seeds collected from a hyper-saline habitat in Seih Shuaib, Abu Dhabi, the UAE (24°53'43"N, 54°55'49"E) and a non-saline habitat in eastern region of Cairo, at Cairo-Suez road (30°06'20"N, 31°35'21"E), Egypt. The average electrical conductivity (EC) was 0.52 and 17.5 mS/cm in Egypt and the UAE, respectively. In addition, the pH was 8.0 and 7.3 in Egypt and the UAE, respectively. The associated species with *A. setifera* in the UAE population were all halophytes but those associated in the non-saline habitats of the Egyptian population were all glycophytes (Table 1). Interestingly, *A. setifera* was found growing neither in non-saline habitat of the UAE nor in saline habitats of Egypt.

Table 1 Habitat characteristics of *Anabasis setifera* in Egypt and the United Arab Emirates (UAE)

Parameter	Egyptian site	UAE site
Seed mass (g/1,000 seeds)	0.43±0.03	0.28±0.008
pH	8.04	7.30
Electrical conductivity (mS/cm)	0.52	17.50
Associated species	<i>Zilla spinosa</i> , <i>Gymnocarpos decandrus</i> , <i>Pulicaria undulata</i> , <i>Ochradenus</i> <i>baccatus</i> , <i>Diploaxis harra</i> , <i>Iphiona</i> <i>mucronata</i> , <i>Centaurea aegyptiaca</i> , <i>Fagonia mollis</i> , <i>Calligonum comosum</i> and <i>Gypsophila capillaris</i>	<i>Salsola drummondii</i> , <i>Suaeda vermiculata</i> , <i>Halopeplis perfoliata</i> and <i>Zygophyllum qatarense</i>

Matured fruits were collected from the shrub canopies of the two populations during December 2013. Fruits were randomly collected from at least 50–60 plants per population and mixed together in order to represent the genetic diversity of the populations. After cleaning the fruit perianths, seeds were stored in brown paper bags at room temperature (22±2°C) until the experiment started (the third week of April 2014). The average seed mass was determined by weighing three replicates, each of 1,000 seeds, from both populations in Egypt and the UAE (Table 1). Five soil samples (0–30 cm) were collected from each site and then pooled together to form one composite sample. Soil samples were air dried, thoroughly mixed and passed through a 2-mm sieve. EC and soil pH were evaluated in 1:5 soil-water extract using electric conductivity meter and a pH meter, respectively.

1.2 Effect of salinity on seed germination

Seeds of *A. setifera* collected from Egypt and the UAE were germinated under different NaCl concentrations (0, 100, 200, 400, 600 and 800 mM NaCl). We selected these salinity levels based on a preliminary test which assessed the salinity tolerance of this species. Three replicates, each of 35 seeds, were used for each treatment. The seeds were germinated in 9-cm diameter Petri dishes on two sheets of Whatman No. 1 filter paper and moistened with 10 mL of the test solution. Petri dishes were sealed with parafilm to minimize evaporation and were then incubated at daily temperature regimes of 25°C/15°C in both continuous darkness and 12-h light/12-h darkness. These conditions were determined to be optimal for the germination of *A.*

setifera. Under darkness treatment, the Petri-dishes were wrapped in two sheets of aluminum foil to prevent any exposure to light. Radicle emergence was the germination criterion and the germinated seeds were counted every other day for 20 days following seed soaking. Seeds incubated in the darkness were only counted after 20 days.

1.3 Effects of salinity on germination recovery

After 20 days, the seeds failed to germinate in both light and darkness conditions of the different NaCl treatments were transferred to distilled water to test their ability for germination recovery. Seeds were incubated under daily temperature regimes of 25°C/15°C with 12-h light/12-h darkness. Germinated seeds were counted every other day for 10 days.

1.4 Calculation and data analysis

Rate of germination was calculated with a modified Timson's germination velocity index: $\sum G/T$, where G is the percentage of seeds germinated on every day and T is the total germination period (Khan and Ungar, 1997). The maximum value of germination rate index (GRI) was 50. The higher the value is, the more rapid the germination. The germination rate was only calculated for seeds incubated under light conditions.

The germination recovery percentage was calculated by the following formula:

$$\text{Recovery percentage} = (a-b)/(c-b) \times 100\%. \quad (1)$$

Where a is the total number of seeds germinated after being transferred to distilled water, b is the total number of seeds germinated in saline solution and c is the total number of seeds.

Three-way ANOVA was used to assess the significance of the main factors (maternal habitat, salinity and light) and their interactions on final germination and germination recovery. Two-way ANOVA was used to assess the impact of maternal habitat and salinity and their interactions on the germination rate index (GRI). Tukey's test (Honestly significant differences, HSD) was used to estimate the least significant range between means. The GRI was log-transformed and germination percentage was arcsine-transformed to meet the assumption of ANOVA. This transformation improved the normality of the distribution of the data. All statistical analyses were performed using SYSTAT, version 13.0.

2 Results

The average mass of seeds collected from Egypt was about 53% greater than that from the UAE. The average mass of 1,000 seeds was 0.43 and 0.28 g for the populations of Egypt and the UAE, respectively (Table 1).

2.1 Germination in different saline solutions

ANOVA test showed significant effects for maternal habitat, salinity and their interaction ($P < 0.001$) but not for light of incubation and its interactions with the other factors ($P > 0.05$; Table 2) on final germination percentage of *A. setifera*. Overall, final germination of the *A. setifera* seeds from Egypt was significantly greater in comparison to the seeds from the UAE. There was a significant reduction in germination percentage in higher salinities compared to lower salinities. Germination was almost inhibited under 800 mM NaCl treatment (Fig. 1).

The interaction between maternal habitat and salinity was significant ($P < 0.001$), indicating that salinity tolerance during germination depends on the maternal habitat. Seeds from Egypt had significantly higher germination than those from the UAE but the difference was much greater in

Table 2 Effects of maternal habitat, salinity and light of incubation on final germination percentage of *Anabasis setifera* seeds

Source of variation	df	Mean square	F value	P value
Habitat (H)	1	1.981	119.50	<0.001
Salinity (S)	5	0.889	53.66	<0.001
Light (L)	1	0.040	2.43	ns
H×S	5	0.171	10.34	<0.001
H×L	1	0.002	0.13	ns
S×L	5	0.033	1.99	ns
H×S×L	5	0.002	0.14	ns

Note: ns means insignificant difference at $P < 0.05$ level.

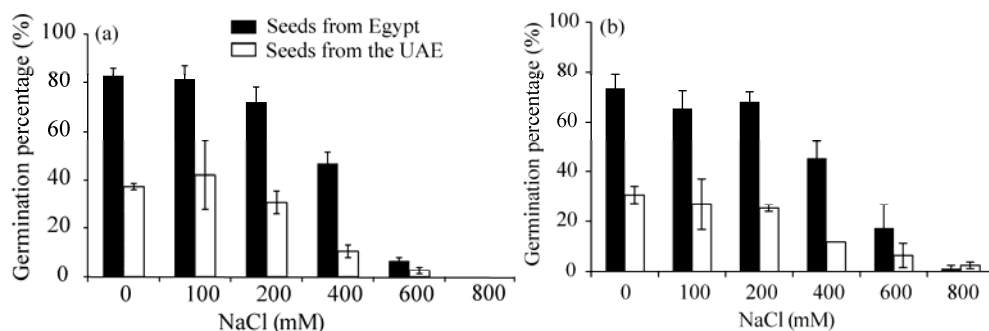


Fig. 1 Effects of maternal habitat, salinity and light of incubation on final germination percentage of *Anabasis setifera* seeds. (a) Germination under light condition; (b) Germination under darkness condition.

higher salinities in comparison to those in lower salinities. The germination was greater by about 130% and 114% under control (distilled water) and 100 mM NaCl conditions, respectively, but by 150%, 350% and 158% under 200, 400 and 600 mM NaCl conditions, respectively (Fig. 1). This result indicates that salinity tolerance was much greater for seeds from Egypt in comparison to that for the seeds from the UAE, especially under higher salinities.

Two-way ANOVA showed significant effects of maternal habitat ($F_{1,19}=10.38$, $P<0.01$) and salinity ($F_{4,19}=6.57$, $P<0.01$) on the germination rate index. Germination was significantly faster for seeds from Egypt (GRI=39.4) than those for seeds from the UAE (GRI=32.1). Germination was significantly faster in distilled water and 100 mM NaCl (GRI=44.1 and 40.3, respectively) than those under 200, 400 and 600 mM NaCl conditions (GRI=34.6, 28.7 and 30.6, respectively) (Fig. 2).

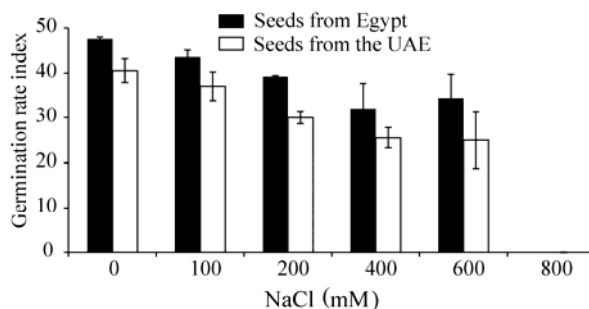


Fig. 2 Effects of maternal habitat and salinity on germination rate index of *Anabasis setifera* seeds

2.2 Germination recovery

The effects of the main factors (maternal habitat, salinity and light of incubation) on germination recovery when ungerminated seeds transferred from saline solution to distilled water were significant ($P<0.05$). The interactions between the maternal habitat and both salinity and light were also significant ($P<0.01$; Table 3). Germination recovery did not differ significantly between the two populations for seeds that were germinated in different salinities and incubated in darkness, except for seeds under 100 mM NaCl condition, seeds from the UAE did not recover from 100 mM NaCl under darkness condition. However, recovery was almost three times greater for seeds from Egypt than those of seeds from the UAE which were germinated in different salinities and incubated in light. In addition, recovery from higher salinities (400, 600 and 800 mM NaCl) was significantly greater for the seed from the UAE under darkness than that under light condition but the reverse was true for seeds from Egypt (Fig. 3).

Table 3 Effects of maternal habitat, salinity and light of incubation on final germination recovery of *Anabasis setifera* seeds

Source of variation	df	Mean square	F value	P value
Habitat (H)	1	0.740	76.33	<0.001
Salinity (S)	5	0.320	33.03	<0.001
Light (L)	1	0.075	7.69	<0.01
H×S	5	0.040	4.09	<0.01
H×L	1	0.305	31.44	<0.001
S×L	5	0.014	1.42	ns
H×S×L	5	0.028	2.93	<0.05

Note: ns means insignificant difference at $P < 0.05$ level.

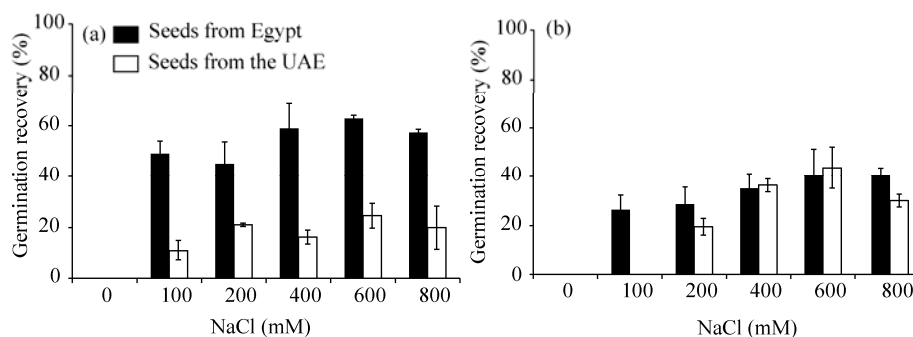


Fig. 3 Effects of maternal habitat, salinity and light of incubation on germination recovery percentage of *Anabasis setifera* seeds. Seeds of the two populations that failed to germinate in different saline solutions in both light and darkness were germinated in distilled water and incubated in 12-h light/12-h darkness. (a) Germination recovery for seeds incubated in 12-h light/12-h darkness; (b) Germination recovery for seed incubated in the darkness.

Two-way ANOVA showed significant effects of salinity ($F=19.8$, $P<0.001$) but not for light ($F=1.4$, $P>0.05$) nor the interaction between salinity and light ($F=1.8$, $P>0.05$) on germination rate index. Recovery was significantly faster for seeds germinated under 100, 200 and 400 mM NaCl conditions (GRI=44.1, 42.8 and 42.2, respectively) than seeds germinated in 600 and 800 mM NaCl conditions (GRI=25.1 and 23.2, respectively) (Fig. 4).

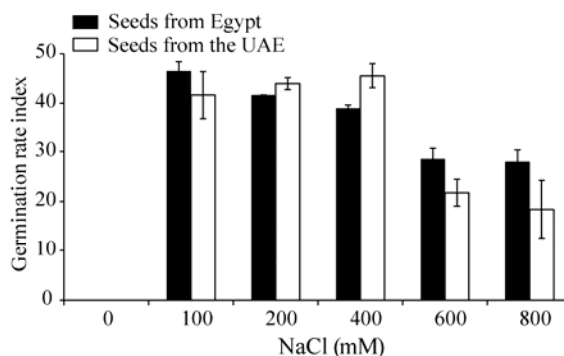


Fig. 4 Effects of maternal habitats and salinity on germination rate index of *Anabasis setifera* seeds recovered in distilled water

3 Discussion and conclusion

Facultative halophytes can grow under saline stress but can grow better in an environment with lower soil salinity (Sabovljevic and Sabovljevic, 2007). *Anabasis setifera* grows very well in both saline and non-saline environments. Interestingly, this species was only recorded in saline habitats in a hyper-arid environment of the UAE, but in non-saline habitats of the Mediterranean climate of Egypt. Unexpectedly, seeds of the non-saline habitat tolerated more salinity, especially at

higher salinity levels. Several studies have reported greater salinity tolerance for seeds matured under saline conditions in comparison to the seeds matured under non-saline conditions. These species include *Prosopis farcta* (Bazzaz, 1973), *Festuca rubra* (Bülow-Olsen, 1983), *Atriplex nummularia* (Uchiyama, 1985), *Iris hexagona* (Van Zandt and Mopper, 2004) and *Suaeda aralocaspica* (Wang et al., 2012). For *Suaeda aegyptiaca*, another facultative halophyte in the hyper-arid environment of the UAE, we reported a result similar to that of *A. setifera* in the present study. Seeds of the non-saline habitat attained higher germination in all salinities in comparison to the seeds in saline habitat.

It has been reported that salinity stress usually increases the level of endogenous abscisic acid (ABA) and decreases endogenous growth promoters such as gibberellic acid (GA) (Kabar, 1987; Bewley and Black, 1994; Tuna et al., 2008). This indicates that GA and ABA act antagonistically in seed germination and plant development (Bewley and Black, 1994; Tuna et al., 2008). In a mutant of *Arabidopsis* with reduced ABA contents, salinity tolerance was higher during germination stage in comparison to a mutant with high ABA (Koornneef et al., 1984). Consequently, we assumed that *A. setifera* seeds in saline conditions would have a lower ratio of GA/ABA, but seeds in non-saline habitats would have a higher ratio of GA/ABA. In many halophytes, exogenous application of GA has resulted in higher salinity tolerance in many species such as *Atriplex griffithii* (Khan et al., 2000), *Salicornia rubra* (Khan et al., 2011), *Suaeda salsa* (Li et al., 2005) and *Prosopis juliflora* (El-Keblawy and Al-Rawai, 2005).

Maternal habitat might directly affect seed mass which, in turn, indirectly affect the salinity tolerance of the offspring (Ungar, 1979; Khan and Ungar, 1984; Philipupillai and Ungar, 1984; Roach and Wulff, 1987; El-Keblawy, unpublished data). For example, in *Salicornia europaea* and *Atriplex triangularis*, two halophytes of Chenopodiaceae, smaller seeds were much less salt-tolerant than large seeds during germination (Ungar, 1979; Khan and Ungar, 1984; Philipupillai and Ungar, 1984). In addition, *Suaeda aegyptiaca* plants that were growing in more favorable non-saline conditions produced larger, heavier seeds that germinated greater and faster and tolerated more salinity stress than those of seeds matured in un-favorable saline conditions (El-Keblawy et al., 2015). In *A. setifera*, the average mass of seeds collected from non-saline habitats of Egypt was >51% heavier than seeds in saline environments of the UAE (average mass of 1,000 seeds from Egypt and the UAE was 0.43 and 0.28 g, respectively). Consequently, the difference in germination between the maternal habitats reported in our study might be attributed to the difference in seed mass of these two habitats. Most of earlier studies that assessed maternal salinity effect on germination did not consider the effect of seed mass. In fact, many of these studies attributed the difference in salinity tolerance to the formation of different ecotypes rather than due to adaptive maternal effects (Bazzaz, 1973; Bülow-Olsen, 1983; Philipupillai and Ungar, 1984; Uchiyama, 1985). Further studies are needed to assess the relation between seed mass and salinity tolerance, especially for facultative halophytes. Seeds with different size from both saline and non-saline habitats could be germinated in different salt concentrations.

In natural habitats, seed germination and seedling establishment are affected by environmental factors such as temperature, light intensity, water availability and soil salinity (Baskin and Baskin, 1998). Maximum halophyte seed germination occurs in distilled water or under reduced salinity stress (El-Keblawy, 2004). The germination success of *A. setifera* seeds with very high speed in the lower salinities (up to 200 mM for the seeds from the UAE and up to 400 mM for the seeds from Egypt) indicates that they would germinate successfully in saline habitats after heavy rainfalls that would dilute soil salinity.

Our results indicated that germination recovery from higher salinities was significantly greater for the UAE's seeds which were previously incubated in darkness, compared with those in the light. The result indicates that *A. setifera* seeds require heavy rainfall to germinate in the hyper-saline habitats of the UAE (EC=17.5 mS/cm). The rainfall would dilute the salinity levels and at the same time lightning storms could help in breaking seed dormancy and consequently stimulate germination (Baskin and Baskin, 1982). The high germination recovery when ungerminated seeds in high saline solutions were transferred to distilled water indicates the ability of *A. setifera* seeds to survive in the saline environment and germinate immediately after rainfalls.

However, emerged seedlings might die if they do not establish within a short period after rainfall because of evaporation. The fast germination observed during recovery from high salinity enables *A. setifera* seedlings to be established before the increase of the soil salinity.

Anabasis setifera produces winged fruits that are dispersed by wind (Lev-Yadun et al., 2009). Consequently, seeds are able to germinate and grow in a habitat that differs from that where they developed and matured. Consequently, seeds matured in the saline habitats of the UAE could reach non-saline habitats and germinate there. However, *A. setifera* plants were not recorded in non-saline habitats of the UAE. In addition, *A. setifera* was not recorded in saline habitats close to the non-saline habitats where it grows in Egypt. One possible explanation for the differential salinity tolerance in the two regions is the dependence of that tolerance on the prevailing temperatures during germination. It has been documented that salinity tolerance during germination depends on temperature. For example, Khan and Gul (2006) reviewed salinity tolerance in different geographical regions and concluded that the tolerance was lower at cooler temperatures in many halophytes of the Great Basin desert (e.g. *Allenrolfea occidentalis*, *Chrysothamnus nauseosus*, *Salicornia rubra* and *Salsola iberica*) but the reverse was true in other halophytes of the subtropical maritime deserts of Pakistan (e.g. *Cressa cretica*, *Atriplex stocksii*, *Haloxylon recurvum*, *Suaeda fruticosa* and *Arthrocnemum macrostachyum*). However, salinity tolerance was greater at moderate temperatures and any increase or decrease in temperatures inhibited germination at all salinities in other species such as *Aeluropus lagopoides*, *Halopyrum mucronatum* and *Zygophyllum simplex* (Khan and Gul, 2006).

To conclude, the salinity tolerance of *A. setifera* seeds during germination cannot explain their natural distribution. Seeds from the non-saline habitats of Egypt tolerated more salinity than those from the saline habitats of the UAE. The smaller seeds of the saline habitats could explain their lower tolerance (Ungar, 1979; Khan and Ungar, 1984; Philipupillai and Ungar, 1984). As far as the effects of maternal habitat is concerned, it is apparent that the big healthy seeds that matured in a stress-free environment of Egypt have more reserves and can often/usually germinate faster and more completely than seeds that matured under stress (the UAE population) and may not have the reserves or machinery to mobilize quickly. Moreover, taking seeds from each population and raising a new generation in a common garden would be interesting to find effects of the grandparent habitat. Further studies on the levels of the different promoting and inhibiting phytohormones under different saline conditions should be assessed in facultative halophytes such as *A. setifera* (the present study) and *S. aegyptiaca* (El-Keblawy, unpublished data) that showed high germination for seeds matured in non-saline habitats and low germination for seeds matured in saline habitats. The carryover of phytohormones from the maternal plants to the seed progeny (Boyko and Kovalchuk, 2011; Migicovsky et al., 2014) supports the possible role of these hormones in the progeny tolerance to salinity stresses. Such studies would enhance our understanding of the importance of the salinity as an environmentally induced maternal effect.

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