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Alleviation of salinity stress and the response to temperature in two seed morphs of *Halopyrum mucronatum* (Poaceae)

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Abstract. *Halopyrum mucronatum* (L.) Stapf. is a coastal dune grass that produces seeds twice during each growing season. Seeds produced during May (summer seed) were black and heavier (2.8 ± 0.09 mg) than brown seeds (2.1 ± 0.04 mg; winter seed) that were produced in November. There was greater than 95% germination in both seed morphs in the non-saline controls at all temperature regimes, but germination was inhibited more by low than high temperatures in the salinity treatments. Summer seeds were more tolerant of salinity than the winter seeds. Highest germination was obtained in all salinity treatments at a 20/30°C (12-h night/12-h day) temperature regime for the winter seeds and at 25/35°C for the summer seeds. Gibberellic acid, thiourea and nitrate partially alleviated the effects of salinity in summer seeds and gibberellic acid, kinetin and betaine were able to alleviate the inhibitory effects of salinity on the germination of winter seeds. The seeds of *Halopyrum mucronatum* exhibited seed dimorphism and a difference in physiological response in the two seed morphs, which could provide them with multiple opportunities to germinate and establish in the hot, dry, saline and unpredictable maritime coastal-dune environment along the Arabian Sea coast of Karachi, Pakistan.

Introduction

Halopyrum mucronatum (L.) Stapf. is a stoloniferous perennial grass that is distributed along the littoral coastal zones from Egypt to Sri Lanka (Jafri 1966). It is an inhabitant of the upper portions of salt marshes, sand flats and dunes of Sandspit beach along the Arabian Sea coast of Karachi, Pakistan. Within established populations, *H. mucronatum* can usually spread by stolons but it is capable of invading new sites through the dispersal of caryopses. Stolons produce new ramets each year and flowering shoots form twice a year, from April to May and from September to November (M. A. Khan, unpubl. data). Black seeds are produced during the summer and are heavier (2.8 ± 0.09 mg) than brown seeds (2.1 ± 0.04 mg) that are formed in the winter. Seeds germinate in the field only after monsoon rains, which occur during July or August (M. A. Khan, pers. obs.).

Somatic seed dimorphism has been reported in a number of annuals that occupy unpredictable environments (Ungar 1991). Differences in the germination responses of seed morphs to environmental conditions are reported for other species (Ungar 1982; Phlipupillai and Ungar 1984; Mohammad and Sen 1988; Khan and Gul 1998). Environmental conditions experienced by parental plants during the growing season often play a significant role in determining the germinability of seeds (Gutterman 1993). Day length, temperature, position of seeds in the inflorescence and time of seed production could affect the degree of dormancy in seeds (Bewley and Black 1994). *Spergularia marina* seeds collected monthly had different germination responses to varying levels of salinity, indicating that parental environments influenced both the salt tolerance and relative germinability of seeds when they were exposed to salt stress (Ungar 1988). Mohammed and Sen (1991) reported that seed polymorphism occurred in a number of halophytic species from India (*Cressa cretica*, *Salsola baryosma*, *Sesuvium sesuvioides*, *Suaeda fruticosa*, *Trianthema triquetra* and *Zygophyllum simplex*). They hypothesised that the differences in seed mass and size could be selected for by different soil salinity levels at the locations where these populations were found growing.

Variation in temperature regime is reported to interact with changing levels of salinity in affecting the seed germination of halophytes (Khan and Ungar 1984; Agami 1986; Ismail 1990). Some halophytes, such as *Atriplex griffithii*, *Cressa cretica*, *Triglochin maritima* and *Zygophyllum simplex* are sensitive to a change in temperature regime (Khan 1991; Khan and Rizvi 1994; Khan and Ungar 1997*a*), while *Arthrocnemum indicum*, *Suaeda fruticosa* and *Haloxylon recurvum* showed only a

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small response to changes in temperature (Khan and Ungar 1996, 1998; Khan and Gul 1998).

Dormancy relieving compounds such as proline and betaine (Khan and Ungar 1997*b*; Gul and Weber 1998; Khan *et al.* 1998), gibberellic acid and kinetin (Ungar 1977; Okusanya and Ungar 1983; Khan and Ungar 1985; Khan and Weber 1986; Yaniv *et al.* 1995; Plyler and Proseus 1996; Khan *et al.* 1998), thiourea and nitrate (Gul and Weber 1998) have been reported to alleviate the effect of salinity on the germination of halophytes. The effect of salinity, temperature and dormancy-relieving compounds on the germination of dimorphic seeds of *H. mucronatum* was investigated to determine how they interact to influence germination. On the basis of its distribution in desert and saline areas, we hypothesise that optimal germination of *H. mucronatum* seeds will occur at high temperatures and that the seeds will be highly salt-tolerant.

Materials and methods

Caryopses of *Halopyrum mucronatum* were collected from a population growing on dunes of Sandspit beach, Karachi, Pakistan, during May 1996 and November 1996 and will be referred to as summer (2.8 ± 0.09 mg; black) and winter seeds (2.1 ± 0.04 mg; brown), respectively. Hulled seeds were separated, cleaned and stored at the room temperature. Germination experiments were begun in December 1996. Seeds were surface-sterilised with the fungicide Phygon and were presoaked in distilled water or respective test solutions for 4 h. Germination was carried out in 20-mm-diameter × 180-mm-long test tubes. Seeds were placed on Whatman No. 1 filter-paper channels (3.5 × 16-cm strip of filter paper folded to form two channels). Filter-paper channels were moistened with either 1.5 mL of test solution or distilled water. All tubes were sealed with parafilm and four replicates of 25 seeds each were used for each treatment. Seeds were considered germinated after the radicle emerged.

Experiment 1

To determine the effect of temperature on germination of the two seed morphs, alternating temperature regimes of 10/20, 15/25, 20/30 and 25/35°C (12-h night/12-h day) were used. Seeds were germinated in programmed refrigerated incubators (Percival) in which the higher temperature (20, 25, 30 and 35°C) coincided with the 12-h light period (Sylvania cool white fluorescent lamps, 25 µmol m^{-2} s^{-1}, 400–700 nm) and the lower temperature (10, 15, 20 and 25°C) coincided with the 12-h dark period. Seeds were germinated in 0, 50, 100, 150 and 200-mM NaCl solutions under the above-mentioned temperature regimes.

Experiment 2

Dormancy-relieving compound treatment concentrations used were 20 mM nitrate, 10 mM thiourea, 100 µM proline, 100 µM betaine, 3 mM gibberellic acid (GA_3), 50 µM kinetin, with distilled water and 100, 200 and 300 mM NaCl at 15/25°C. Preliminary results indicated that these concentrations of dormancy-relieving compounds were capable of stimulating seed germination.

Percentage germination was recorded every 2 days for 20 days in both experiments. The rate of germination was estimated by a modified Timson index of germination velocity = $\Sigma G/t$, where G is the percentage seed germination at 2-day intervals and t is the total germination period (Khan and Ungar 1984). The maximum value possible using this index with our data was 50 (i.e. 1000/20). The higher the value, the more rapid was the rate of germination.

Germination data were arcsine transformed for the statistical analysis. These data were analysed using SPSS, V. 7 (SPSS Inc. 1996). A three-way ANOVA was used to demonstrate the significance of the main effects (salinity, temperature regime, seed type) and their interaction on the rate and percentage of germination in the first experiment. A two-way ANOVA was used to demonstrate the significance of main effects (salinity and growth regulators) and their interaction on the rate and percentage of germination in the second experiment. When significant differences were found among means, a Bonferroni post-hoc test was used to determine whether significant ($P < 0.05$) differences occurred between individual treatments.

Results

Experiment 1

A three-way ANOVA of final germination indicated significant ($P < 0.001$) effects of salinity ($F = 287$, $P < 0.001$), temperature regime ($F = 10.2$, $P < 0.001$), seed type ($F = 20.6$, $P < 0.001$) and all their interactions ($P < 0.001$). Germination of both summer- and winter-seed morphs in the non-saline control was over 95% but was reduced by salinity treatments to an extent dependent on temperature regime (Figs 1, 2, 3). Lower temperature regimes (10/20 and 15/25°C) caused a substantial reduction in the germination of summer seeds when salinity was increased (Fig. 1). Summer seeds had higher germination than winter seeds at high salinity levels at 25/35°C (Figs 1–3). At the highest temperature regime (25/35°C), summer seeds had 80% germination in 200 mM NaCl (Fig. 1). Final germination percentages of winter seeds in the control and 50 mM NaCl were similar in all temperature

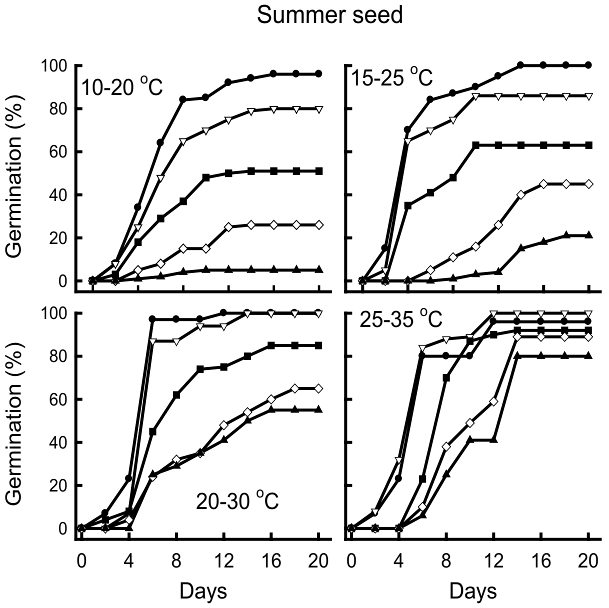

Fig. 1. Mean germination percentage as a function of time of summer seeds in 0 (●), 50 (▽), 100 (■), 150 (◇) and 200 (▲) mM NaCl at thermoperiods of 10–20, 15–25, 20–30 and 25–35°C.

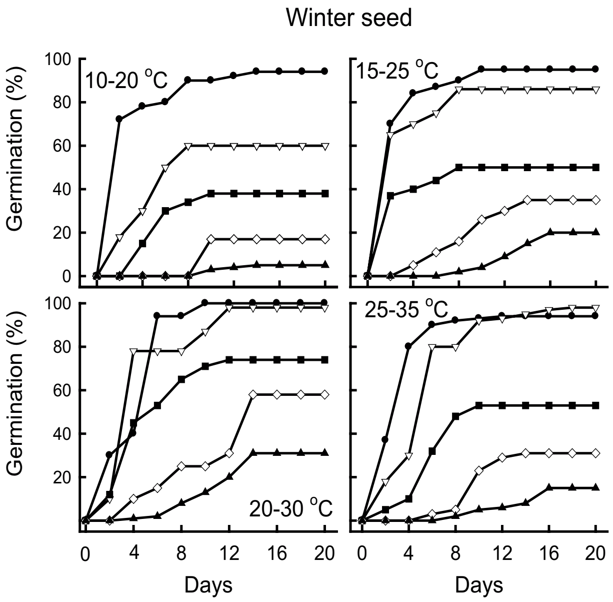

Fig. 2. Mean germination percentage as a function of time of winter seeds in 0 (●), 50 (▽), 100 (■), 150 (◇) and 200 (▲) mM NaCl at thermoperiods of 10–20, 15–25, 20–30 and 25–35°C.

regimes except 10/20°C, whereas in 200-mM NaCl the highest germination was found at 20/30°C (Figs 2, 3).

A three-way ANOVA of germination rate indicated significant main effects of salinity ($F = 413.7$, $P < 0.001$), temperature regime ($F = 6.7$, $P < 0.001$), seed type ($F = 13.3$, $P < 0.001$) and all their interactions ($P < 0.001$). Germination velocity of summer seeds was similar in controls at all temperatures, but the velocity of germination increased with an increase in temperature at higher salinities (Fig. 4). The germination rate of winter seeds showed no effect of changes in temperature regime in the non-saline controls, but the lower temperature regime (10/20°C) significantly reduced the rate of germination in all salinity treatments. At 100 mM or higher concentration of NaCl, the highest velocity of germination was obtained in the 20/30°C treatment (Fig. 4)

Experiment 2

A two-way ANOVA of percentage germination for salinity and dormancy-relieving compounds showed that there were highly significant individual effects of salinity (summer seed, $F = 13.7$, $P < 0.0001$; winter seed, $F = 298.8$, $P < 0.0001$) and dormancy-relieving compounds (summer seed, $F = 158.4$, $P < 0.0001$; winter seed, $F = 38.2$, $P < 0.0001$) and an interaction (summer seed, $F = 6.9$, $P < 0.0001$; winter seed, $F = 7.3$, $P < 0.0001$). A two-way ANOVA for velocity of germination showed that there were highly significant effects of salinity (summer seed, $F = 16.3$, $P < 0.0001$; winter seed, $F = 344.8$, $P < 0.0001$) and dormancy-relieving compounds (summer seed, $F = 211.8$, $P < 0.0001$; winter seed, $F = 35.2$, $P < 0.0001$) and an interaction (summer seed, $F = 6.5$, $P < 0.0001$; winter seed, $F = 6.6$, $P < 0.0001$). Kinetin did not alleviate salinity-enforced inhibition of germination in summer seeds, whereas GA_3 partially alleviated the inhibitory effects of salinity on germination (Fig. 5). Gibberellic acid reduced the inhibitory effect of salinity in winter seeds and kinetin promoted seed germination in the higher salinity treatments (Fig. 5). Proline was ineffective in alleviating the inhibitory effects of salinity in both summer and winter seeds, whereas betaine promoted germination of winter seeds at 100 and 200 mM NaCl (Fig. 6). Thiourea and nitrate alleviated the inhibitory effect of salinity in summer seeds but failed to have a significant influence on winter seeds (Fig. 7)

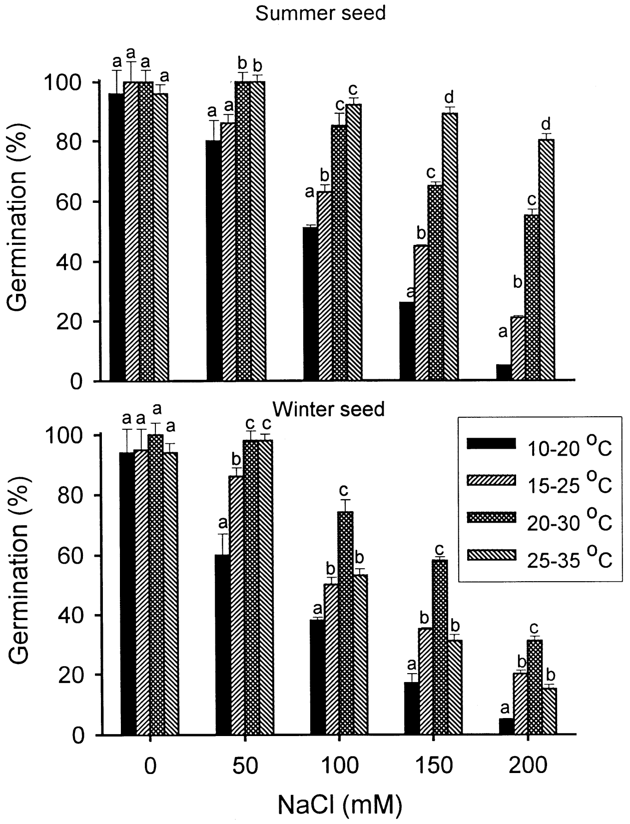

Fig. 3. Mean (± s.e.) final germination percentages of seeds in 0, 50, 100, 150 and 200 mM NaCl at thermoperiods of 10–20, 15–25, 20–30 and 25–35°C. For each NaCl concentration, values of final germination percentages having the same letter are not significantly different at $P = 0.05$, Bonferroni test.

The velocity of germination of summer seeds decreased with increasing salinity. Thiourea and nitrate enhanced the velocity of germination in NaCl treatments (Table 1). At 100–300 mM NaCl, GA_3 and kinetin significantly promoted the velocity of germination in winter seeds.

Discussion

We hypothesised that that seeds of *H. mucronatum* would have their highest germination at warmer temperature regimes, but both seed morphs had 95% or higher

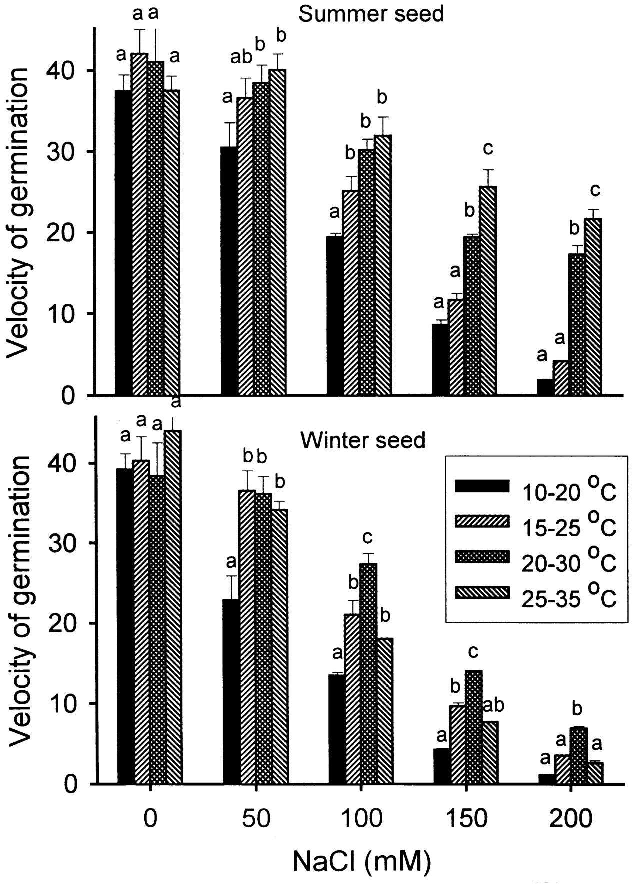

Fig. 4. Index of velocity of germination (mean ± s.e.) of winter seeds in 0, 50, 100, 150 and 200 mM NaCl at thermoperiods of 10–20, 15–25, 20–30 and 25–35°C. For each NaCl concentration, values of final germination percentages having the same letter are not significantly different at $P = 0.05$, Bonferroni test.

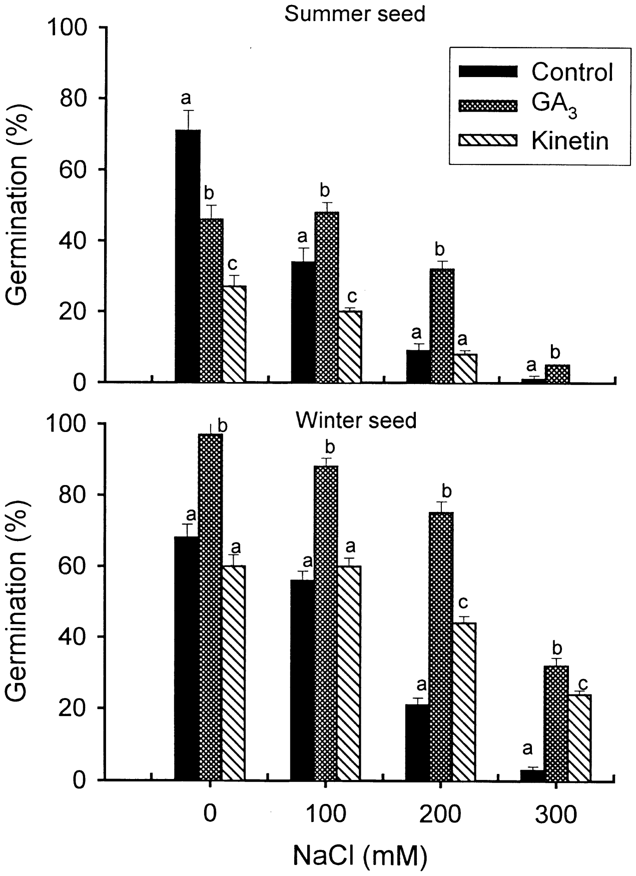

Fig. 5. Final germination percentages (mean ± s.e.) of seeds in 100, 200 and 300 mM NaCl, 3.0 mM GA_3 and 50 µM kinetin at 15–25°C. For each NaCl concentration, values of final germination percentages having the same letter are not significantly different at $P = 0.05$, Bonferroni test.

germination in distilled water in all of the temperature treatments. However, lower temperature regimes inhibited the germination of both seed types in the salinity treatments, with summer seeds (2.8 mg ± 0.09) germinating at higher salinities than winter seeds (2.1 ± 0.04 mg). Germination of summer seeds at the higher salinities (150 and 200 mM NaCl) was substantially reduced at lower temperatures (10/20°C), but at high temperatures (25/35°C) 80% of the seeds germinated in 200 mM NaCl, indicating that there was a salinity × temperature interaction affecting the germination response to salinity. Germination for winter seeds in 200 mM NaCl was only 30% at 20/30°C.

The parental environment in which seeds develop has a strong effect on their germinability (Ungar 1995). Okusanya and Ungar (1983) determined that *Spergularia marina* seeds collected from plants at different times during the growing season had different levels of dormancy, depending on the month of seed collection. A number of halophytes, including species in the genera *Arthrocnemum*, *Atriplex*, *Salicornia*, *Chenopodium* and *Spergularia* exhibit some form of seed dimorphism or polymorphism in their germination response (Khan and Ungar 1984; Philipupillai and Ungar 1984; Mohammed and Sen 1988; Ungar 1988; Khan and Gul 1998). Because of differences in germination requirements, these polymorphic seeds provide multiple opportunities for the recruitment by seeds in these unpredictable, hot, dry and saline semi-desert coastal environments.

In contrast to other species growing in this coastal habitat, *H. mucronatum* seeds are relatively intolerant of salinity at germination. Both *Cressa cretica* and *Arthrocnemum indicum* seeds collected from adjacent areas could germinate in up to 1000 mM NaCl (Khan 1991; Khan and Gul 1998); however, only a few *H. mucronatum* seeds germinated at 300 mM NaCl. Other co-occurring species such as *Atriplex griffithii* showed a similar level of salt tolerance to *H. mucronatum* during germination (Khan and Rizvi 1994). Salinity and temperature interact to regulate the seed germination of halophytes, but the effect of temperature regime on seed germination under saline conditions varies among species (Ungar 1995). Species such as *Atriplex*

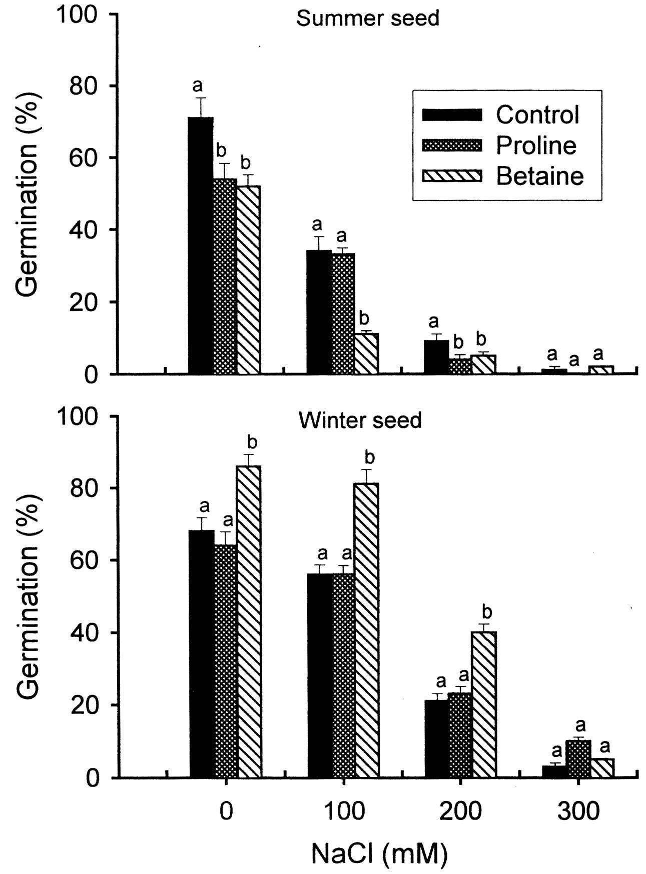

Fig. 6. Final germination percentages (mean ± s.e.) of seeds in 100, 200 and 300 mM NaCl, 1.0 mM proline and 1.0 mM betaine at 15–25°C. For each NaCl concentration, values of final germination percentages having the same letter are not significantly different at $P = 0.05$, Bonferroni test.

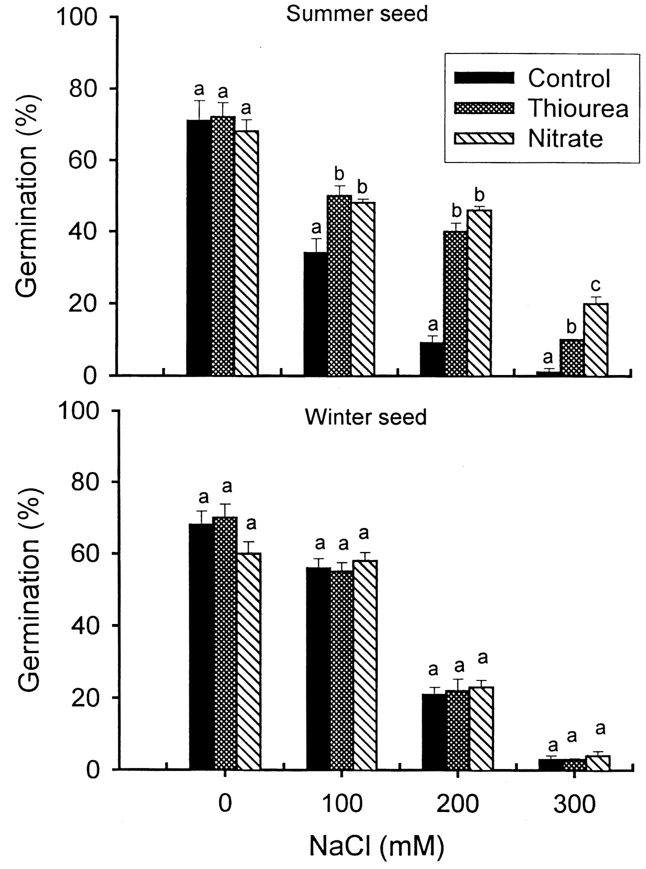

Fig. 7. Final germination percentages (mean ± s.e.) of seeds in 100, 200 and 300 mM NaCl, 20 mM nitrate and 10 mM thiourea at 15–25°C. For each NaCl concentration, values of final germination percentages having the same letter are not significantly different at $P = 0.05$, Bonferroni test.

triangularis, *Puccinellia ciliata*, *Triglochin maritima* and *Zygophyllum simplex* are sensitive to changes in temperature regime (Khan and Ungar 1984, 1997*b*; Myers and Couper 1989), whereas, as *H. mucronatum*, other species such as *Arthrocnemum indicum*, *Haloxylon recurvum* and *Suaeda fruticosa* are relatively less sensitive to changes in the temperature regime (Khan and Ungar 1996, 1998; Khan and Gul 1998)

The two seed morphs of *H. mucronatum* differed in their response to GA_3 and kinetin treatments under saline conditions. Kinetin did not stimulate germination of summer seeds but increased germination of winter seeds in high salinities (200 and 300 mM). Gibberellic acid increased germination of summer seeds and was also stimulatory at 200 mM NaCl. It also increased germination of winter seeds under saline conditions. Khan and Ungar (1985) showed that GA_3 and kinetin were more effective in alleviating the inhibitory effects of salinity in small seeds in comparison to the medium and large seed morphs of *Atriplex triangularis*. There was little difference in the response of brown and black seeds of *Arthrocnemum indicum* to GA_3 and kinetin under saline conditions (Khan *et al.* 1998). Seed germination of other species increased significantly in salt treatments with an application of GA_3 (Ungar 1984, 1991; Khan 1991) or kinetin (Kabar and Baltepe 1990; Khan and Ungar 1996). It may be that the production of growth-promoting substances is inhibited in seeds by salt stress and that exogenous applications overcome this deficiency, but further research is necessary to determine the endogenous levels of these growth regulators under salt-stress conditions (Ungar 1991)

Proline failed to alleviate the inhibitory effect of salinity on the germination of both summer and winter seeds. Betaine did not stimulate germination of summer seeds, but winter-seed germination was significantly promoted in 100 and 200 mM NaCl. Poljakoff-Mayber *et al.* (1994) found that there were low levels of proline and significant amounts of betaine in dry seeds of *Kosteletzkya virginica*, and these may alleviate the inhibitory effects of salinity by acting as osmoregulators or osmoprotectants of proteins in the

Table 1. Effect of dormancy-relieving compounds and salinity on the velocity of germination (Timson index, max. = 50) of summer and winter seeds of *Halopyrum mucronatum*

Values in each row with the same letter are not significantly different ($P = 0.05$), Bonferroni test

NaCl (mM)	Control	Proline	Betaine	Thiourea	Nitrate	GA_3	Kinetin
			Summer seeds				
0	19 ± 0.5a	13 ± 3.6b	14 ± 0.7b	18 ± 3.6a	20 ± 0.7a	18 ± 0.9a	10 ± 1.8b
100	2 ± 2.3a	1 ± 0.8a	1.4 ± 0.7a	9 ± 2.9b	10 ± 2.7b	9 ± 1.2b	3 ± 1.0a
200	0.5 ± 1.7a	0 ± 0 a	0.7 ± 0.9a	8 ± 0.8b	9 ± 0.9b	1 ± 0.2a	0 ± 0a
300	0 ± 0a	0 ± 0 a	0 ± 0a	1 ± 0b	2 ± 0b	0 ± 0.2a	0 ± 0a
			Winter seeds				
0	22 ± 0.5a	21 ± 3.6a	30 ± 0.7b	18 ± 3.6b	20 ± 0.7a	37 ± 0.9c	25 ± 1.8a
100	5 ± 1.3a	7 ± 0.8a	8 ± 0.7a	6 ± 2.9a	7 ± 2.7a	23 ± 1.2c	15 ± 1.0d
200	1 ± 1.7a	2 ± 0a	1 ± 0.9a	1 ± 0.8a	1 ± 0.9a	9 ± 0.2 b	7 ± 0.3c
300	0 ± 0a	0 ± 0a	0 ± 0a	0 ± 0a	0 ± 0a	3 ± 0.03b	2 ± 0.02b

cytoplasm. However, external application of proline and betaine to *K. virginica* seeds in both the control and saline media had no effect on seed germination. Khan and Ungar (1996) reported that both proline and betaine alleviated the effects of low salinity and innate dormancy of *Zygophyllum simplex* seeds but neither was effective at high salinities. Proline and betaine also alleviated the inhibition of germination by salinity in *Allenrolfea occidentalis* seeds (Gul and Weber 1998). Khan *et al.* (1998) showed that proline and betaine failed to alleviate either innate dormancy or the inhibitory effects of salinity in both the brown and black seeds of *Arthrocnemum indicum*.

Thiourea and nitrate significantly alleviated the inhibitory effects of salinity in the summer seeds of *H. mucronatum* but did not stimulate germination of winter seeds. Nitrate was shown to promote seed germination (Roberts and Smith 1977) and it alleviated the inhibitory effect of salinity on seeds (Gul and Weber 1998; Khan and Ungar 1998). Thiourea could stimulate seed germination and was shown to alleviate the negative effects of salinity on germination (Esashi *et al.* 1979; Aldosaro *et al.* 1981; Gul and Weber 1998). The inhibitory effect of salinity on *Allenrolfea occidentalis* seeds was partially alleviated by nitrate and thiourea (Gul *et al.* 2000). Khan and Ungar (1997*b*) determined that both thiourea and nitrate significantly improved germination of *Z. simplex* seeds at low salinities. Nitrogen compounds such as thiourea may counteract the effect of reduced promoter (cytokinins and gibberellins) and increased inhibitor substances, such as abscisic acid, in seeds when they are exposed to salt stress (Kabar and Baltepe 1990), but more research is needed to determine the endogenous levels of these growth regulators in seeds to determine the precise effects of these nitrogen compounds on seed germination (Ungar 1991)

Halopyrum mucronatum seeds exhibited both physiological differences in germination response and morphological dimorphism. Neither summer nor winter seeds had an innate dormancy; however, lower temperatures (10/20°C) inhibited germination in the presence of salinity (>100 mM NaCl). Summer seeds showed optimal germination at 25/35°C and winter seeds at 20/30°C. They also responded differently to different germination-promoting compounds. Betaine, GA_3 and kinetin alleviated the inhitory effect of salinity in winter seeds, while thiourea, nitrate and GA_3 were stimulatory to summer seeds. *Halopyrum mucronatum* populations have been inundated during high tides; however, seed germination only occurred after the monsoon rains when salinity levels would be reduced. High temperatures, salinity and drought characterise this habitat, except during the monsoon period. Even monsoon periods are unpredictable, since some years have only one or two brief periods of precipitation and then the soil dries out quickly, exposing seedlings to high salinity (≥ 3.5% soil solution salinity = 600 mM) and drought stress, while in other years the monsoon period persists for a couple of months providing opportunities for the establishment of *H. mucronatum* seedlings. Differences in the physiological requirements of summer large (2.8 ± 0.09 mg) and winter small seeds (2.1 ± 0.04 mg) of *H. mucronatum* may provide alternative temporal and spatial conditions for germination and recruitment in its stressful and unpredictable coastal environment. Our results corroborate the hypothesis that germination is optimal at high temperatures, but *H. mucronatum* could not germinate at the high salinities reported for other species growing in the same environment. Results indicate that seed germination in *H. mucronatum* is more closely associated with heavy monsoon rains than are the germination of associated species, which are capable of germinating at higher salinities.

Acknowledgments

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