

Effect of Temperature, Light and Salinity on Seed Germination and Radicle Growth of the Geographically Widespread Halophyte Shrub *Halocnemum strobilaceum*

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• **Background and Aims** The small leafy succulent shrub *Halocnemum strobilaceum* occurs in saline habitats from northern Africa and Mediterranean Europe to western Asia, and it is a dominant species in salt deserts such as those of north-west China. The effects of temperature, light/darkness and NaCl salinity were tested on seed germination, and the effects of salinity were tested on seed germination recovery, radicle growth and radicle elongation recovery, using seeds from north-west China; the results were compared with those previously reported on this species from 'salt steppes' in the Mediterranean region of Spain.

• **Methods** Seed germination was tested over a range of temperatures in light and in darkness and over a range of salinities at 25 °C in the light. Seeds that did not germinate in the NaCl solutions were tested for germination in deionized water. Seeds from which radicles had barely emerged in deionized water were transferred to NaCl solutions for 10 d and then back to deionized water for 10 d to test for radicle growth and recovery.

• **Key Results** Seeds germinated to higher percentages in light than in darkness and at high than at low temperatures. Germination percentages decreased with an increase in salinity from 0.1 to 0.75 M NaCl. Seeds that did not germinate in NaCl solutions did so after transfer to deionized water. Radicle elongation was increased by low salinity, and then it decreased with an increase in salinity, being completely inhibited by ≥ 2.0 M NaCl. Elongation of radicles from salt solutions < 3.0 M resumed after seedlings were transferred to deionized water.

• **Conclusions** The seed and early seedling growth stages of the life cycle of *H. strobilaceum* are very salt tolerant, and their physiological responses differ somewhat between the Mediterranean 'salt steppe' of Spain and the inland cold salt desert of north-west China.

Key words: *Halocnemum strobilaceum*, halophyte, inland salt desert, radicle growth, radicle growth recovery, seed germination, seed germination recovery.

INTRODUCTION

Plants can be divided into two broad groups with respect to salt tolerance: halophytes (salt tolerant) and glycophytes (salt intolerant). Halophytes can grow and complete their life cycle in saline environments, whereas glycophytes cannot (Ungar, 1991). The responses of seeds of halophytes to salt differ from those of non-halophytes. Thus, compared with glycophytes, seeds of halophytes germinate at higher salinities, and they maintain viability even under extreme salinity or osmotic stress, recovering and germinating when the water potential of the medium increases (Ungar, 1995).

Germination of halophytes in the field is controlled by several environmental factors, in particular light (Gutterman, 1993; Huang and Gutterman, 1998, 1999a), temperature (Badger and Ungar, 1989) and salinity (Ungar, 1995; Khan *et al.*, 2002). A survey of the light and temperature requirements for germination of 91 halophytes of salt marshes and salt deserts included information on the light/dark requirements for germination of 23 species and on the optimum temperature requirements for

germination of all 91 species. Seeds of four species required light for germination, four germinated to higher percentages in light than in dark, 13 germinated equally well in light and dark, and two germinated to higher percentages in dark than in light. The optimum temperature for germination ranged from 5 to 35/25 °C, and the mean optimum was about 21 °C (Baskin and Baskin, 1998).

Halophyte species vary in their tolerance to salinity during seed germination (Ungar, 1995; Khan *et al.*, 2002). Seeds of halophytes can recover the capacity to germinate after exposure to salt stress that inhibits their germination (Woodell, 1985). Further, following pre-treatment of seeds of halophytes with salt solutions, the rate and percentage of germination often increase after they are transferred to fresh water (Katembe *et al.*, 1998). Germination of *Limonium stocksii* (Plumbaginaceae) seeds was only 5% at 0.5 M NaCl, but ungerminated seeds germinated to nearly 100% after they were transferred to distilled water (Zia and Khan, 2004). Osmotic pre-treatment significantly stimulated germination recovery of seeds of two *Atriplex* species (Chenopodiaceae), and their germination was 90% 2 d after transfer to distilled water (Katembe *et al.*, 1998). However, whereas germination of *Halogeton glomeratus*

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(Chenopodiaceae) seeds was 45–85% in fresh water after they were soaked in low salinity solutions, it was only 0–8% for seeds given a high salinity pre-treatment (Khan *et al.*, 2001).

Halocnemum strobilaceum (Chenopodiaceae) occurs in saline habitats from northern Africa and Mediterranean Europe to western Asia (Liu, 1985). In China, this species is distributed mainly in the north-west provinces of Xinjiang and Gansu. It is an ecologically important semi-shrub in saline soils on the plain in front of the south slopes of Tianshan Mountain, Xinjiang. In this area, *H. strobilaceum* is one of the dominant or co-dominant halophytic species in saline lowlands and on the shores of salt lakes, margins of alluvial fans and salt crusts of fluvial plains (Liu, 1985). In highly saline patches or on shores of salt lakes, *H. strobilaceum* often forms monodominant communities or co-occurs with *Kalidium foliatum* (Chenopodiaceae) and *Salicornia europaea* (Chenopodiaceae). In slightly saline habitats, it is commonly found in association with other species such as *Halostachys caspica* (Chenopodiaceae), *Tamarix hispida*, *T. ramosissima* (Tamaricaceae), *Atriplex verrucifera* and *Lycium ruthenicum* (Solanaceae) (Wu, 1980). *Halocnemum strobilaceum* is very tolerant to salinity, and thus plants of this species can grow naturally in soil with a total salt content of 38% (soil dry-weight basis) in the 0–10 cm soil depth layer and of 29% in the 10–30 cm layer. They can even survive in soil covered by a 5–10 cm layer of salt crust (Wu, 1980).

Although the effect of salinity on seed germination of *H. strobilaceum* from 'salt steppes' in the Mediterranean region of south-eastern Spain has been investigated by Pujol *et al.* (2000, 2001), there are few studies on the responses of this species to other environmental factors such as temperature and light (Song *et al.*, 2006). Most importantly, different ecotypes of the same species occurring in different habitats may have different adaptation strategies to the special environmental conditions during seed germination and seedling growth in their local sites. To this end, the present study investigated the seed germination ecophysiology of *H. strobilaceum* in salt deserts of China. The specific goals of this research were to (a) test the effect of temperature, light/dark and salinity on seed germination and of salinity on seed germination recovery, radicle growth and radicle elongation recovery using seeds collected from the temperate cold desert of north-west China; and (b) compare the responses of seeds of the geographically widespread *H. strobilaceum* from the cold desert of north-west China with those from the Mediterranean region of Spain reported by Pujol *et al.* (2000, 2001).

MATERIALS AND METHODS

Seeds and field site description

Seeds of *H. strobilaceum* (Pall.) M. Bieb. are oblate and brown with small dense protuberances on the surface. The embryo is fully developed and located in a peripheral position, rarely encircling the endosperm. Thus, the type of seed produced by *H. strobilaceum* is peripheral (Martin, 1946). The mean (\pm s.e.) mass of four groups of 1000 seeds

each was 86.25 ± 4.23 mg, and the mean (\pm s.e.) seed diameter ($n = 20$) was 0.66 ± 0.02 mm.

Mature seeds were collected in November 2004, from plants of *H. strobilaceum* growing in a salt desert near the Fukang Desert Ecological Station of the Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences ($87^{\circ}45' - 88^{\circ}05'E$; $43^{\circ}45' - 44^{\circ}30'N$; 460 m a.s.l.). This area is a temperate inland desert in the hinterland of the Eurasian continent. The site has typical desert vegetation, alkali-saline grey desert soil and a continental climate. Mean annual temperature is $6.6^{\circ}C$ and mean temperatures of the coldest (January) and hottest (July) months are -17 and $25.6^{\circ}C$, respectively. Annual precipitation (including rain and snow) is 164 mm, 66% of which occurs in spring and summer, and in winter snow covers the ground to a depth of only 3–29 mm. Annual potential evaporation is >2000 mm. Salts accumulate on the soil surface in the dry season; however, salt concentration is diluted by water from melting snow in spring and by rain in summer (Li, 1990).

Soil samples collected from ten randomly chosen areas within the study population of *H. strobilaceum* in November 2004 and analysed by the residue drying quality measure (Bao, 2000) had mean (\pm s.e.) total soil salinities in the 0–2, 2–5 and 5–10 cm soil layers of $0.65 \pm 0.03\%$, $1.66 \pm 0.06\%$ and $1.83 \pm 0.07\%$, which are equal to NaCl concentrations of 0.11 ± 0.005 , 0.28 ± 0.010 and 0.31 ± 0.012 M, respectively. Since there were few or no differences between the effects of NaCl, Na_2SO_4 , $MgCl_2$ and $MgSO_4$ on germination of *H. strobilaceum* in the present study (unpublished data) or in that of Pujol *et al.* (2000), data only for NaCl are presented. Another reason for considering only NaCl is that apparently it is the major component of salinity in the deserts of north-west China (Fan *et al.*, 1993; Tobe *et al.*, 2000). Minimum and maximum soil salinities in the study site were 0.02 and 0.88 M NaCl, respectively.

Seeds were incubated in 50 mm diameter Petri dishes on three layers of Whatman No. 1 filter paper moistened with 2.5 ml of deionized water or with different concentrations of NaCl solution. Petri dishes were sealed by plastic film to prevent evaporation. An emerged radicle was the criterion for germination (Côme, 1982).

Effects of temperature and light on germination

Seeds that had been stored dry at $4^{\circ}C$ for 1 month were incubated at 5, 10, 15, 20, 25, 30 and $35^{\circ}C$ in constant fluorescent light ($100 \mu mol m^{-2} s^{-1}$, 400–700 nm; hereafter light) and in constant darkness. Germination in the light was monitored every 24 h, at which time germinated seeds were counted and removed from the Petri dishes. After 15 d, when no additional seeds had germinated for 5 d, experiments in light were terminated, and seed germination in darkness was checked first and only at this time.

Effects of salinity on germination and recovery

The effects of 0.0 (deionized water control), 0.1, 0.2, 0.3, 0.4, 0.5, 0.75, 1.0, 2.0, 4.0 and 6.0 M concentrations of NaCl

on germination of seeds (stored dry at 4 °C for 3 months) were tested at 25 °C in the light. Germination was monitored every 24 h, and germinated seeds were counted and removed from the dishes. The time taken for germination percentages of all the replicates to reach 50 % was recorded as TG_{50} (Tobe *et al.*, 2000). Final germination percentages were calculated after incubation for 15 d.

Ungerminated seeds from the 15 d NaCl pre-treatments were rinsed three times in deionized water and then incubated in deionized water. Seed germination recovery was monitored every 24 h, at which time germinated seeds were counted and removed from the dishes. The time taken for germination recovery percentages of all the replicates to reach 50 % was recorded as TG_{r50} . Final germination recovery percentages were calculated after 15 d of incubation using the following formula:

$$[(A - B)/(C - B)] \times 100$$

where *A* is the number of seeds germinated in salt solutions plus those that recovered to germinate in the deionized water, *B* is the number of seeds germinated in salt solutions and *C* is the total number of seeds tested (Khan and Ungar, 1984). Final germination was recorded as $(A/C) \times 100$.

Effects of salinity on radicle growth and recovery

Seeds stored dry at 4 °C for 3 months were incubated initially in deionized water at 25 °C in the light. When the radicles had barely emerged (<1.0 mm), 20 of these young seedlings were transferred into Petri dishes containing 0.0 (deionized water control), 0.1, 0.2, 0.3, 0.4, 0.5, 0.75, 1.0, 2.0 and 3.0 M NaCl solutions. Seedling incubation was terminated after 10 d and mean radicle length recorded. Then, seedlings incubated in different NaCl concentrations for 10 d were rinsed three times with deionized water and transferred to filter paper saturated with deionized water for an additional 10 d, at which time final radicle lengths of the seedlings were measured.

Data analysis

Seed germination percentage and radicle length were expressed as mean ± s.e. One-way or two-way analysis of variance (ANOVA; $P < 0.05$) was used to compare treatment effects (Sokal and Rohlf, 1995). If ANOVA showed significant effects, Tukey's test was used to determine differences among treatments.

RESULTS

Effects of temperature and light on germination

After 15 d of incubation, the germination percentage over the 10–35 °C temperature range was significantly higher in light than in darkness ($P < 0.001$) (Fig. 1). Germination percentages in the light and in darkness increased significantly with the increase in temperature ($P < 0.001$). Although seeds germinated to a high percentage at 35 °C, seedlings were distorted, or they died.

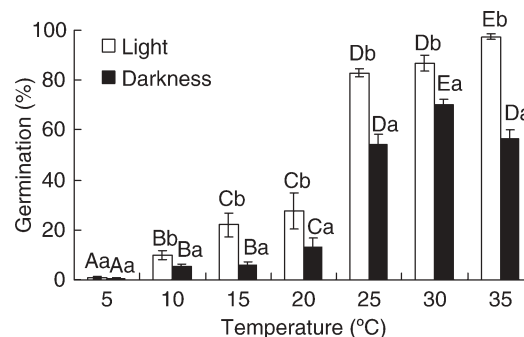


FIG. 1. Effect of temperature and light on germination of *Halocnemum strobilaceum* seeds after 15 d of incubation in deionized water. Different upper case letters indicate significant differences in germination percentage across the range of temperatures for seeds incubated in the light and for those incubated in the dark, and different lower case letters indicate significant differences between seeds incubated in the light and darkness at a given temperature. Values are means ± s.e.

A two-way ANOVA showed that germination was significantly affected by temperature, light and their interaction (Table 1).

Effects of salinity on germination and recovery

Germination was significantly affected by salinity ($P < 0.001$). As salinity increased from 0.0 to 0.5 M NaCl, the rate and percentage of germination decreased, and it was significantly inhibited by higher salinities (Fig. 2). No seeds germinated at salinities of ≥ 0.75 M. At NaCl concentrations of 0–0.3 M, TG_{50} increased, i.e. germination rate decreased. Seed germination percentage did not reach 50 % (TG_{50}) at salinities exceeding 0.3 M until after 15 d of incubation (Table 2). As the pre-treatment concentration of salinity increased, the percentage and rate of germination recovery increased, and for all salinities germination recovery percentages were significantly higher than that of the control ($P < 0.001$). Even seeds pre-treated with 6.0 M NaCl recovered. Germination recovery did not differ significantly among seeds transferred from 2.0–6.0 M NaCl solutions to deionized water ($P > 0.05$).

Effects of salinity on radicle growth and recovery

Concentrations of 0.1–0.3 M NaCl significantly increased radicle elongation ($P < 0.001$), whereas concentrations of 0.75–3.0 M significantly inhibited it ($P < 0.001$). No radicle elongation occurred at NaCl concentrations of ≥ 2.0 M (Fig. 3). Radicle growth recovered after seedlings

TABLE 1. Two-way ANOVA analysis of effects of temperature, light and their interactions on seed germination of *Halocnemum strobilaceum*

Source of variance	d.f.	SS	MS	F-value	P-value
Temperature	5	443.107	88.621	207.167	<0.001
Light	1	21.870	21.870	51.125	<0.001
Temperature × light	5	9.890	1.978	4.624	0.002

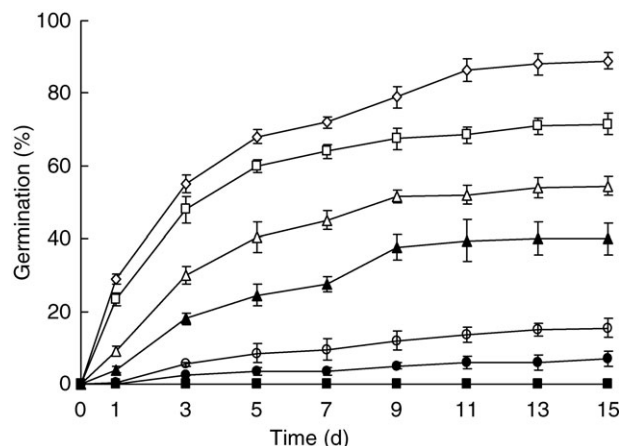


FIG. 2. Effect of NaCl concentration on germination of *Halocnemum strobilaceum* seeds incubated at 25 °C in the light for 15 d. (1) Open diamond, deionized water (control); (2) open square, 0.1 M NaCl; (3) open triangle, 0.2 M NaCl; (4) filled triangle, 0.3 M NaCl; (5) open circle, 0.4 M NaCl; (6) filled circle, 0.5 M NaCl; (7) filled square, 0.75 and 1.0 M NaCl. Values are means \pm s.e.

were transferred to deionized water. However, elongation recovery decreased with the increase in pre-treatment salinities. Seedlings from solutions ≥ 3.0 M NaCl showed no capacity for recovery (Fig. 4).

DISCUSSION

In the life cycle of a plant, seeds have the highest resistance to extreme environmental stresses, whereas seedlings are most susceptible, and this is especially true for desert species (Gutterman, 1993). Therefore, successful establishment of a plant population is dependent on the adaptive aspects of seed germination and of early seedling growth. Germination of many halophytes occurs when the combination of photoperiod, temperature regime, soil water and

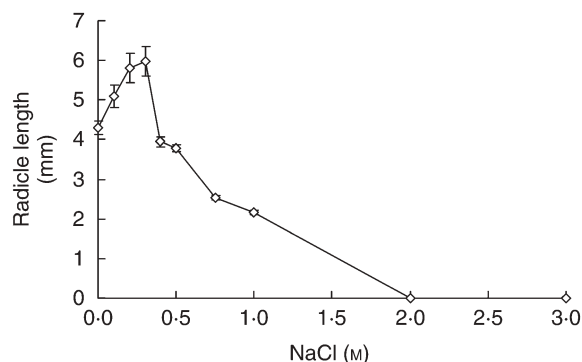


FIG. 3. Effect of NaCl concentration on radicle elongation of *Halocnemum strobilaceum* at 25 °C in the light after 10 d of incubation. Values are means \pm s.e.

soil salinity is optimal for plant growth (Naidoo and Naicker, 1992; Gutterman, 1993; Zia and Khan, 2004). Thus, for example, seeds of perennial plants in the *Artemisietum herbae-albae* plant community type of the Negev Desert, Israel, germinate *en masse* only once in several years (Evenari and Gutterman, 1976).

Germination percentages of *H. strobilaceum* seeds were higher in light than in darkness at all temperatures tested, indicating that a considerable portion of the seed population is light sensitive. This characteristic of *H. strobilaceum* is similar to that of the desert shrubs *Artemisia monosperma* (Asteraceae) (Huang and Gutterman, 1998), *A. sphaerocephala* (Huang and Gutterman, 1999b) and *A. ordosica* (Huang and Gutterman, 2000). The light requirement for germination of *H. strobilaceum* seeds ensures that they will germinate successfully on or near the soil surface when other conditions are suitable for seedling emergence. If buried at soil depths to which light cannot penetrate, they may become part of a persistent soil seed bank. Song *et al.* (2006) reported that *H. strobilaceum* seeds could germinate to high percentages when they were incubated in continuous darkness. However,

TABLE 2. Effects of NaCl on germination and its recovery in deionized water of seeds of *Halocnemum strobilaceum*

Salinity (M)	Seed germination (% \pm s.e.)				
	Initial solution, B/C \times 100	Recovery* [(A - B)/(C - B)] \times 100	Final [†] , A/C \times 100	TG ₅₀ (d)	TG _{r50} (d)
0	89.0 \pm 1.3 ^a	17.5 \pm 6.8 ^a	91.5 \pm 1.7 ^a	3	>15
0.1	73.5 \pm 4.9 ^b	43.8 \pm 4.8 ^b	84.5 \pm 3.8 ^b	4	>15
0.2	54.5 \pm 3.0 ^c	58.8 \pm 8.6 ^c	79.5 \pm 2.6 ^{cde}	12	>15
0.3	40.0 \pm 4.4 ^d	62.8 \pm 7.0 ^c	76.0 \pm 5.9 ^{def}	>15	4
0.4	15.5 \pm 2.8 ^e	68.3 \pm 4.1 ^c	73.5 \pm 2.6 ^f	>15	4
0.5	7.0 \pm 1.7 ^e	73.5 \pm 2.6 ^{cd}	75.5 \pm 1.0 ^f	>15	4
0.75	0	74.5 \pm 1.0 ^d	74.5 \pm 1.0 ^f	>15	3
1.0	0	77.0 \pm 1.7 ^d	77.0 \pm 1.7 ^{ef}	>15	3
2.0	0	88.0 \pm 2.8 ^e	88.0 \pm 2.8 ^{ab}	>15	3
4.0	0	85.5 \pm 2.4 ^c	85.5 \pm 2.4 ^b	>15	2
6.0	0	84.5 \pm 2.8 ^c	84.5 \pm 2.8 ^{bcd}	>15	2

* Recovery is the percentage of ungerminated seeds in the NaCl pre-treatment solution that germinated after transfer to deionized water [(A - B)/(C - B)] \times 100, where A is the sum of the number of seeds germinated in the salt solutions plus the number that recovered to germinate in deionized water, B is the number of seeds germinated in the initial salt solutions and C is the total number of seeds tested.

[†] Final germination was recorded as (A/C) \times 100, where A is the sum of the number of seeds germinated in salt solutions and of those that recovered to germinate in the deionized water, and C is the total number of seeds tested.

Values followed by the same letter do not differ significantly.

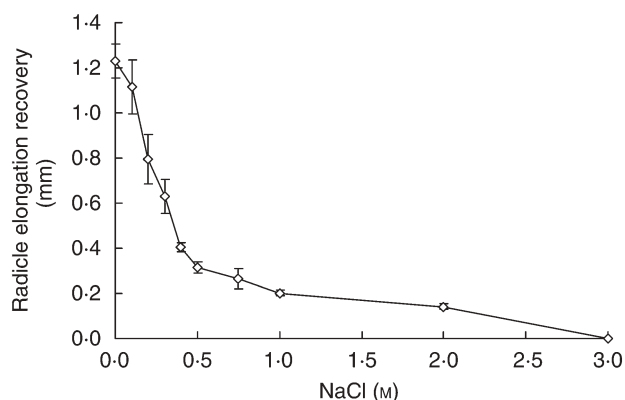


FIG. 4. Radicle elongation recovery in *Halocnemum strobilaceum* after transfer from different concentrations of NaCl to deionized water. Radicle length recovery was recorded after 10 d of incubation in deionized water at 25 °C in the light. Values are means \pm s.e.

they monitored germination daily but do not say if seeds were examined under a green ‘safe light’ or under ‘white light’. If the latter, then they did not incubate seeds in ‘continuous’ darkness. In which case, the seeds of *H. strobilaceum* probably were light stimulated as they were being checked daily for germination (Baskin and Baskin, 1998). This could explain why seeds of *H. strobilaceum* germinated to higher percentages in the dark in the Song *et al.* (2006) study than they did in the present study. Further, even a green ‘safe light’ can satisfy the light requirement of some positively photoblastic seeds (Walck *et al.*, 2000).

Seeds of *H. strobilaceum* germinated to >50 % only at 25, 30 and 35 °C, and at each of these temperatures they germinated to a higher percentage in light than in darkness. These responses are similar to those of seeds of some salt marsh and salt desert species, i.e. the best conditions for germination are high temperatures in light (Baskin and Baskin, 1998). In north-west China, seeds of *H. strobilaceum* mature in November, when the average temperature is <0 °C and thus too low for germination (Fig. 1). In the field, seeds of this species germinate primarily from April to July. Thus, seed germination begins in spring, when soil moisture is high, due to snow melt, and average temperatures are 0–10 °C. However, in light, only 5–35 % of the seeds of *H. strobilaceum* germinated even at 10–20 °C, whereas >80 % of the seeds germinated at 25–35 °C, which is coincident with temperatures in its natural habitat in July. In this summer rainy season, rain-water washes away salts on the soil surface and at shallow depths. Thus, seeds heretofore prevented from germinating can germinate under this optimal combination of low salinity, high soil moisture and high temperatures. The ability of seeds of *H. strobilaceum* to germinate in spring to early summer, when soil moisture is available for seedling establishment, is a life history/ecophysiological adaptation of this species to its dry saline desert habitats.

Halophyte seeds respond to salinity in two ways: (a) germination is inhibited by high salinity, but seeds do not lose their viability; and (b) salinity stress delays germination but does not induce dormancy or kill the seeds (Ungar, 1978, 1995; Levitt, 1980). Seeds of *Salicornia*

rubra and *Halogeton glomeratus* even germinated in a 1.0 M NaCl solution (Khan *et al.*, 2000, 2001), and *Salicornia bigelovii* seeds did so in a 0.856 M NaCl solution (Rivers and Weber, 1971). However, seeds of *Salicornia pacifica* var. *utahensis* germinated to only 3 % in a 0.856 M NaCl solution (Khan and Weber, 1986), and those of *Allenrolfea occidentalis* (Chenopodiaceae) did not germinate when salinity exceeded 0.8 M NaCl (Gul and Weber, 1999). Although germination of *H. strobilaceum* seeds decreased with increase in salinity, 7 % of them germinated in a 0.5 M NaCl solution. Song *et al.* (2006) also found that only a low percentage of *H. strobilaceum* seeds germinated at 0.5 M NaCl. Cold stratification caused a significant increase in germination of *H. strobilaceum* seeds incubated at 0.2, 0.4 and 0.6 M NaCl at 25 °C in the light (Qu, 2006). In general, the difference between germination percentages of seeds at low salinities and that in deionized water is insignificant, but they gradually decrease with further increase of salinity (Khan and Ungar, 1997; Katembe *et al.*, 1998; Gul and Weber, 1999; Khan *et al.*, 2000; Huang *et al.*, 2003).

Seeds of most halophytes exposed to salinities that inhibit germination will recover and germinate after they are transferred to distilled water. Further, final germination percentages are even increased by salt pre-treatment in most species (Khan and Ungar, 1997; Gul and Weber, 1999; Khan *et al.*, 2000; Huang *et al.*, 2003). For example, seeds of *Allenrolfea occidentalis* recovered to germinate rapidly and to high percentages after they were transferred from high salinity solutions to distilled water (Gul and Weber, 1999). The recovery germination percentage was about 20 % in *Haloxyton ammodendron* seeds pre-soaked in a 0.2 M NaCl solution, but about 56 % in those pre-soaked in solutions of 0.8–1.4 M NaCl (Huang *et al.*, 2003). However, seed germination of some species is permanently inhibited by high salinity. For instance, seeds of *Zygophyllum simplex* (Zygophyllaceae) could hardly recover to germinate after they were transferred from a high salinity solution to distilled water (Khan and Ungar, 1997). In the present experiments, ungerminated seeds of *H. strobilaceum* germinated well after they were transferred from solutions of high salinity to deionized water. Germination recovery increased gradually with increase of pre-treatment salinity and was quite high even for seeds pre-treated in a 6.0 M NaCl solution, which is near the molarity of a saturated solution of NaCl. Thus, seeds of *H. strobilaceum* are well adapted to saline habitats via a high capacity for germination recovery.

The mean salinity of soil collected at ten sites in the present study area ranged from 0.11 to 0.31 M at a 0–10 cm depth, and minimum and maximum soil salinity across all sites were 0.02 and 0.88 M NaCl, respectively. Wu (1980) reported that plants of *H. strobilaceum* are highly tolerant to salinity, and they can grow naturally in soil with a total salt concentration of 38 % (equal to 6.5 M NaCl) in the 0–10 cm soil layer and of 29 % (equal to 5.0 M NaCl) in the 10–30 cm depth layer. They even can survive in soil covered by a 5–10 cm layer of salt crust. In sites where the soil salinity is \leq 0.5 M NaCl, seeds of *H. strobilaceum* can germinate successfully. However, in sites where soil salinity exceeds 0.5 M NaCl, seeds do not

germinate, and thus they may remain in the soil seed bank until the salt is diluted by water from melting snow or until precipitation, temperature and light are not limiting for germination. As such, soil salinity could act as a 'rain gauge' for seed germination (Gutterman, 1993), in which case it would play an important ecological role in the successful establishment of *H. strobilaceum* populations.

Seedlings of halophytes can develop in solutions with low concentrations of salts; however, radicle growth may be greatly retarded by high salinity (Malcolm *et al.*, 2003). As expected, growth of *H. strobilaceum* radicles was increased by low salinities (≤ 0.3 M) and decreased by high salinities (≥ 0.5 M). These physiological responses are similar to those of *Annona muricata* and *A. squamosa* (Annonaceae), in which inhibition of radicle elongation was significantly related to increase in salinity (Passos *et al.*, 2005). Tobe *et al.* (2000) found that although 0.1–0.2 M NaCl solutions did not affect the viability of *Kalidium caspicum* seeds, they promoted mortality of radicles. However, young roots of *H. strobilaceum* have high salinity tolerance (up to 1.0 M) and recovery ability (up to 2.0 M). Thus, for successful establishment of *H. strobilaceum* seedlings, the high salinity on the soil surface and at shallow soil depths needs to be diluted by precipitation or by melt water from snow. During the rainy season in spring and summer, the salinity on the soil surface would be decreased by precipitation, and then seeds could germinate successfully and seedlings become established. In the desert area near the Dead Sea, seedlings of *Mesembryanthemum nodiflorum* (Aizoaceae) appear in the winter, only after several rains, which dilute the salt accumulated during the summer from the upper layer of the soil. The seeds of this halophyte do not germinate in high salinity, and seedlings appear mainly in depressions and runnels, where more water penetrates into the soil (Gutterman, 1980/81).

Germination of seeds of *H. strobilaceum* from both north-west China and southeastern Spain decreased with increase in salinity. However, seeds from southeastern Spain could germinate at a higher salinity [0.86 M NaCl (Pujol *et al.*, 2001)] than those from north-west China (0.5 M NaCl). Germination recovered rapidly after seeds of *H. strobilaceum* from both Spain and China were transferred to fresh water, but the recovery rate of seeds from southeastern Spain ($TG_{r50} = 2$ d) (Pujol *et al.*, 2000) was a little faster than that of seeds from north-west China ($TG_{r50} = 3-4$ d). Growth of seedlings of *H. strobilaceum* from both southeastern Spain and north-west China was stimulated at low salinities [0.17–0.51 M NaCl, southeastern Spain (Pujol *et al.*, 2001) and ≤ 0.3 M NaCl, north-west China] but completely inhibited at higher salinities [≥ 0.68 M NaCl, southeastern Spain (Pujol *et al.*, 2001) and ≥ 0.75 M NaCl, north-west China]. Thus, tolerance to salinity of seedlings from southeastern Spain apparently is higher than that of those from north-west China.

In north-west China, *H. strobilaceum* occurs in inland salt deserts, where the amount and frequency of precipitation are highly unpredictable, resulting in periods of salt and drought stress. The ability of *H. strobilaceum* seeds to germinate at low salinity and to recover from high salinity,

and of seedlings to grow in low salinity, survive at high salinity and resume growth after the soil solution is diluted by water is an adaptation to its saline desert habitat. When salinity is high in the dry season, seeds do not germinate, but they do germinate when salinity is diluted by precipitation. Although evaporation following precipitation will decrease soil water potential, radicles of *H. strobilaceum* can continue to elongate. When evaporation and soil salinity are low, radicle elongation is even accelerated. Thus, following an increase in soil moisture, seedlings of *H. strobilaceum* can resume growth and their roots can grow to a sufficient soil depth to become established before the next rain occurs. Clearly, then, the seed germination and early seedling growth stages of the life cycle of *H. strobilaceum* are parts of the adaptive strategy of this species that allows it to inhabit harsh saline conditions such as those in the deserts of north-west China.

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