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Effects of sodium chloride on seed germination and growth of two Chinese desert shrubs, *Haloxylon ammodendron* and *H. persicum* (Chenopodiaceae)

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Abstract. The effects of sodium chloride (NaCl), polyethylene glycol-6000, temperature and light on germination and the effects of NaCl on growth were investigated in two Chinese desert shrubs, *Haloxylon ammodendron* (C.A.Mey.) Bunge and *H. persicum* Bunge ex Boiss. et Buhse. Both species occur in non-saline sand dunes; *H. ammodendron* also occurs in saline land, although it is not dominant there. Percentage germination of *H. ammodendron* and *H. persicum* in -3.0 MPa (667 mmol kg⁻¹) NaCl was 91 and 64%, respectively. Hydroponic culture of each species for *c.* 3 months with NaCl solutions of 0, 200, 400 and 600 mmol kg⁻¹ showed that the survival of *H. ammodendron* was highest (82.3%) at 400 mmol kg⁻¹ NaCl, while that of *H. persicum* decreased with increasing NaCl concentration and was low (11.1%) at 400 mmol kg⁻¹ NaCl. Sodium concentration in shoot tissues of 99-day-old seedlings grown at 400 mmol kg⁻¹ NaCl exceeded 1000 mmol kg⁻¹ in both species, while Na concentration in non-transpiring young seedlings grown in 400 mmol kg⁻¹ NaCl was 240 and 350 mmol kg⁻¹ for *H. ammodendron* and *H. persicum*, respectively. The results indicate that both species have relatively low adaptability to salinity at the older seedling stage compared with that at the germination and young seedling stage, and that *H. ammodendron* shows higher adaptability to salinity at the older seedling stage than *H. persicum*. It was concluded that salinity adaptability in the later developmental stage of these species determines their distribution with respect to salinity.

Introduction

In order for plants to become established in saline environments, adaptation at both the germination and mature stage is crucial (Ungar 1991, 1995). There have been many studies on the effects of salinity at both the germination and later developmental stages (e.g. West and Taylor 1981; Stumpf *et al.* 1986; Partridge and Wilson 1987; Ungar 1996). However, it is still unclear how adaptation to salinity at different developmental stages is correlated with the distribution of species in locations with different degrees of salinity (Ungar 1991). It is also unclear how salt accumulation in plant tissues is related to adaptation of species to salinity.

Haloxylon ammodendron (C.A.Mey.) Bunge and *H. persicum* Bunge ex Boiss. et Buhse (Chenopodiaceae) are shrubs found in desert regions of north-western China (Fu and Jin 1992). *Haloxylon ammodendron* occurs on both saline and non-saline lands, although it is not a dominant species on saline land. In contrast, *H. persicum* is found only on non-saline land. In both species, the leaves are very small and the green branches photosynthesise. The seeds of these species have no

endosperm and only a fully differentiated spiral seedling coated by pericarp. The germination process of this type of seed seems to consist simply of water absorption by the dry spiral seedling and its subsequent stretching (Wallace *et al.* 1968; Sharma and Sen 1989). In China, both species serve as livestock feed and firewood, and are also planted in sand dunes to stabilise them (Fu and Jin 1992).

It is unclear why only *H. ammodendron* occurs on saline land, while *H. persicum* is limited to non-saline land. The present study was undertaken to investigate at what developmental stage their geographical distribution is determined. Because sodium chloride (NaCl) is the most abundant salt in many salinised locations in Chinese desert (Fan *et al.* 1993), it was used to examine the responses of plants to salinity. We examined the effects of moistening with polyethylene glycol (PEG)-6000 and NaCl solutions on the germination of these two species. Seed longevity, responses of germination to temperature and light were also examined because these factors determine the time and locations of germination, and could affect the feature of responses of seeds to salinity. The

effects of NaCl on survival and growth of transpiring older seedlings were also investigated. Additionally, ion concentrations in plants treated with different concentrations of NaCl were examined in both non-transpiring young seedlings and shoots of transpiring older seedlings.

Materials and methods

Seeds

Seeds of *H. ammodendron* (seed weight: (mean \pm s.e.) 3.48 ± 0.48 mg; $n = 20$) and *H. persicum* (seed weight: (mean \pm s.e.) 5.89 ± 0.87 mg; $n = 20$) were collected soon after ripening in November of 1995 and 1997 from plants growing in a non-saline location in the Turpan Botanical Garden of the Xinjiang Institute of Pedology, Biology and Desert Research, Turpan, China ($42^{\circ}56'N$, $89^{\circ}2'E$) and irrigated regularly. The collected seeds were initially stored at *c.* $5^{\circ}C$ until transport to Japan in the following January or March. After transport to Japan, most of the seeds were stored at *c.* $-18^{\circ}C$ to avoid loss of germinability, and the germination experiments were carried out within 12 months after the ripening of the seeds; some seeds were stored either at *c.* $23^{\circ}C$ for 11 months or at *c.* $2^{\circ}C$ or *c.* $-18^{\circ}C$ for 23 months to examine their longevity at different temperatures.

Experiments at germination and young seedling stage

In all the experiments on germination and young seedling stage, 25 seeds were sown in 90-mm Petri dishes on three layers of filter paper (Toyo, No.1) moistened with 10 mL of deionised water or a solution of NaCl or PEG-6000. The Petri dishes were covered with lids and maintained at a constant temperature in an incubator. About two-thirds of the volume of the water or solution in each Petri dish was replaced daily to avoid change in the Ψ_w of the solution. The seeds were considered to have germinated when the emerging seedlings had almost completely uncoiled and elongated to a length exceeding 10 mm.

(a) Seed longevity

Seeds stored at different temperatures for 11 or 23 months were moistened with deionised water and maintained at $20^{\circ}C$ in darkness for 10 days. Seed viability was evaluated by the final percentage germination.

(b) Effects of temperature and light on seed germination

Seeds were moistened with deionised water and maintained at a constant temperature (5 – $35^{\circ}C$) in either under continuous darkness or continuous illumination with fluorescent lamps (photon flux density at the surface of the seeds: 80 – $90 \mu\text{mol m}^{-2}\text{s}^{-1}$ over the waveband 400 – 700 nm) for 10 days.

(c) Effects of NaCl and PEG on seed germination

Seeds were moistened with either deionised water or a NaCl or PEG-6000 solution of a known water potential (Ψ_w) between -1.0 and -6.0 MPa and maintained at $20^{\circ}C$ in continuous darkness for 21 days. NaCl solutions of known Ψ_w were prepared according to Lang (1967). Solutions of PEG-6000 were prepared so that each was almost isotonic

with the corresponding NaCl solution; the Ψ_w of the PEG solutions was determined with an isopiestic psychrometer (Boyer and Knipling 1965) at $20^{\circ}C$ with NaCl solutions of known Ψ_w as standards.

(d) Na and K concentrations in young seedlings

Sodium and potassium concentrations in young seedlings were measured after moistening the seeds with water or a solution of NaCl (200 , 400 , or 600 mmol kg^{-1}) for 1–3 days, until they had germinated and the seedlings had elongated to a length of *c.* 20 mm; thereafter, 40 – 60 seedlings were blotted dry and quickly weighed, dipped into water and quickly blotted dry again to remove salt on their surface, and dried at $80^{\circ}C$ for more than 3 days. After determining the dry weights of the seedlings, they were ground, decomposed with HNO_3 on a hot plate, and finally dissolved in a 100 -mL aqueous solution, which was analysed for Na and K content by ICP spectrometry (ICAP-750, Nippon Jarrell-Ash, Japan). From the results, Na and K concentrations expressed on a tissue water basis were calculated.

Experiments at older seedling stage

Experiments were carried out in a greenhouse (temperature, $25^{\circ}C$; relative humidity, 60%). Each species was grown in wet coarse sand for the first week after sowing the seeds; thereafter, seedlings with a height of 50 – 70 mm were transferred to four 15 -L tanks filled with a nutrient solution ($6 \text{ mmol kg}^{-1} \text{ KNO}_3$, $4 \text{ mmol kg}^{-1} \text{ Ca}(\text{NO}_3)_2$, $4 \text{ mmol kg}^{-1} \text{ NH}_4\text{H}_2\text{PO}_4$, $2 \text{ mmol kg}^{-1} \text{ MgSO}_4$, $54 \mu\text{mol kg}^{-1} \text{ Fe-EDTA}$, $46 \mu\text{mol kg}^{-1} \text{ H}_3\text{BO}_3$, $9.1 \mu\text{mol kg}^{-1} \text{ MnCl}_2$, $0.32 \mu\text{mol kg}^{-1} \text{ CuSO}_4$, $0.76 \mu\text{mol kg}^{-1} \text{ ZnSO}_4$, $0.56 \mu\text{mol kg}^{-1} \text{ Na}_2\text{MoO}_4$), so that the roots were immersed in the solution. Seventeen or 18 seedlings each of the two species were transferred to each tank. One week after the transfer, NaCl was added daily for 1 week to three of the tanks so that their final NaCl concentrations became 0 , 200 , 400 , or 600 mmol kg^{-1} ; these NaCl concentrations were maintained throughout the experimental period. The solution in each tank was aerated and renewed once a week. Dead plants and branches were removed. In this study, plants were regarded as dead when most parts of their green branches had died. Ninety-nine days after sowing, the surviving plants were harvested and the fresh weights of roots and shoots were determined. Dry weights of the roots and shoots were measured after oven-drying at $80^{\circ}C$ for more than 3 days. Sodium and potassium concentrations expressed on a tissue water basis in the shoots were determined in some of shoot samples by the method described above.

Results

Seed longevity and effects of temperature and light on seed germination

Percentage germination of seeds stored at *c.* 2 or *c.* $-18^{\circ}C$ for 23 months exceeded 90% in both species. However, percentage germination of seeds stored at *c.* $23^{\circ}C$ for 11 months was $20 \pm 7.1\%$ and $3 \pm 1.0\%$ (mean \pm s.e.) for *H. ammodendron* and *H. persicum*, respectively.

Table 1. Effects of temperature on percentage germination in two *Haloxylon* species
Seeds were moistened with deionised water for 10 days in continuous darkness. Data are means of four replications \pm s.e.

Species	Percentage germination (%) at						
	$5^{\circ}C$	$10^{\circ}C$	$15^{\circ}C$	$20^{\circ}C$	$25^{\circ}C$	$30^{\circ}C$	$35^{\circ}C$
<i>Haloxylon ammodendron</i>	96 ± 3.3	100 ± 0.0	100 ± 0.0	98 ± 2.3	93 ± 6.0	91 ± 2.0	54 ± 8.3
<i>H. persicum</i>	95 ± 3.8	96 ± 3.3	95 ± 3.8	95 ± 2.2	81 ± 8.9	59 ± 8.9	32 ± 9.2

Effects of temperature on the germination was examined (Table 1). For both species, percentage germination exceeded 50% within 1 day after moistening at temperatures of 15–30°C; however, at 5 and 10°C, percentage germination of both species exceeded 50% after 2 and 3 days, respectively (data not provided). The final percentage germination of both species exceeded 50% at temperatures below 30°C (Table 1). For both species, the effect of light illumination on germination was not significant under any temperature regime (Student's *t*-test; $P = 0.05$) (data not provided).

Effects of NaCl and PEG on seed germination

Because both the final percentage germination and germination rate were high at 20°C in both species in the above experiment, the optimal germination temperature can be regarded to be near at 20°C; therefore, effects of NaCl and PEG on seed germination were examined at 20°C.

When the seeds were moistened with solutions of NaCl or PEG, germination in both species was retarded as the Ψ_w decreased: percentage germination after 1 and 2 days was considerably decreased with decreasing Ψ_w in both species in both treatments. (Fig. 1). In NaCl treatment, the final percentage germination was not conspicuously changed with changing Ψ_w at Ψ_w higher than -3.0 MPa (*H. ammodendron*) or -2.0 MPa (*H. persicum*); but it decreased considerably with decreasing Ψ_w at lower Ψ_w (Fig. 2). The final percentage germination of PEG-treated seeds was high at Ψ_w higher than -1.9 MPa (*H. ammodendron*) or -0.9 MPa (*H. persicum*); but at lower Ψ_w , it decreased with decreasing Ψ_w , and was almost zero for both species when Ψ_w was lower than -4.1 MPa (Fig. 2). For the NaCl treatment, the final percentage germination was higher between -3.0 and -6.0 MPa in *H. ammodendron* than in *H. persicum* (Fig. 2). The final percentage germination of seeds treated with PEG solutions of -1.9 and -3.1 MPa was lower in *H. persicum* than in *H. ammodendron*. The inhibitory effect on germination was considerably less for both species in NaCl than in isotonic PEG solutions (Fig. 2).

Although seedling elongation in both species was considerably slower with decreasing Ψ_w of the solution for both the NaCl and PEG treatments, the emerging seedlings continued to elongate until their length exceeded 10 mm (data not provided). Furthermore, no visible evidence was detected of any injurious or toxic effects on the seedlings from the NaCl or PEG solutions.

Concentrations of Na and K in young seedlings

When seeds were moistened with either water or a solution of NaCl, the time taken by the emerging seedlings to reach a length of *c.* 20 mm became longer as the NaCl concentration in the external medium increased (data not provided).

As the external NaCl concentration increased, Na concentration in the seedlings increased in both species (Fig. 3). The concentration of K decreased with increasing NaCl concen-

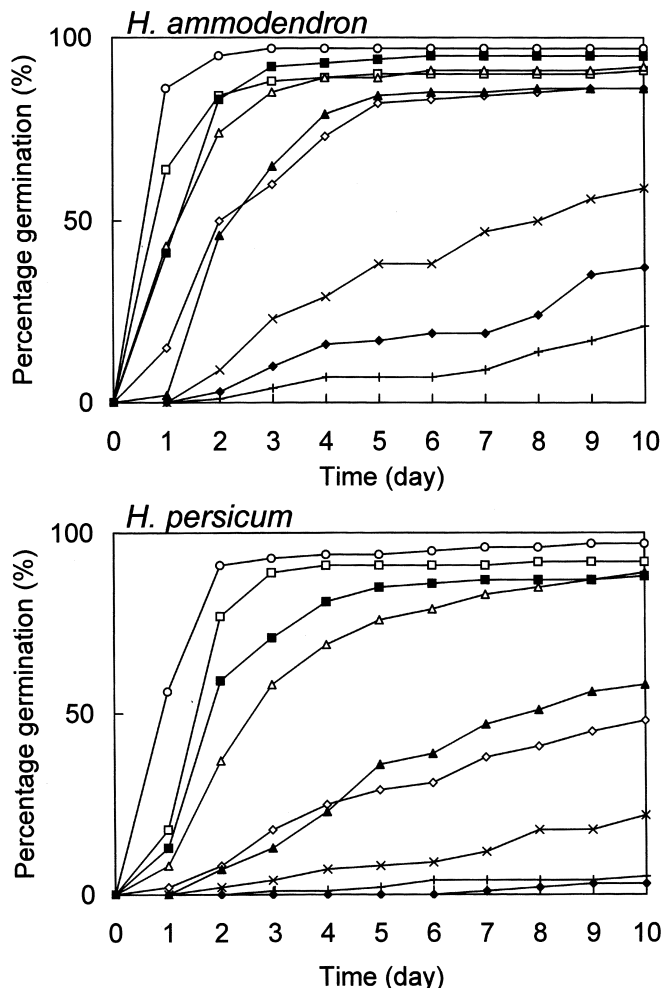


Fig. 1. Changes over time in percentage germination in the initial 10 days when the seeds were moistened with deionised water (○), a NaCl solution of -1.0 MPa (223 mmol kg^{-1}) (□), -2.0 MPa (446 mmol kg^{-1}) (△), -3.0 MPa (667 mmol kg^{-1}) (◇), -4.0 MPa (883 mmol kg^{-1}) (×) or -5.0 MPa ($1095 \text{ mmol kg}^{-1}$) (+) or a PEG solution of -0.9 MPa (■), -1.9 MPa (▲), -3.0 MPa (◆) in continuous darkness at 20°C. Each point represents the mean of four replications.

tration in the external medium (Fig. 3) because of the increasing duration of exposure of the seedlings to water or solutions and resultant more leakage of K from them. Both the increase in Na concentration and the decrease in K concentration in the seedlings with increasing external NaCl concentration were more pronounced in *H. persicum* than in *H. ammodendron*.

Effect of NaCl on growth and ion concentrations in shoots

When hydroponically cultivated, the branches of all plants treated with NaCl (200 – 600 mmol kg^{-1}) became succulent (branch diameter 2.0 – 3.0 mm) in both species, while the branches of all plants that were not treated with NaCl (0 mmol kg^{-1}) remained non-succulent (branch diameter 1.0 – 1.5 mm). Some plants in both species died (Table 2); for both species, shoot death preceded the death of the roots.

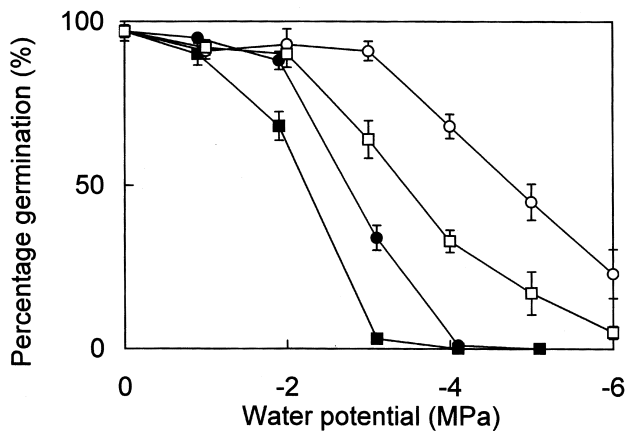


Fig. 2. Percentage germination 21 days after moistening seeds of *H. ammodendron* (○, ●) and *H. persicum* (□, ■) with deionised water (at 0 MPa), or NaCl (○, □) or PEG (●, ■) solutions with different Ψ_w (water potential) in continuous darkness at 20°C. Corresponding NaCl concentration is shown in the legend of Fig. 1. Each point represents the mean of four replications; error bars indicating s.e. are shown only where s.e. was larger than point size.

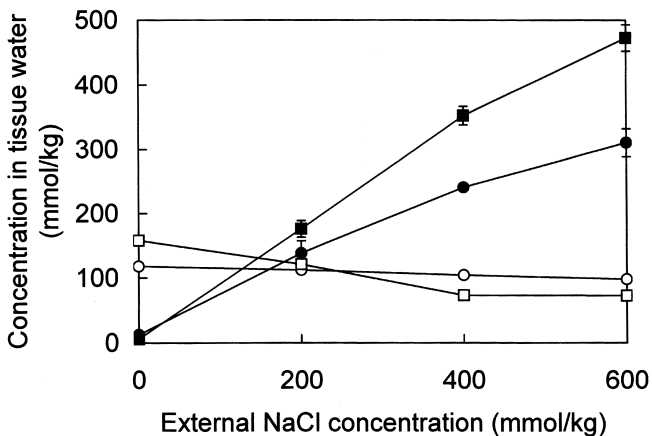


Fig. 3. Sodium (●, ■) and potassium (○, □) concentrations in *c.* 20-mm-long seedlings of *H. ammodendron* (○, ●) and *H. persicum* (□, ■) as a function of the NaCl concentration in the external medium in which the seeds were germinated at 20°C. Each point represents the mean of five replications; error bars indicating s.e. are shown only where s.e. was larger than point size.

Marked differences in response to NaCl between *H. ammodendron* and *H. persicum* were detected (Table 2). While *H. ammodendron* showed highest survival at 400 mmol kg⁻¹ NaCl, survival of *H. persicum* decreased with increasing NaCl concentration and was zero at 600 mmol kg⁻¹ NaCl (Table 2). Highest mean dry weight of surviving plants was between 200 and 400 mmol kg⁻¹ NaCl for *H. ammodendron* and at 200 mmol kg⁻¹ NaCl in *H. persicum* in both shoots and roots (Table 2).

In 0 mmol kg⁻¹ NaCl treatment, the mean Na concentration of *H. ammodendron* was about nine times higher than that of *H. persicum*. Sodium concentration in *H. persicum*

shoots continued to increase beyond 200 mmol kg⁻¹ external NaCl concentration, whereas that of *H. ammodendron* shoots remained at about 1000 mmol kg⁻¹ in external NaCl concentrations of 200–600 mmol kg⁻¹ (Fig. 4). In both species, K concentration decreased when external NaCl concentration increased from 0 to 200 mmol kg⁻¹, but did not show marked changes with changing external NaCl concentration at higher external NaCl levels.

Discussion

In typical habitats of these species in China, annual precipitation is *c.* 200 mm or less; monthly mean temperature is lower than 0°C from November to March and 23 to 27°C from June to August (Fu and Jin 1992). Measurement of Na content in 0–0.5 m deep soil layer in saline locations where *H. ammodendron* was distributed showed that Na content at four sites ranged between 29 and 311 mmol (kg dry soil)⁻¹ (X. Li, unpubl. data). Precipitation from late November to early March is usually as snow, which covers the ground in these regions during winter, and melting snow in the early spring leaches salt from the surface in saline locations and supplies water to the seeds, causing their germination. On summer days, the ground surface temperature rises to 60–80°C (Fu and Jin 1992).

Seeds of both *H. ammodendron* and *H. persicum* lost most of their germinability within 11 months when they were stored at *c.* 23°C, i.e. at a high temperature, but at temperatures lower than *c.* 2°C, their germinability was maintained for 23 months. These results concur with the fact that, in typical habitats of these species in China, the seeds ripen in November, overwinter without significant decline in germinability, and germinate with sufficient water supply after winter; however, in the hot season, very high soil temperatures would cause loss of their germinability more rapidly than did storage at *c.* 23°C. Thus, for these short-lived seeds, rapid germination and low dependence of germination on environmental conditions would prevent loss of germinability before germination and increase the possibility of establishment.

In many saline environments, viability of seeds in hypersalinity is one of the important factors in determining whether a species occurs in saline environments (Ungar 1991, 1995). However, this factor would not limit the distribution of these species in saline environments: the best chance of germination of these species would be spring in the year following ripening; from ripening to early spring, the seeds of these species are not moistened with saline solution because of the cold climate.

For both species tested, the percentage germination in NaCl was significantly higher than that in isotonic PEG solutions. This would be due to NaCl movement into the seedlings (Fig. 3). When NaCl enters the seeds, it decreases the Ψ_w in the seeds and promotes water uptake by them. Seeds that germinate better in NaCl than in isotonic PEG solutions have been reported for some other species (Sharma 1973; Romo and Eddleman 1985; Tobe *et al.* 1999).

Table 2. Percentage survival and shoot and root dry weight of plants grown at different NaCl concentrations
Dry weight was measured only for survived plants. In each column, the values followed by the same letter are not significantly different from each other at $P = 0.05$ (Student's t -test)

External NaCl concentration (mmol kg ⁻¹)	<i>H. ammodendron</i>			<i>H. persicum</i>		
	Percentage survival (%)	Dry weight (mg)		Percentage survival (%)	Dry weight (mg)	
		Shoot	Root		Shoot	Root
0	47.1	704ab	87a	83.3	500a	90a
200	64.7	1053a	103a	44.4	768a	100a
400	82.3	1165a	142a	11.1	210a	44a
600	23.5	542b	126a	0	—	—

The Ψ_w of the NaCl solution that inhibited germination of both *H. ammodendron* and *H. persicum* was rather low compared with those that inhibit germination of many halophytic species (Partridge and Wilson 1987; Myers and Morgan 1989; Khan and Rizvi 1994; Khan and Ungar 1996; Ungar 1996). For example, the seeds of two tested species germinated in a NaCl concentration about twice the maximum possible for seeds of a halophyte *Haloxylon recurvum* (Khan and Ungar 1996). It is unlikely, that the higher percentage germination of *H. ammodendron* than *H. persicum* in NaCl solutions of Ψ_w lower than -3.0 MPa determines their geographical distribution. Moreover, the seedlings emerging at high salinity continued to elongate without any detectable signs of injurious or toxic effects of NaCl. These results show that both *H. ammodendron* and *H. persicum* are well adapted to highly saline environments at the germination and young seedling stage.

The adverse effects of NaCl were more conspicuous in the older seedling stage in both species (Table 2). This would be associated with the considerably higher Na concentration in the shoots of transpiring plants (Fig. 4) than in the non-transpiring small seedlings (Fig. 3) grown at the same external NaCl concentration. This would be because transpiration stream causes continuous salt transport to plant tissues. The Na concentrations in the shoots (Fig. 4) were higher than those reported for many halophytes grown under comparable NaCl concentrations (Jefferies *et al.* 1979; Neales and Sharkey 1981; Esel 1985; Robinson and Downton 1985; Demmig and Winter 1986; Matoh *et al.* 1988). Na concentrations in the shoots of these halophytes grown at 400–600 mmol kg⁻¹ were within a range 100–800 mmol kg⁻¹, while that in the shoots of two tested species grown at 400–600 mmol kg⁻¹ exceeded 1000 mmol kg⁻¹ (Fig. 4). Maintaining a low internal accumulation of salt is an important strategy for plants to survive in saline environments (Clemens *et al.* 1983; Luard and El-Lakany 1984; Aswathappa and Bachelard 1986; Matoh *et al.* 1988). The higher salt accumulation in the shoot of both species may be related to the fact that neither species is dominant in saline environments. Our findings that NaCl in the root medium causes succulence and

decreased K concentration are in accord with the results of previous research (Handley and Jennings 1977; Neales and Sharkey 1981; Esel 1985; Robinson and Downton 1985; Demmig and Winter 1986).

NaCl caused more adverse effects on *H. persicum* than on *H. ammodendron* in the older seedling stage (Table 2). This would explain why *H. persicum* is excluded from saline locations. *Haloxylon ammodendron* appears to be better able to regulate its internal Na concentration. Indeed, the Na concentration in the shoot of this species was considerably higher than that in *H. persicum* at 0 mmol kg⁻¹ (Fig. 4), and was almost constant in the range of 200–600 mmol kg⁻¹ (Fig. 4).

We conclude that salinity adaptability in the older seedling stage of the tested species is correlated with their geographical distribution with respect to salinity.

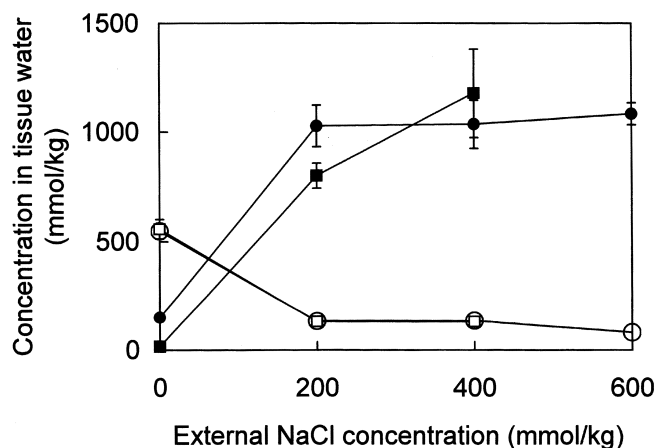


Fig. 4. Sodium (●, ■) and potassium (○, □) concentrations in shoots of *H. ammodendron* (○, ●) and *H. persicum* (□, ■) as a function of NaCl concentration in the root medium. Each point represents the mean of five replications except for 600 mmol kg⁻¹ NaCl-treated *H. ammodendron* ($n = 4$) and 400 mmol kg⁻¹ NaCl-treated *H. persicum* ($n = 2$). Error bars indicating s.e. are shown only where the s.e. was larger than point size.

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