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Effects of sodium, magnesium and calcium salts on seed germination and radicle survival of a halophyte, *Kalidium caspicum* (Chenopodiaceae)

Kazuo Tobe[AD], *Xiaoming Li*[B] *and Kenji Omasa*[C]

[A]Laboratory of Intellectual Fundamentals for Environmental Studies, National Institute for Environmental Studies,
16-2 Onogawa, Tsukuba, Ibaraki 305-8506, Japan.
[B]Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, 40 South Beijing Rd,
Urumqi, Xinjiang 830011, People's Republic of China.
[C]Graduate School of Agricultural and Life Sciences, University of Tokyo, 1-1-1 Yayoi, Bunkyo,
Tokyo 113-8657, Japan.
[D]Corresponding author; email: tobe@nies.go.jp

Abstract. *Kalidium caspicum* (L.) Ung.-Sternb. is a common species of highly saline habitats of north-western China, which in previous germination research has been shown to be rather sensitive to NaCl toxicity. To investigate the effects of different salts on the seed germination and radicle survival of this halophytic shrub, seeds were incubated in various salt (NaCl, Na_2SO_4, $MgCl_2$, or $MgSO_4$ with or without $CaCl_2$) or polyethylene glycol-6000 solutions. The germination percentage and the percentage of emerging radicles surviving to a length of at least 4 mm were examined. The survival of *K. caspicum* radicles depended mainly on the cation composition of the media: both Na^+ and Mg^{2+} had toxic effects on the radicles, while Ca^{2+} alleviated the toxicity of these cations. Mg^{2+} was more toxic than Na^+ and a higher concentration of Ca^{2+} was needed to alleviate its toxicity. It was suggested that the establishment of seedlings of *K. caspicum* in the field is facilitated by the marked alleviation of salt toxicity by Ca^{2+} and that the proportion of soluble Na, Mg and Ca ions in the soil determines the distribution of *K. caspicum* in the field.

Introduction

Kalidium caspicum (L.) Ung.-Sternb. (Chenopodiaceae) is a stem-succulent halophytic shrub distributed in highly saline locations in the desert regions of north-western China (Lanzhou Institute of Desert Research 1985). In a previous study (Tobe *et al.* 2000*a*), we reported that the radicles of *K. caspicum* were very sensitive to NaCl toxicity and that most of them were killed in media with NaCl concentrations at which the radicles of many halophytic and non-halophytic species survive. This unexpected result encouraged us to examine more closely the effects of salinity on *K. caspicum* radicles.

Saline soils contain multiple salt constituents that may have different physiological effects on plant tissues. The main salt components in saline soils are Na^+, Mg^{2+} and Ca^{2+} cations and $Cl^–$ and $SO_4{}^{2–}$ anions (Shainberg 1975). However, many studies examining the effects of salinity on plants have been carried out with only Na salts or dilutions of sea water and only a few (e.g. Younis and Hatata 1971; Redmann 1974; Janzen and Chang 1987; Hardegree and Emmerich 1990; Pujol *et al.* 2000) have compared the effects of Na, Mg and other salts on the germination or growth of plants. Since the effects of salinity on the radicles of *K. caspicum* are mainly salt-specific (Tobe *et al.* 2000*a*), different salt components in saline soils may have different effects on radicle survival. Therefore, to understand the establishment of this species in saline areas, we need to investigate the responses of its radicles to each of these salt components.

It is well known that Ca^{2+} alleviates the adverse effects of NaCl on many plant species (Jennings 1976; Greenway and Munns 1980; Rengel 1992; Marschner 1995). Adding Ca^{2+} to root media with NaCl favours plant growth in both halophytic (Colmer *et al.* 1996) and non-halophytic species (LaHaye and Epstein 1969; Cramer *et al.* 1986; Kurth *et al.* 1986; Suhayda *et al.* 1992; Kinraide 1999). However, little is known about the interaction of Ca^{2+} with Mg salts, which are often abundant in saline soils. Furthermore, the implications of the effects of Ca^{2+} on the establishment of species in saline areas are not clear. It is possible that the establishment of *K. caspicum* in saline areas is facilitated by the alleviation of salt toxicity to its radicles by the Ca^{2+} present in saline soils.

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The objectives of this study were to investigate (1) how different salts act on *K. caspicum* radicles and (2) whether Ca^{2+} ameliorates the responses of *K. caspicum* radicles to Na and Mg salts. We compared the effects of NaCl, Na_2SO_4, $MgCl_2$, $MgSO_4$ and $CaCl_2$ on seed germination and radicle survival and examined the effects of low concentrations of $CaCl_2$ on the response of the radicles to a Na or Mg salt. To evaluate the osmotic effects of the medium on seeds and radicles, we also examined seed and radicle responses to solutions of polyethylene glycol (PEG)-6000, which cannot permeate plant cell walls (Carpita *et al.* 1979) and acts solely as an osmoticum on seeds and radicles (Sharma 1973; Redmann 1974; Hardegree and Emmerich 1990). The laboratory results were related to the composition of soluble salts at 90 saline locations in China to understand how salt composition in the soil might affect the establishment of *K. caspicum* in saline areas.

Materials and methods

Materials

Seeds of *K. caspicum* [seed weight: 171 ± 45 µg (mean ± s.d.; $n = 20$)] were collected in November 1996 from plants growing on saline soil in Fukang, China (44°18′N, 87°55′E). The annual precipitation and annual mean temperature in Fukang are 172 mm and 6.1°C (means from 1958 to 1980). Seeds were initially stored at about 5°C in the dark until being transported to Japan in March 1997. In Japan, the seeds were stored at *c.* –18°C in the dark. During this storage period, seed germinability was assayed at times by incubating the seeds with deionised water at 20°C in dark and we found neither an indication of seed dormancy nor a reduction of seed germinability. The germination experiments were carried out during the period from September 2000 to February 2001.

Methods

Twenty-five seeds were sown on three layers of filter paper (Toyo, no. 1) in a 90-mm plastic Petri dish. The filter paper was moistened with about 10 mL of deionised water, a salt solution (NaCl, Na_2SO_4, $MgCl_2$ or $MgSO_4$ with or without $CaCl_2$, or $CaCl_2$ alone) or a PEG-6000 solution of known water potential. The concentrations of the salt solutions and the water potentials of the PEG solutions used were determined from the results of preliminary experiments so as to make the results clearly indicate the dependence of seed germination and radicle survival on salt concentrations. About half the volume of each seed was immersed in the solution. Each salt solution was prepared by dissolving a commercial reagent-grade salt in deionised water and the PEG solution of known water potential was prepared according to a calibration curve that was determined from isopiestic psychrometer (Boyer and Knipling 1965) measurements at 20°C. The Petri dishes were covered with lids and the seeds were incubated for 15 days. Because seeds of *K. caspicum* germinate most favourably in the dark and at 20°C (Tobe *et al.* 2000*a*), all the experiments were carried out under these conditions.

The seeds were observed daily in dim light through a magnifying glass with a scale; the numbers of both germinated seeds and seeds with radicles longer than 4 mm were counted and seeds with radicles longer than 4 mm were discarded. About two-thirds of the volume of the solution in each Petri dish was replaced daily with the treatment solution to avoid a change in the solute concentration of the solution; because no decrease in the volume of solution in each dish caused by evaporation or seed water uptake was detectable, the daily solution replacement would have sufficed for maintaining the solute concentration in the dish constant. The seeds were considered to have germinated when the radicles emerged. After 15 days of incubation, we determined the final germination percentage (G_F) and the final percentage of seeds with radicles longer than 4 mm (S_F); the survival percentage of radicles was evaluated as (S_F/G_F) × 100. Each treatment was replicated four times.

To statistically test the difference between two means, the Student's *t*-test was used. For comparison of multiple means, one-way ANOVA and Tukey's tests were used. Percentage values were arcsine transformed before statistical analysis. All statistical tests were conducted at $P = 0.05$.

Results

Effects of individual salts and PEG on germination and radicle survival

When *K. caspicum* seeds were moistened with deionised water, or a solution of a salt (NaCl, Na_2SO_4, $MgCl_2$, $MgSO_4$, or $CaCl_2$) or PEG, the percentages of both germinated seeds and seeds with emerging radicles longer than 4 mm reached maximum levels after 15 days (Fig. 1).

For all salt treatments, G_F was higher than 50% at a total ion (cation + anion) concentration (TIC) <540 mmol kg^{-1}, but varied between 4% (NaCl) and 61% ($MgSO_4$) at a TIC of 720 mmol kg^{-1} (Fig. 2). In contrast, S_F decreased markedly at a relatively low TIC for both Na and Mg salts but was high at a wide range of TICs for $CaCl_2$ treatments. When seeds were treated with a Na salt of TIC >120 mmol kg^{-1} or with a Mg salt of TIC >12 mmol kg^{-1}, some or most of the emerging radicles died before their lengths exceeded 4 mm. In these solutions, most radicles, including those elongated

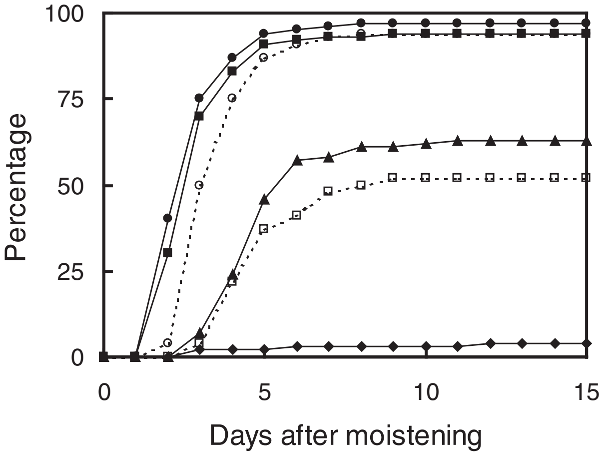

Fig. 1. Changes over time in the percentage of germinated seeds (closed symbols connected with solid lines) and seeds with emerging radicles longer than 4 mm (open symbols connected with dotted lines) for the following treatments: deionised water (●, ○), 60 mmol kg^{-1} NaCl (■, □), 240 mmol kg^{-1} NaCl (▲) and 360 mmol kg^{-1} NaCl (◆). The percentages of seeds with emerging radicles longer than 4 mm for 240 and 360 mmol kg^{-1} NaCl treatments were zero throughout 15 days and the data were not indicated. Each point represents the mean of four replications.

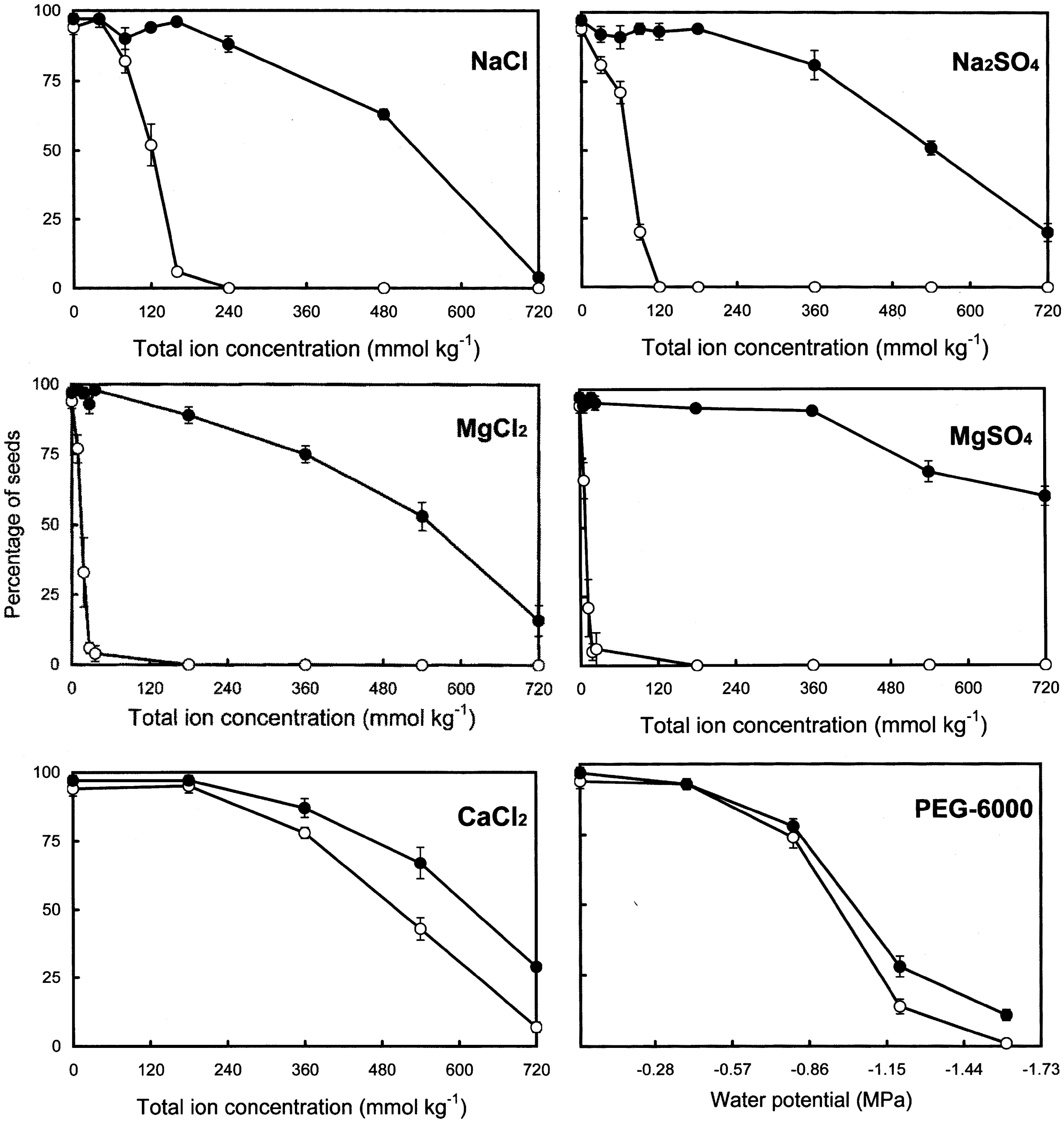

Fig. 2. Effect of total ion (cation + anion) concentration (TIC) of single salts and water potential of PEG on final germination percentage (G_F, ●) and final percentage of seeds from which radicles longer than 4 mm emerged (S_F, ○). Calculated from van't Hoff's law, the lowest water potential in the horizontal axis for PEG (–1.73 MPa) is isotonic to 720 mmol kg^{-1} TIC. Each point represents the mean of four replications; bars indicating s.e. are shown only where s.e. is larger than point size.

beyond 4 mm, were dark brown and had an unhealthy appearance. In contrast, with the $CaCl_2$ treatment, more than 90% of the emerging radicles elongated beyond 4 mm at a TIC < 360 mmol kg^{-1}. Although some radicles remained shorter than 4 mm at a TIC > 540 mmol kg^{-1}, they appeared healthy. PEG-treated seeds showed high survival percentages at a water potential higher than –0.8 MPa; some or most radicles remained shorter than 4 mm at water potentials lower than –1.2 MPa but appeared healthy. The similarity in the response of $CaCl_2$-treated seeds to that of PEG-treated seeds suggests that suppression of S_F at higher $CaCl_2$ concentrations resulted mainly from osmotic inhibition of the medium and that the toxic effect of Ca^{2+} or Cl^- on the radicles, if any, was rather small even at relatively high concentrations. On the other hand, the unhealthy appearance of radicles treated with a Na or Mg salt at high concentrations was clearly distinguishable from the healthy appearance of radicles treated with $CaCl_2$ or PEG. Thus, the adverse effects of a Na or Mg salt on radicles are most likely attributed to salt-specific toxicity. These results also suggest a close relationship between salt toxicity and cation.

To investigate the relationships between cation concentration and radicle survival, the survival percentage of emerging radicles [$(S_F/G_F) \times 100$, %] was plotted against the cation concentrations for Na and Mg salts at a range of 0–80 mmol kg^{-1} (Fig. 3). This plot indicates that Mg^{2+} had toxic effects on the radicles at concentrations several times lower than those for Na^+. At given Mg^{2+} concentrations, $MgCl_2$ and $MgSO_4$ had essentially the same suppressive effect on the survival percentage. Because we expected that Cl^- would have none or very little toxicity to the radicles, the toxicity of Mg salts can be attributed mostly to the Mg^{2+}. For similar reasons, the toxicity of the Na salts would be expected to originate largely from the presence of Na^+. However, the survival percentage of radicles was smaller with Na_2SO_4 than with NaCl treatments, although the TIC at a given Na^+ concentration was *c.* 1.3 times higher in NaCl than in Na_2SO_4 solutions. This suggests that SO_4^{2-} either had toxic effects on radicles or intensified the toxic effects of Na^+ on the radicles.

Interactive effects of $CaCl_2$ and other salts on radicle survival

To investigate whether Ca^{2+} alleviates the toxic effects of Na and Mg salts, we examined the survival percentages of radicles in various salt solutions with or without 1.0 mmol kg^{-1} $CaCl_2$ (Table 1). In this experiment, the salt concentration in each solution was that at which the S_F approached zero without Ca^{2+} in the solution. Thus, the salt concentration in each solution was relatively low and the G_F was high in all treatments. Also KCl was incorporated in this examination (Table 1) and we found that its toxicity was slightly less than that of NaCl [S_F for KCl was significantly higher than that for NaCl at $P = 0.05$ (Student's *t*-test)]. Therefore, $CaCl_2$ alleviated the toxic effects of salts on radicles for all tested salts; while the survival percentage was less than 17% in the absence of $CaCl_2$, it exceeded 90% in all the solutions with 1.0 mmol kg^{-1} $CaCl_2$. All of the radicles that emerged in solutions without $CaCl_2$ had an unhealthy appearance, but most radicles emerging in solutions containing 1.0 mmol kg^{-1} $CaCl_2$ were healthy and continued to elongate beyond 4 mm. Because the addition of a small amount of $CaCl_2$ to, for example, an 80 mmol kg^{-1} NaCl solution (causing a very small increase in the proportion of Cl^- in the solution) markedly improved the survival percentage of radicles, we considered that the alleviatory effect of $CaCl_2$ on salt toxicity resulted from the action of Ca^{2+}.

Table 1. Effect of 1.0 mmol kg^{-1} Ca^{2+} on the germination percentage (G_F) and survival percentage [$(S_F/G_F) \times 100$, %] of *Kalidium caspicum* radicles treated with different salts

Data are the means of four replications, s.e. is indicated in parentheses. TIC, total ion (cation + anion) concentration

Salt in the medium	0 mmol kg^{-1} Ca^{2+}		1.0 mmol kg^{-1} Ca^{2+}	
	G_F (%)	Survival (%)	G_F (%)	Survival (%)
80 mmol kg^{-1} NaCl (TIC = 160 mmol kg^{-1})	95 (1.0)	6 (1.2)	97 (1.9)	100 (0)
40 mmol kg^{-1} Na_2SO_4 (TIC = 120 mmol kg^{-1})	93 (3.0)	0 (0)	94 (2.0)	98 (1.2)
12 mmol kg^{-1} $MgCl_2$ (TIC = 36 mmol kg^{-1})	98 (1.2)	4 (3.0)	92 (1.6)	97 (1.1)
12 mmol kg^{-1} $MgSO_4$ (TIC = 24 mmol kg^{-1})	95 (2.5)	6 (6.0)	95 (1.9)	99 (1.0)
80 mmol kg^{-1} KCl (TIC = 160 mmol kg^{-1})	88 (2.8)	17 (4.3)	89 (4.1)	99 (1.0)

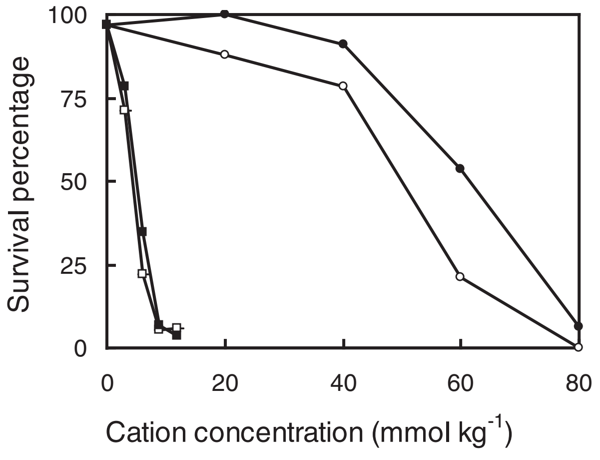

Fig. 3. Dependence of the survival percentage [$(S_F/G_F) \times 100$, %] of *Kalidium caspicum* radicles treated with a Na or Mg salt on the cation concentration in each solution. Each point represents the mean of four replications; bars indicating s.e. are shown only where s.e. is larger than point size. NaCl (●), Na_2SO_4 (○), $MgCl_2$ (■), $MgSO_4$ (□).

To examine whether Ca^{2+} alleviates the toxic effects of salts at much higher concentrations and to investigate the relationship between the alleviatory effect of Ca^{2+} and the salt composition in the solution, we examined the survival percentage of radicles in solutions with higher concentrations of NaCl or $MgCl_2$ to which various concentrations of $CaCl_2$ had been added (Tables 2, 3). The final germination percentage (G_F) was not dependent on Ca^{2+} concentrations at either concentration of NaCl or $MgCl_2$ (ANOVA, $P = 0.05$), but the survival percentage depended on Ca^{2+} concentrations for both concentrations of NaCl or $MgCl_2$ (ANOVA, $P = 0.05$). For both NaCl and $MgCl_2$ treatments, the survival percentages were higher at higher concentrations of Ca^{2+}. For NaCl treatments, the survival percentages were high at Ca^{2+} concentrations higher than 1.0 mmol kg^{-1} (Table 2). At 120 mmol kg^{-1} NaCl, most radicles were healthy at Ca^{2+} concentrations higher than 1.0 mmol kg^{-1} (ratio $Ca^{2+} : Na^+ = 0.0083$); however, at 240 mmol kg^{-1} NaCl, most radicles were

Table 2. Dependence of the germination percentage (G_F) and survival percentage [(S_F/G_F) × 100, %] of *Kalidium caspicum* radicles treated with 120 or 240 mmol kg^{-1} NaCl on Ca^{2+} concentration in the medium

In each column, the values followed by the same letter are not significantly different from each other at $P = 0.05$ (Tukey's test). Data are the means of four replications, s.e. is indicated in parentheses

Ca^{2+} concentration (mmol kg^{-1})	120 mmol kg^{-1} NaCl		240 mmol kg^{-1} NaCl	
	G_F (%)	Survival (%)	G_F (%)	Survival (%)
0.2	89a (7.6)	70a (5.5)	70a (2.6)	3a (1.7)
1.0	90a (2.6)	99b (1.1)	72a (4.9)	80b (7.3)
5.0	85a (3.8)	99b (1.2)	59a (4.4)	97b (1.8)

Table 3. Dependence of the germination percentage (G_F) and survival percentage [(S_F/G_F) × 100, %] of *Kalidium caspicum* radicles treated with 60 or 120 mmol kg^{-1} MgCl$_2$ on Ca^{2+} concentration in the medium

In each column, the values followed by the same letter are not significantly different from each other at $P = 0.05$ (Tukey's test). Data are the means of four replications, s.e. is indicated in parentheses

Ca^{2+} concentration (mmol kg^{-1})	60 mmol kg^{-1} MgCl$_2$		120 mmol kg^{-1} MgCl$_2$	
	G_F (%)	Survival (%)	G_F (%)	Survival (%)
1.0	93a (2.5)	3a (2.1)	88a (1.6)	0a (0)
5.0	92a (3.7)	79b (8.4)	87a (3.4)	13b (2.7)
25	87a (1.9)	96c (1.8)	85a (1.9)	76c (10.8)

healthy only at 5.0 mmol kg^{-1} (Ca^{2+} : Na^{+} = 0.021), and, at 1.0 mmol kg^{-1} (Ca^{2+} : Na^{+} = 0.0042), many radicles appeared unhealthy even though their lengths exceeded 4 mm. The adverse effect of Mg^{2+} on radicle survival was alleviated by a concentration of Ca^{2+} that was about 10 times higher than that for Na^{+} (Table 3). For the 60 mmol kg^{-1} MgCl$_2$ treatment, the survival percentage was high and most radicles were healthy only at 25 mmol kg^{-1} Ca^{2+} (Ca^{2+} : Mg^{2+} = 0.42). At 120 mmol kg^{-1} MgCl$_2$, 25 mmol kg^{-1} Ca^{2+} (Ca^{2+} : Mg^{2+} = 0.21) did not suffice to completely recover the high survival percentage and some radicles appeared unhealthy. When this result is compared with the 12 mmol kg^{-1} MgCl$_2$ treatment (Table 1), in which 1.0 mmol kg^{-1} Ca^{2+} (Ca^{2+} : Mg^{2+} = 0.083) sufficed to alleviate the Mg^{2+} toxicity, it is seen that a higher Ca^{2+} : Mg^{2+} ratio is needed to alleviate the toxicity of higher concentrations of Mg^{2+}.

The results indicate that a high proportion of Mg^{2+} and/or a lower proportion of Ca^{2+} in the medium jeopardises the survival of *K. caspicum* radicles. We roughly estimated from the results (Tables 1–3) that the required ratios for *K. caspicum* radicles to elongate beyond 4 mm without an indication of unhealthy appearance are Ca^{2+} : Na^{+} > 0.01 and Ca^{2+}/Mg^{2+} > 0.1.

Salt composition in the field and its implication for the establishment of K. caspicum

To relate the results obtained above to field conditions, we investigated the composition of soluble salts near the soil surface at 90 different saline locations in arid regions of China, on the basis of data from Wang *et al.* (1993) that presented the concentrations of Na + K, Mg and Ca in the soil at each location. The ratios of Ca : (Na + K) and Ca : Mg near the soil surface were calculated for each saline location (Fig. 4). The mean ratios of Ca : (Na + K) and Ca : Mg were 0.033 and 0.32, respectively. The data showed that the

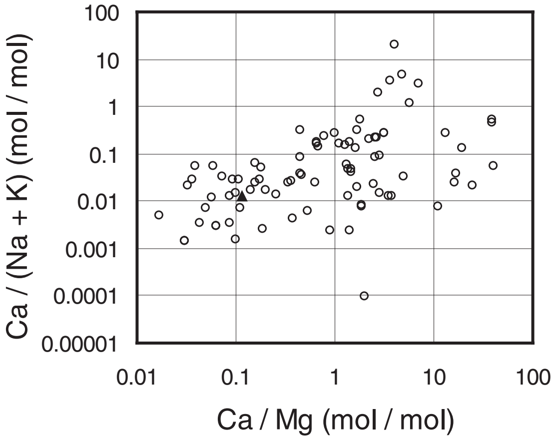

Fig. 4. The ratios of Ca : (Na + K) and Ca : Mg near the soil surface at 90 saline locations in arid regions of China [data from Wang *et al.* (1993)]. Each point (○) corresponds to a location. For reference, the value for sea water is shown by the symbol (▲).

composition of cations in the soil varied greatly among locations. Because the toxicity of K is similar to that of Na (Table 1) and the concentration of K is usually much smaller than that of Na, the value Ca : (Na + K) can be regarded as Ca : Na as far as the toxicity to *K. caspicum* radicles is concerned. Then, two-thirds of the locations fulfill the above requirement (Ca : Na >0.01 and Ca : Mg >0.1) for survival of *K. caspicum* radicles.

Discussion

Effects of different salts on the initial developmental stage of plants

The toxicity of Na and Mg salts to *K. caspicum* radicles was attributed mainly to the cations. The fact that the toxic effects of Na^+, Mg^{2+} and K^+ on radicles were alleviated by Ca^{2+} suggests that the toxicity of different salts to radicles originated from a common mechanism. The radicles treated with a Na or Mg salt of a relatively higher concentration in the absence of Ca^{2+} showed an unhealthy appearance, which was clearly different from that of the radicles inhibited osmotically from elongating by PEG. Thus, the adverse effects of a Na or Mg salt on radicle survival would not originate mainly from the inhibition of cell extension.

According to some researchers (Cramer *et al.* 1985; Kent and Läuchli 1985; Marschner 1995), the toxicity of salt to plant tissues is attributable to the displacement of Ca^{2+} bound to the external surface of the plasma membrane of plant cells with metal cations and the subsequent impairment of the integrity and permeability of plasma membrane, and Ca^{2+} in the external medium restores the cation-displaced Ca^{2+} on the membrane. This explanation seems to be applicable to the interpretation of the interactive effects of Na, Mg and Ca salts on *K. caspicum* radicles. The fact that $CaCl_2$ caused a much smaller adverse effect on the survival of *K. caspicum* radicles than Na and Mg salts would be due to the fact that $CaCl_2$ treatment did not cause the displacement of membrane-bound Ca^{2+} with other cations. Higher toxicity and a higher requirement of Ca^{2+} for toxicity alleviation in Mg^{2+} than in Na^+ or K^+ would reflect the higher displacement ability of Mg^{2+} compared with that of Na^+ or K^+ with Ca^{2+} bound to the surface of plasma membrane. This may be because Mg^{2+}, which has the same valence as Ca^{2+} and a hydrated ionic radius similar to that of Ca^{2+}, is more replicable to membrane-bound Ca^{2+} than is Na^+ or K^+.

The toxic effects of salt on seed germination have been reported in many halophytic and non-halophytic species (Redmann 1974; Bal and Chattopadhyay 1985; Bliss *et al.* 1986; Hardegree and Emmerich 1990; Katembe *et al.* 1998; Tobe *et al.* 1999, 2001). However, these reports are based on germination experiments with single salt components (especially NaCl). It is possible that Ca^{2+}, which exists more or less in saline soils, can alleviate salt toxicity to the seed germination of these species. Thus, germination experiments with a single salt component may not always simulate the seed germination behaviour of species in the saline field.

Distribution of species in saline soils

Seedlings are the most vulnerable stage in the life cycle of plants (Kigel 1995) and adaptation of plants to salinity at the early developmental stage is crucial in facilitating the distribution of species in saline areas (Ungar 1991, 1995). In this study, we investigated the effects of salt composition in the media on seed germination and radicle survival of a halophyte *K. caspicum* and, as a result, suggest that Ca^{2+} plays a critical role in allowing the establishment of *K. caspicum* in saline areas. Seeds treated with a Na or Mg salt demonstrated a high germination percentage in a wide range of salt concentrations, but, in the absence of Ca^{2+}, all the emerging radicles were killed except at very low salt concentrations. This indicates that seed germination in Na or Mg salts without Ca^{2+} results in the death of a very high proportion of radicles. The toxicity of Mg salts was much higher than that of Na salts and a higher concentration of Ca^{2+} was needed to alleviate the toxicity of Mg salts compared with that of Na salts. From this result, we concluded that the proportion of soluble Na, Mg and Ca in the soil determines whether or not *K. caspicum* can become established in saline areas. As a criterion for the survival of *K. caspicum* radicles, we tentatively proposed ratios of $Ca^{2+}:Na^+ > 0.01$ and $Ca^{2+}:Mg^{2+} > 0.1$. However, this criterion was based on only a very early stage of development and a higher proportion of Ca^{2+} may be needed for the successful establishment of this species in saline areas.

The seedlings or radicles of some halophytic and non-halophytic species have been shown to continue to grow in up to 200–400 mmol kg^{-1} NaCl in the absence of Ca^{2+} (Khan and Ungar 1984; Khan and Rizvi 1994; Tobe *et al.* 1999, 2001). Furthermore, in two *Haloxylon* species distributed in the same region as *K. caspicum*, the radicles continued to elongate without suffering from salt toxicity in a medium with a NaCl concentration higher than 650 mmol kg^{-1} and without the addition of Ca^{2+} (Tobe *et al.* 2000*b*). In contrast, *K. caspicum* radicles were very sensitive to Na and Mg salts without Ca^{2+}. For example, at 80 mmol kg^{-1} NaCl, only 6% of the radicles survived beyond 4 mm. *Kalidium caspicum* is distinguished by its absolute requirement for Ca^{2+} for radicle survival in saline media. We have also found that the toxic effect of salt on seed germination of several non-halophytic species is markedly alleviated by the addition of Ca^{2+} (K. Tobe, unpubl. data). Moreover, Bliss *et al.* (1986) found that Ca^{2+} alleviates NaCl toxicity in the germination (plumule emergence) of barley seeds. Thus, some species require external Ca^{2+} to become established in saline soils, while others do not. The reason for this interspecific difference in a Ca^{2+} requirement is unknown, but these results suggest that the proportion of Ca^{2+} in the soil in a saline location can be an important factor determining which species dominate.

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