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HIGH SALT TOLERANCE IN GERMINATING DIMORPHIC SEEDS OF *ARTHROCNEMUM INDICUM*

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Arthrocnemum indicum L. is a stem-succulent perennial in the family Chenopodiaceae and is widely distributed in the tidal marshes of Pakistan. Seeds were collected from a coastal salt marsh situated on the Arabian Sea coast at Sands Pit, Karachi, Pakistan. *Arthrocnemum indicum* produces dimorphic brown and black seeds, and brown seed was significantly ($P < 0.05$) heavier. Experiments were conducted to determine the effect of salinity and temperature on the germination of seeds. Results indicated that both seeds are highly salt tolerant, and 3% of the brown seeds germinated at 1000 mM NaCl. Germination was significantly higher at 15°–25°C thermoperiod at 600 and 800 mM NaCl. Rate of germination decreased with increase in salinity and there was no significant difference among various thermoperiods on the rate of germination in both seed types. When the seeds were transferred to distilled water after 20-d exposure to salinity, most recovered in 24 h, with recovery percentages at highest salinity varied from 72% to 86% at various thermoperiods.

Introduction

Seed dimorphism (or polymorphism) is of selective advantage because it helps plants to respond directly to changing environmental conditions (Khan and Ungar 1984; Venable 1985; Ungar 1995). Polymorphic seeds vary in their dormancy level, thereby providing an extended period of germination in salt marsh and salt desert environments (Ungar 1995). A number of halophytic taxa, including *Atriplex, Salicornia, Chenopodium, Spergularia, Cakile, Trianthema, Plantago, Halopyrum,* and *Salsola* have evolved some form of plasticity in their germination responses (Okusanya and Ungar 1983; Khan and Ungar 1984; Philipupillai and Ungar 1984; Galinato and van der Valk 1986; Mohammad and Sen 1988; Ungar 1988; Maun and Payne 1989; Noor and Khan 1995). Mohammad and Sen (1991) reported that seeds of a number of halophytic species from India (*Cressa cretica, Salsola baryosma, Sesuvium sesuvioides, Suaeda fruticosa, Trianthema triquetra,* and *Zygophyllum simplex*) were polymorphic. They hypothesized that the differences in seed mass and size could be selected for by different soil salinity levels at the locations where these populations are growing.

Subtropical halophytes vary in their germination responses to various thermoperiods (Khan and Ungar 1997*a*, 1997*b*) and variation in thermoperiod is reported to interact with various levels of salinity in affecting the seed germination of halophytes (Macke and Ungar 1971; Rivers and Weber 1971; Ungar 1977; Okusanya and Ungar 1983; Khan and Ungar 1984; Berger 1985; Agami 1986; Khan and Weber 1986; Khan et al. 1987; Ismail 1990; Khan 1991; Khan and Rizvi 1994; Noor and Khan 1995; Khan and Ungar 1996, 1997*b*). Species like *Atriplex griffithii, C. cretica,* and *Z. simplex* are sensitive to change in thermoperiod (Khan 1991; Khan and Rizvi 1994; Khan and Ungar 1997*b*), while others like *S. fruticosa* and *Haloxylon recurvum* are less sensitive to change in thermoperiod (Khan and Ungar 1996, 1998*c*).

Arthrocnemum indicum Willd. (Chenopodiaceae) is a stem-succulent perennial halophytic shrub, commonly found in tropical coastal salt marshes, which are frequently inundated with seawater. Karim and Qadir (1979) described that *A. indicum* is a low shrub that occurs in almost pure patches or, rarely, with other species like *Limonium stocksii, C. cretica, Aleuropus insignis,* and *Suaeda monoica.* Our study was conducted in a population of *A. indicum* in coastal salt marsh located at Sands Pit, Karachi, Pakistan. Flowering and seed set of *A. indicum* occur in May to July. *Arthrocnemum indicum* propagates itself primarily by vegetative means (rhizomes); a large number of seeds is produced, but recruitment through seed is rare. We found black and brown seeds from the seed collection of Sands Pit population. Brown seeds were heavier than black seeds. Dimorphic seeds of *A. indicum* could also vary in their response to salinity and temperature. This physiological dimorphism could provide various opportunities for *A. indicum* populations in new habitats.

The objective of this investigation was to determine the effect of thermoperiod and salinity on the germination of the dimorphic seeds of *Arthrocnemum indicum.*

Material and Methods

Seeds of *Arthrocnemum indicum* L. were collected during July 1994 from Karachi, Pakistan, and were brought to Ohio University. Seeds were separated from the inflorescence and were stored at 4°C. Germination studies were started in December 1995. Seeds were surface sterilized using the fungicide Phygon. Germination was carried out in 50 × 9-mm (Gelman no. 7232) tight-fitting plastic petri dishes with 5 mL of test solution. Each dish was placed in a 10-cm-diameter plastic petri dish as an added precaution against loss of water by evaporation. Four replicates of 25 seeds each were used for each treatment. Seeds were considered to be germinated with emergence of the radicle.

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Table 1 Results of Three-Way ANOVA of Characteristics by Seed Color, Salinity, and Thermoperiod Treatments

Independent variable	Seed color (SC)	Salinity (S)	Thermoperiod (T)	SC × S	SC × T	T × S	SC × T × S
Final germination	0.2^{ns}	287.0***	10.2***	0.8^{ns}	2.8***	2.5*	2.5***
Rate of germination	13.3***	413.7***	6.7***	1.3^{ns}	6.3***	2.0*	3.2***
Total germination after recovery	0.04^{ns}	5.0***	3.8**	1.8^{ns}	5.8***	1.6^{ns}	2.0**
Rate of recovery	4.3*	9.1***	3.4**	4.1**	3.5**	1.9*	2.0**
Percent recovery	1.9^{ns}	40.2***	3.8**	3.9**	4.9**	3.1***	2.9***

Note. Number represents F-values. ns = not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

To determine the effect of temperature on germination, alternating temperature regimes of 10°–20°, 10°–30°, 15°–25°, and 25°–35°C were used. The higher temperature (20°, 25°, 30°, and 35°C) coincided with the 12-h light period (Sylvania cool white fluorescent lamps, 25 μM m^{-2} s^{-1}, 400–750 nM) and the lower temperature (10°, 15°, and 25°C) coincided with the 12-h dark period. Seeds were germinated in distilled water and 200-, 400-, 600-, 800-, and 1000-mM NaCl solutions under the above-mentioned temperature regimes. Percentage of germination was recorded every 2 d for 20 d. Ungerminated seeds from the NaCl treatments were transferred to distilled water after 20 d to study the recovery of germination, which was also recorded at 2-d intervals for 20 d. The recovery percentages were determined by the following formula: $(a - b) / (c - b) \cdot 100$, where a is the total number of seeds germinated after being transferred to distilled water, b is the total number of seed germinated in saline solution, and c is the total number of seeds. The rate of germination was estimated by using a modified Timson index of germination velocity $\sum G / t$, where G is the percentage of seed germination at 2-d 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 the rate of germination.

Germination data (20 d and rate of germination) were transformed (arcsine) before statistical analysis. These data were analyzed using SPSS, version 7 (SPSS Inc. 1996). A three-way ANOVA was used to demonstrate the significance of main effects (salinity, thermoperiod, and seed type) and their interaction in affecting the rate and percentage germination. A Bonferroni test was used to determine if significant ($P < 0.05$) differences occurred between individual treatments.

Results

A three-way ANOVA of germination indicated significant ($P < 0.0001$) effects of salinity and thermoperiod and nonsignificant effect of seed color (table 1). All interactions except between seed color and salinity are significant. Seed germination of *Arthrocnemum indicum* decreased with the increase in salinity, as expected, in both seed types and all thermoperiods studied (figs. 1, 2). Germination of black seeds was maximal in nonsaline treatment at 10°–30°C thermo-

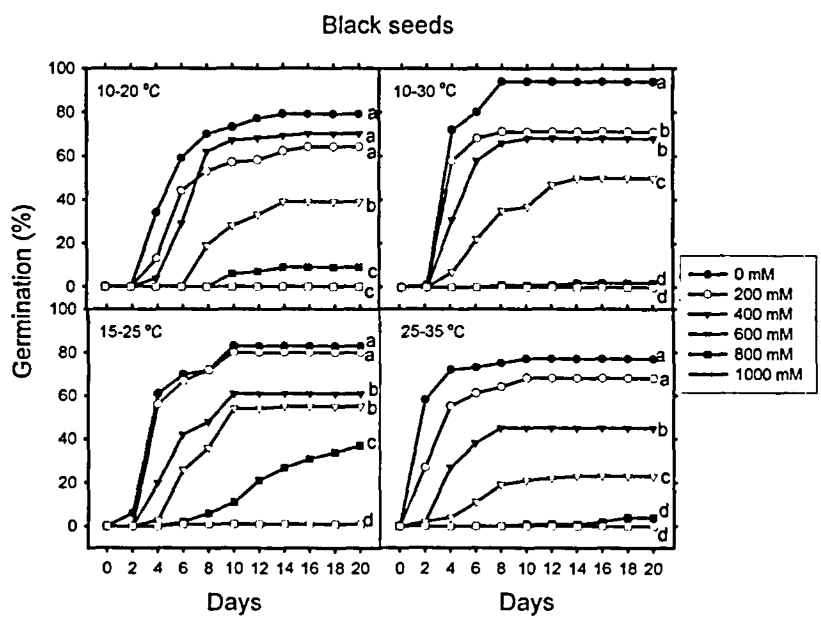

Fig. 1 Percentage germination of *Arthrocnemum indicum* black seeds in 0, 200, 400, 600, 800, and 1000 mM NaCl at thermoperiods of 10°–20°C, 10°–30°C, 15°–25°C, and 25°–35°C. Values of final germination percentages having the same letter are not significantly different at $P > 0.05$, Bonferroni test.

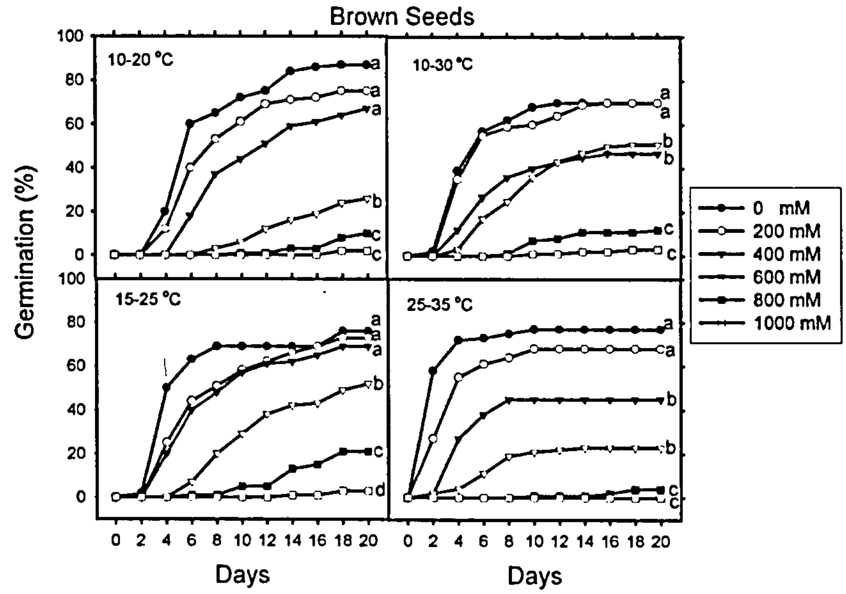

Fig. 2 Percentage germination of *Arthrocnemum indicum* brown seeds in 0, 200, 400, 600, 800, and 1000 mM NaCl at thermoperiods of 10°–20°C, 10°–30°C, 15°–25°C, and 25°–35°C. Values of final germination percentages having the same letter are not significantly different at $P > 0.05$, Bonferroni test.

period (fig. 1). The effect of salinity was more pronounced at 10°–20°C and 25°–35°C, whereas higher thermoperiod (15°–25°C) stimulated germination at high salinity concentrations (800 mM). Final germination percentages showed that 10°–30°C is more suitable for germination at low salinity and 15°–25°C is more suitable at higher salinities. Germination of brown seeds in nonsaline control was higher at 10°–20°C (fig. 2). Brown seeds could germinate at 1000 mM NaCl although germination was extremely low (3%). At 10°–30°C and 15°–25°C thermoperiods high salinity (600 and 800 mM NaCl) showed higher germination percentages.

A three-way ANOVA of germination rate indicated significant ($P < 0.0001$) main effects of salinity, thermoperiod, seed color, and all interactions except for between salinity and seed color (table 1). At 0 and 200 mM NaCl the rate of germination was similar in all thermoperiods (fig. 3). At 400 mM NaCl higher thermoperiods (15°–25°C and 25°–35°C) had a higher germination rate. At 600 mM NaCl treatment rate of germination at 10°–20°C was substantially lower in comparison to the other thermoperiods (fig. 3). In black seeds the rate of germination was higher at 10°–30°C in nonsaline control (fig. 4). At high salinity (600 and 800 mM NaCl) a better germination rate was found at 15°–25°C thermoperiod.

A three-way ANOVA of rate of recovery indicated

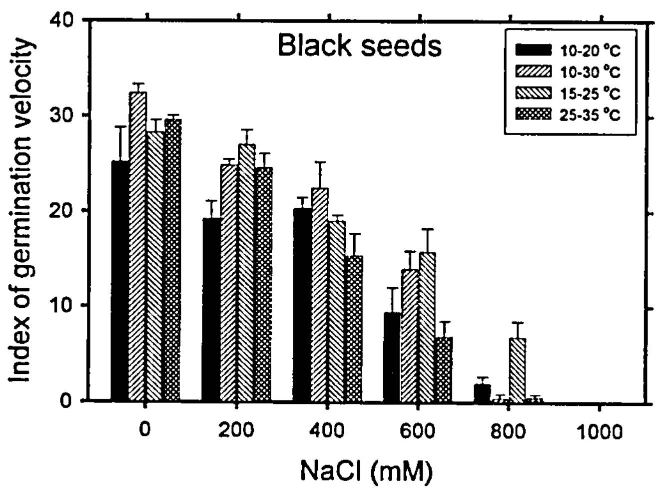

Fig. 3 Rate of germination of *Arthrocnemum indicum* black seeds in 0, 200, 400, 600, 800, and 1000 mM NaCl at thermoperiods of 10°–20°C, 10°–30°C, 15°–25°C, and 25°–35°C.

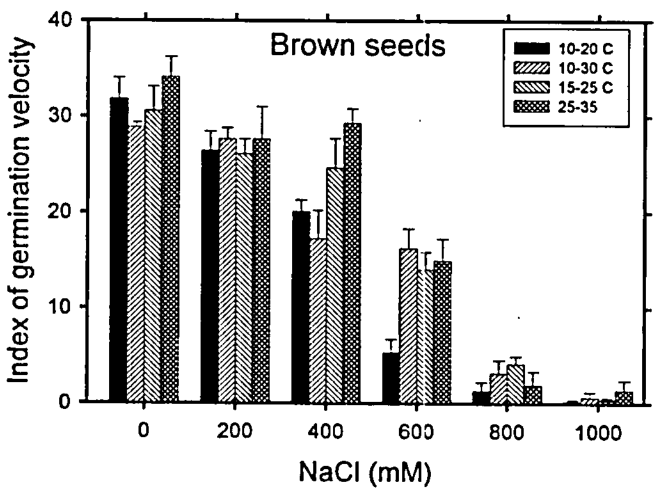

Fig. 4 Rate of germination of *Arthrocnemum indicum* brown seeds in 0, 200, 400, 600, 800, and 1000 mM NaCl at thermoperiods of 10°–20°C, 10°–30°C, 15°–25°C, and 25°–35°C.

significant ($P < 0.0001$) main effects of salinity, thermoperiod, seed color, and all interactions (table 1). When seeds were transferred to distilled water after 20 d of salinity treatment, the recovery percentages increased with increases in pretransfer salinity treatments. Those black seeds, which were subjected to high salinity, had higher recovery percentages (table 2). Seeds recovered at all temperature regimes and at all salinity treatments, and change in thermoperiod had little effect on recovery. The lowest thermoperiod had 63% recovery in comparison to about 85% in other treatments. Recovery in brown seeds was similar to that of black seeds (table 3). A three-way ANOVA of percentage of recovery indicated significant ($P < 0.0001$) main effects of salinity, thermoperiod, seed color, and all interactions (table 1). Change in thermoperiod had no significant effect on the recovery responses (tables 2, 3). Both black and brown seeds apparently can tolerate 1000 mM salinity and retain viability. Rate of recovery for the brown and black seeds does not change with change in temperature or salinity (data not given).

Discussion

Arthrocnemum indicum usually grows in coastal salt marshes and produces seeds during May and June (Gul 1993). Seed size of *A. indicum* varies from 0.5 mm to 1.60 mm, with 80% seeds falling in the size range 1–1.2 mm. *Arthrocnemum indicum* also produces black and brown seeds, and black seeds are heavier (248 ± 12 μg) than brown seeds (200 ± 8 μg). A number of halophytic taxa, *Atriplex, Halopyrum, Salicornia, Chenopodium, Spergularia, Cakile, Trianthema, Plantago,* and *Salsola,* found growing in saline habitats exhibit some form of seed dimorphism or polymorphism in their germination response (Khan and Ungar 1984; Philipupillai and Ungar 1984; Galinato and van der Valk 1986; Mohammad and Sen 1988; Ungar 1988; Morgan and Myers 1989; Noor and Khan 1995). Differences in seed size and time of germination among the seeds produced by a single parent have been shown to influence the population biology of progeny, resulting in a differential competitive ability, survivorship, and fecundity (Khan and Ungar 1986; Harper 1977; Cook 1979; Cideciyan and Malloch 1982). In response to variable environments, plants have evolved dimorphism in seed character.

Both brown and black seed were highly tolerant to salinity during germination. Few brown seeds (3%) germinated at 1000 mM NaCl, but no black seeds germinated at this concentration. Malcolm (1964) studied the seed germination of *Arthrocnemum halocnemoides* var. *pterygosperma* and *perganulatum.* He tested the germination of both varieties at 75, 300, and 500 mM NaCl and eight temperature regimes. He reported reduction and delay in germination with increase in salinity. A 50% reduction in germination occurred at about 75 mM NaCl for var. *pterygosperma* and at about 344 mM NaCl for var. *pergranulatum,* with an interaction between salinity and temperature on ger-

Table 2 Mean Percentage Germination (±SE: $n = 4$) of Black Seeds in Treatment, Initial Salinity Effects (S), Germination Recovery in Distilled Water (R), and Total Germination (T)

NaCl	10–20°C			10°–30°C			15°–25°C			25°–35°C		
mM	S	R	T	S	R	T	S	R	T	S	R	T
0 ..	79 ± 9.8^{a}	13 ± 12.5^{a}	81 ± 10.0^{a}	94 ± 2.9^{a}	0 ± 0.0^{a}	94 ± 3.4^{a}	83 ± 4.4^{a}	0 ± 0.0^{a}	83 ± 4.4^{a}	77 ± 1.0^{a}	18 ± 10.5^{a}	81 ± 3.2^{a}
200 ..	64 ± 5.4^{a}	16 ± 13.5^{a}	69 ± 7.3^{a}	71 ± 1.9^{b}	40 ± 15.1^{b}	82 ± 5.0^{a}	80 ± 9.8^{a}	84 ± 15.2^{b}	95 ± 5.0^{a}	68 ± 5.1^{a}	37 ± 15.0^{ab}	79 ± 5.2^{a}
400 ..	70 ± 4.1^{a}	34 ± 12.7^{a}	81 ± 3.4^{a}	68 ± 8.5^{b}	8 ± 5.1^{a}	72 ± 5.8^{b}	61 ± 1.9^{b}	41 ± 19.0^{c}	77 ± 5.7^{a}	48 ± 6.9^{b}	45 ± 1.0^{abc}	71 ± 6.4^{a}
600 ..	39 ± 11.5^{b}	31 ± 10.3^{a}	59 ± 9.8^{a}	50 ± 4.7^{c}	44 ± 7.6^{b}	72 ± 4.3^{b}	55 ± 9.3^{b}	47 ± 9.8^{c}	76 ± 5.7^{a}	23 ± 5.8^{c}	74 ± 7.1^{bcd}	80 ± 5.8^{a}
800 ..	9 ± 3.7^{c}	88 ± 5.2^{b}	89 ± 5.0^{a}	2 ± 2.0^{d}	80 ± 6.8^{c}	81 ± 6.8^{b}	37 ± 8.0^{c}	84 ± 2.8^{b}	91 ± 1.6^{a}	4 ± 2.8^{d}	90 ± 4.6^{d}	91 ± 4.4^{b}
1000 ..	0 ± 0^{c}	63 ± 5.9^{b}	63 ± 5.9^{a}	0 ± 0.0^{d}	86 ± 3.8^{c}	86 ± 4.0^{b}	1 ± 1.0^{d}	86 ± 7.8^{b}	86 ± 7.3^{a}	0 ± 0.0^{d}	82 ± 7.4^{cd}	82 ± 7.4^{a}

Note. Values in each column having the same letter are not significantly different at $P > 0.05$, Bonferroni test.

Table 3 Mean Percentage Germination (±SE: n = 4) of Brown Seeds in Treatment, Initial Salinity Effects (S), Germination Recovery in Distilled Water (R), and Total Germination (T)

NaCl	10–20°C			10°–30°C			15°–25°C			25°–35°C		
mM	S	R	T	S	R	T	S	R	T	S	R	T
0	87 ± 6.8[a]	44 ± 25.3[a]	96 ± 2.3[a]	70 ± 1.2[a]	7 ± 7.0[a]	72 ± 2.8[a]	76 ± 5.7[a]	100 ± 0.0[a]	100 ± 0.0[a]	74 ± 4.2[a]	6 ± 6.0[a]	75 ± 5.0[a]
200	75 ± 6.4[a]	32 ± 19.3[a]	87 ± 1.9[b]	70 ± 3.5[a]	59 ± 18.3[b]	86 ± 6.6[b]	73 ± 4.4[a]	46 ± 23.2[b]	84 ± 7.3[b]	61 ± 7.5[a]	27 ± 16.0[ab]	74 ± 6.0[a]
400	67 ± 1.9[a]	54 ± 9.8[a]	84 ± 3.6[b]	47 ± 9.3[b]	22 ± 8.4[c]	61 ± 4.4	69 ± 7.7[a]	22 ± 10.0[c]	77 ± 5.7[b]	69 ± 3.0[a]	25 ± 3.1[b]	77 ± 1.9[a]
600	26 ± 3.8[b]	72 ± 6.6[a]	80 ± 5.6[b]	51 ± 6.6[b]	50 ± 17.6[b]	77 ± 6.1	52 ± 2.8[b]	45 ± 9.8[b]	74 ± 3.5[b]	36 ± 5.2[b]	68 ± 2.6[c]	80 ± 0.0[a]
800	10 ± 7.6[c]	71 ± 4.5[a]	77 ± 1.9[b]	12 ± 4.6[c]	81 ± 4.6	84 ± 4.3[b]	21 ± 4.4[c]	78 ± 8.4[d]	84 ± 5.9[b]	5 ± 3.8[c]	67 ± 8.5[c]	68 ± 9.9[a]
1000	2 ± 2.0[c]	80 ± 3.4[b]	81 ± 3.4[b]	3 ± 3.0[c]	75 ± 8.0[d]	76 ± 8.1[a]	3 ± 1.0[d]	86 ± 4.6[d]	86 ± 4.7[b]	5 ± 3.8[c]	72 ± 4.3[c]	73 ± 4.7[a]

Note. Values in each column having the same letter are not significantly different at $P > 0.05$, Bonferroni test.

mination. Both varieties germinated better at a thermoperiod of 5°–35°C. He also reported that scarification increased the germination and interacted with temperature.

Seeds of halophytes vary greatly in their ability to germinate under hypersaline conditions (Ungar 1991). The maximum salinity tolerance ranges from 200 to 1034 mM for halophytes like *Aster tripolium, Limonium vulgare, Salicornia europaea, Spartina alterniflora,* and *Suaeda linearis* (Ungar 1972; Woodell 1985). Khan and Weber (1986) reported that the germination of the inland perennial halophyte *Salicornia pacifica* var. *utahensis* was reduced from 55% in distilled water controls to 3% germination at 856 mM NaCl. Khan (1991) reported that *Cressa cretica* seed germination improved with scarification, and scarified seed had the ability to germinate at 856 mM NaCl. Germination of other perennial halophytes is reported to occur up to 345 mM NaCl (*Atriplex griffithii;* Khan and Rizvi 1994), 500 mM (*Suaeda fruticosa;* Khan and Ungar 1998*c*), 500 mM (*Triglochin maritima;* Khan and Ungar 1998*b*), and 500 mM (*Haloxylon recurvum;* Khan and Ungar 1996).

In this study, a change in thermoperiod at the lower salinities did not have any significant effect; however, a temperature regime of 15°–25°C promoted germination at higher salinities. Rate of germination decreased with increase in salinity, and there was no significant difference among various thermoperiods on the rate of germination in both seed types. Rate of germination of brown seeds was slightly higher than black seeds. Salinity and temperature have been reported to interact to affect the seed germination of halophytes (Ungar 1995), and the greatest inhibition is usually found at the minimum and maximum limits of tolerance for the temperature (Ungar 1978; Khan and Ungar 1997*a*, 1997*b*). Further, limits of salt tolerance may be greater at one thermoperiod than at another (Khan and Weber 1986; Myers and Couper 1989; Ismail 1990; Khan 1991; Khan and Rizvi 1994; Khan and Ungar 1996, 1997*b*, 1998*b*, 1998*c*). The response to salinity also may vary with temperature in that the initial inhibition of germination may occur at higher concentrations at some thermoperiods than at others (Malcolm 1964; Ungar 1965; Binet 1968; Rivers and Weber 1971; Khan and Ungar 1984; Philipupillai and Ungar 1984; Badger and Ungar 1989). Species like *S. fruticosa* and *H. recurvum* showed less response in germination when thermoperiods varied (Khan and Ungar 1996, 1998*b*), while species like *C. cretica, A. griffithii, T. maritima,* and *Polygonum aviculare* are more sensitive to change in temperature (Khan 1991; Khan and Rizvi 1994; Khan and Ungar 1998*a*, 1998*c*).

When the seeds were transferred to distilled water after 20 d of exposure to salinity, they recovered quickly. Recovery germination percentages at the highest salinity treatment varied from 72% to 86% at various thermoperiods. This indicates that very high salinity and change in thermoperiod do not significantly affect the germination ability of *A. indicum* seeds once salinity stress is relieved. Keiffer and Ungar (1995) exposed seeds of five halophytes (*Atriplex prostrata, Hordeum jubatum, S. europaea, Spergularia marina,* and *Suaeda calceoliformis*) to an extended period of salinity and determined their recovery responses after seeds were transferred to distilled water. *Hordeum jubatum* seeds failed to germinate after 2 yr of exposure, seeds of *S. marina* were stimulated after short-term exposure but substantially reduced after long exposures, *A. prostrata* decreased over time, and *S. europaea* and *S. calceoliformis* were stimulated by the exposure of salinity and had higher germination in comparison to control. Seeds of *S. fruticosa* recovered quickly from hypersaline conditions when transferred to distilled water at all thermoperiods (Khan and Ungar 1998*b*), but only those exposed to high salinity at a lower thermoperiod showed salt stimulation of germination. *Haloxylon recurvum* and *T. maritima* seed had about 50% recovery at low to moderate thermoperiods (Khan and Ungar 1996, 1998*a*).

Arthrocnemum indicum is a shrub with an extensive woody rhizome system. It usually grows in an area where part of the population is exposed to diurnal tidal inundation. It has been observed to propagate primarily through rhizomes, although it produces a large number of seeds and maintains a persistent seed bank (B. Gul and M. A. Khan, unpublished data). However, during 5 yr of field observations, no successful establishment of seedlings was reported. Our study demonstrates that seeds are extremely salt tolerant and exposure to high salinity and temperature does not affect their viability. Most seeds promptly germinated under laboratory conditions when salinity was reduced. *Arthrocnemum indicum* seeds could be categorized as one of the most salt tolerant at germination stage known so far. Few (3%) brown seed germinated at 1000 mM NaCl treatment, a salinity concentration much higher than seawater (600 mM NaCl). This indicates that lack of recruitment through seeds in *A. indicum* populations is not prevented by the following factors: (1) nonavailability of seeds, (2) innate seed dormancy, and (3) induced dormancy by high salinity and temperature. Although high salinity induced dormancy in most of the seeds by inhibiting compounds regulating germination activity (Khan et al. 1998), few seeds should still be able to germinate. It seems that proximate strategy of *A. indicum* is to use vegetative methods for the recruitment of a new individual, a less costly form of recruitment. Production of a large number of seeds appears to be an ultimate strategy of *A. indicum* populations in order to introduce a new genotype at an appropriate time to maximize the fitness.

Arthrocnemum indicum is a dominant late successional species of the coastal swamps of Arabian Sea coast. It is not unusual that seeds do not recruit dominating plants. However, further investigations are necessary to understand the ecophysiological causes preventing *A. indicum* seeds from germinating under natural conditions.

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