

Effects of cold stratification, temperature, light and salinity on seed germination and radicle growth of the desert halophyte shrub, *Kalidium caspicum* (Chenopodiaceae)

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Abstract We tested the effects of cold stratification, temperature, light and NaCl on seed germination and germination recovery and of NaCl on radicle growth and radicle elongation recovery of *Kalidium caspicum*, a small leafy succulent shrub dominant in saline deserts in northwest China. In all conditions of temperature and light/darkness, germination percentages and rates of cold-stratified seeds were significantly higher than those of nonstratified seeds. Germination of a high percentage of both nonstratified and stratified seeds was inhibited by 0.2 M NaCl, and 0.6 M NaCl completely inhibited germination. Nongerminated seeds germinated after they were transferred from NaCl solutions to distilled water. Radicle elongation significantly decreased with increase in salinity, and it was completely inhibited by ≥ 1.0 M NaCl; radicle elongation recovered in young seedlings pretreated by 10 days of incubation in ≤ 0.4 M NaCl. Results show that seed germination and early seedling growth of *K. caspicum* are salt tolerant, and these characteristics help explain why this species can survive and dominate salt

habitats, such as those in the Junggar desert in Xinjiang, northwest China.

Keywords Adaptative strategy · Desert halophyte · *Kalidium caspicum* · Radicle growth · Seed germination

Introduction

Seed germination and seedling establishment are the most critical stages for survival of plants under extreme conditions (Kitajima and Fenner 2000), and this is particularly true in saline deserts such as the cold Junggar desert in northwestern China, where rainfall is low and unpredictable. Many salt desert halophytes belong to families known to have physiological dormancy (*sensu* Baskin and Baskin 2004), which can be broken by cold stratification (Baskin and Baskin 1998). Cold stratification can increase germination percentages and rates (Bewley and Black 1982; Huang et al. 2004, b) and change temperature and light requirements for germination. After dormancy is broken, the ability of seeds to germinate in higher salinity may increase (Baskin and Baskin 1998). The responses of seeds of halophytes to salt differ from those of non-halophytes (glycophytes). Seeds of halophytes germinate at higher salinities, and they maintain viability even under extreme salinity or osmotic stress, recovering when the water potential of the medium increases (gets less

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negative). Seeds of many species of halophytes tolerate salinity levels two to three times higher than the growing plant (Ungar 1995), whereas seedlings are the most vulnerable stage in the life cycle of plants (Kitajima and Fenner 2000).

Kalidium caspicum (L.) Ung.-Sternb. (Chenopodiaceae) is an ecologically important semi-shrub halophyte of the saline desert vegetation of central Asia (Liu 1985). In Xinjiang province, Northwest China, it mainly occurs in saline lowlands and on shores of salt lakes (Liu 1985; Zhang and Hai 2002). Plants of this species can tolerate high salinity and physiological drought, and they can grow in sites with a low water table and a high concentration of dissolved salts (Zhang and Hai 2002). In the saline desert near Fukang and Miquan, there are large areas of pure stands of *K. caspicum*, which is one of the most important plants for ecological conservation in Xinjiang (Liu 1985). In its natural habitat, seeds of *K. caspicum* mature in November, at which time the average temperature in Xinjiang is $<0^{\circ}\text{C}$ (Li 1990). Thus, hypothetically seeds go through a long and cold winter in their natural habitat. Therefore, knowledge of environmental conditions for seed dormancy break and germination responses of *K. caspicum* is crucial in understanding its ecological adaptations to natural saline desert environments.

Tobe et al. (2000, 2002) tested the effects of (1) several constant and daily alternating temperatures in constant darkness and at a 12 h dark/12 h light period in deionized water, and (2) different salts and PEG on seed germination of *K. caspicum*. They concluded that seeds of *K. caspicum* were nondormant. However, according to the geographic distribution of this species, we expected that freshly matured seeds of *K. caspicum* seeds would be dormant, which should be important for this plant species to survive cold winters of temperate zones. Thus, we (1) compared germination of 4-week cold stratified and nonstratified seeds under different conditions of light and temperature in distilled water, (2) tested the effect of cold stratification on seed germination in NaCl solutions and on total germination percentage after nongerminated seeds in NaCl solutions were transferred to distilled water and (3) monitored radicle growth of *K. caspicum* in NaCl solutions and radicle elongation recovery after NaCl-pretreated seedlings were transferred to distilled water.

Material and methods

Seeds

Mature fruits (utricles, hereafter seeds) were collected in November 2004 from plants of *K. caspicum* growing in a salt desert near the Fukang Desert Ecological Station of the Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences ($87^{\circ}45'–88^{\circ}05' \text{E}$; $43^{\circ}45'–44^{\circ}30' \text{N}$; 460 m a.s.l.). Vegetation consists of plants such as *K. caspicum*, *K. foliatum*, *Suaeda physophora*, *Haloxylon ammodendron* (Chenopodiaceae) and *Reaumuria soongorica* (Zygophyllaceae). The mean annual temperature is 6.6°C , and mean temperatures of the coldest (January) and hottest (July) months are -17 and 25.6°C , respectively. Annual precipitation (including rain and snow) is 164 mm. About 66% of the rainfall occurs in spring and summer. Annual potential evaporation is $>2,000$ mm (Li 1990).

Freshly matured seeds were collected from dry inflorescences by manually shaking the plants. The seeds were cleaned and air-dried, by which time they were 2 weeks old. Some of these seeds were used immediately to begin a cold stratification treatment, and the others were stored at -18°C until used in experiments.

Seed mass was determined for four groups of 1,000 seeds each and seed size by measuring the diameters of 20 seeds. Internal morphology of the seed was observed under a dissecting microscope, and type of seed was determined following Martin (1946).

General procedures for seed germination

For each treatment, four replicates of 50 seeds each were incubated in 50-mm-diameter Petri dishes on three layers of Whatman No. 1 filter paper moistened with 2.5 ml of distilled water or with different concentrations of NaCl solutions. Petri dishes were sealed by plastic film to prevent evaporation. An emerged radicle was the criterion for germination (Côme 1982). Since NaCl is the major component of salinity in the deserts of northwest China (Fan et al. 1993) and chloride is the most abundant ion in the habitat of *K. caspicum* (Zhang and Hai 2002), we tested the effect of NaCl only in our experiments.

Effects of cold stratification on germination in a range of temperatures in light and in darkness

Rinsed sand moistened with distilled water was placed beneath two layers of filter paper in $20 \times 10 \times 2$ cm deep metal boxes. Two-week-old seeds were placed on the filter paper in metal boxes, which were closed and placed in a chamber in darkness for 4 weeks at 3–5°C. Seeds that had been stratified for 4 weeks and those that had not been stratified (stored dry at –18°C) were incubated at 15, 20, 25, 30 and 35°C in constant fluorescent light ($100 \mu\text{mol m}^{-2} \text{s}^{-1}$, 400–700 nm, hereafter light) and in constant darkness. Germination in light was monitored every 24 h, at which time germinated seeds were counted and removed from the Petri dishes. The time taken for germination of all four replicates to reach 50% was recorded as TG_{50} . After 20 days, when no additional seeds had germinated for 5 days, experiments in light were terminated, and germination in darkness was checked the first and only time.

Effects of cold stratification and salinity on seed germination and germination recovery

Seeds cold stratified 4 weeks on sand moistened with distilled water and seeds that had been stored for 4 weeks at –18°C were incubated in 0.0 (distilled water control) and in 0.2, 0.4, 0.6, 0.8, 1.0, 2.0 and 4.0 M NaCl solutions at 25°C in light. Germination was monitored every 24 h, at which time germinated seeds were counted and removed from the Petri dishes. Germination percentages were calculated after incubation for 20 days. Nongerminated seeds incubated for 20 days in NaCl solutions were rinsed three times in distilled water and then incubated in distilled water for an additional 20 days. Seed germination percentage in the initial solutions was recorded as

$$(A/C) \times 100$$

and the final germination percentage after recovery as

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

where A is the number of seeds germinated in initial salt solutions, B the number of seeds which recovered to germinate in distilled water and C total number of seeds tested (Khan and Ungar 1984).

Effects of salinity on radicle growth and radicle growth recovery

Seeds stored at –18°C for 4 weeks were incubated initially in distilled water at 25°C in light. After 12 h, when the radicles were 5 cm long, 20 of these young seedlings each were transferred into Petri dishes containing 0.0 (distilled water control), 0.2, 0.4, 0.6, 0.8, 1.0, 2.0 and 4.0 M NaCl solutions. Incubation of the seedlings was terminated after 10 days, and radicle elongation was recorded as mean length of the radicles after 10-day incubation – 5 cm. Then, the seedlings incubated in different concentrations of NaCl for 10 days were rinsed three times with distilled water and transferred to filter paper containing 2.5 ml distilled water for an additional 10 days, at which time final lengths of the radicles were measured. Elongation recovery was defined as total radicle length after the 20-day incubation period minus radicle length after the first 10-day incubation period in initial NaCl solutions.

Data analysis

Germination percentages and radicle lengths were expressed as mean \pm SE. Germination data and recovery germination data were transformed (arcsine) before statistical analysis in order to ensure homogeneity of variance. One-, two- or three-way ANOVA ($P < 0.05$) was used to compare treatment effects. If ANOVA showed significant effects, Tukey's test was used to test for differences among treatments (Sokal and Rohlf 1995).

Results

Seed

Seeds of *K. caspicum* are ovate to round, rufous and with small dense protuberances on the surface. Mass of 1,000 seeds was 157.35 ± 2.63 mg (mean \pm SE), and seed diameter was 0.90 ± 0.22 mm. The embryo is fully developed and located in a peripheral position, rarely encircling the endosperm. Thus, the type of seed produced by *K. caspicum* is peripheral (Martin 1946).

Effects of cold stratification on seed germination in a range of temperatures in light and in darkness

After 20 days of incubation, germination percentage for seeds stratified for 4 weeks was significantly higher (Fig. 1) and TG_{50} significantly lower (Table 1) than those of the nonstratified seeds over the 15–35°C temperature range in light and in darkness (Fig. 1). At 15°C, nonstratified seeds germinated to significantly higher percentages in darkness than in light. However, after 4 weeks of stratification, seeds germinated equally well in light and in darkness at all temperature/light regimes (Fig. 1).

Three-way ANOVA showed that percentages of seed germination were significantly influenced by temperature, light, cold stratification and their interactions (Table 2).

Effect of cold stratification and NaCl concentration on germination

Regardless of whether seeds were nonstratified or cold stratified for 4 weeks, germination was significantly inhibited by salinity ($P < 0.05$; Fig. 2). As salinity increased from 0.0 to 0.4 M NaCl, rate and

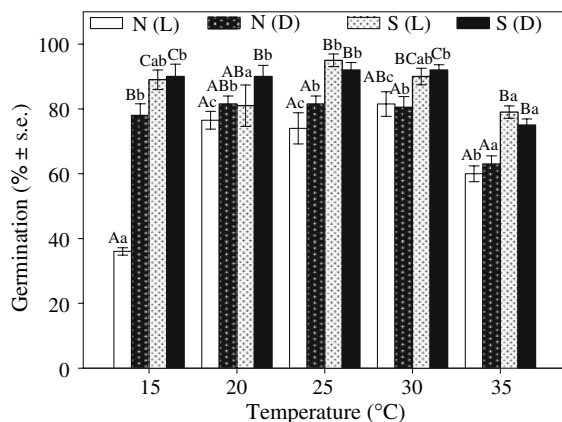


Fig. 1 Effects of light/darkness and temperature on germination percentages of nonstratified and of 4-week cold stratified *Kalidium caspicum* seeds after 20 days of incubation. Different uppercase letters indicate significant differences in germination percentages among different treatments at the same temperature. Different lowercase letters indicate significant differences in germination percentages of seeds with the same treatment across all temperatures. N(L), nonstratified seeds germinated in light; N(D), nonstratified seeds germinated in darkness; S(L), stratified seeds germinated in light; S(D), stratified seeds germinated in darkness

Table 1 TG_{50} for 4-week cold stratified and for nonstratified *Kalidium caspicum* seeds incubated in distilled water at five temperatures in light

Pre-treatment	TG_{50}				
	15°C	20°C	25°C	30°C	35°C
Nonstratified	>20 ^{Aa}	10.5 ^{Ab}	10.5 ^{Ab}	10.0 ^{Ab}	11.5 ^{Ab}
Stratified	6.0 ^{Ba}	6.0 ^{Ba}	2.0 ^{Bb}	2.0 ^{Bb}	2.3 ^{Bb}

For the same temperature, different uppercase letters indicate significant differences between germination rates of nonstratified and stratified seeds. For nonstratified or stratified seeds, different lowercase letters indicate significant differences in germination rates across the five temperatures

percentage of germination significantly decreased. Germination of a high percentage of both nonstratified and stratified seeds was inhibited by 0.2 M NaCl (Fig. 2), and 0.6 M NaCl completely inhibited germination (data not shown). Cold stratification significantly promoted germination also in NaCl solution ($P < 0.05$, Fig. 2, Table 3). Rate and percentage of germination were much higher for stratified seeds than they were for nonstratified seeds ($P < 0.05$; Fig. 2, Table 3). After 40 days of incubation (20 days of incubation in NaCl solutions plus an additional 20 days in distilled water for seeds that did not germinate in initial NaCl solutions), percentages of seeds that germinated in NaCl solutions plus those that did so after transfer to distilled water were lower than those in the distilled water control; difference among pre-treatments of salinity and stratification were not significant (Fig. 3).

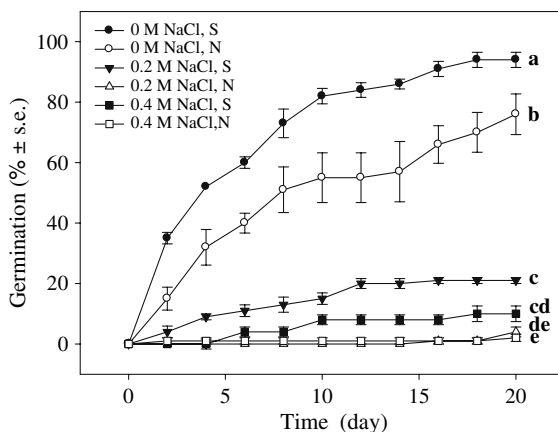
A two-way ANOVA showed that seed germination in NaCl solutions was significantly affected by cold stratification and salinity, but not by the interaction between cold stratification and salinity (Table 3).

Effects of salinity on radicle growth and recovery

Salinity significantly inhibited radicle elongation ($P < 0.05$), which decreased with increase in NaCl concentration from 0.0 to 1.0 M. Very little radicle growth occurred at ≥ 0.4 M and none at > 0.8 M (Fig. 4a). Radicles of seedlings transferred to distilled water after 10 days of incubation in NaCl solutions continued to elongate. However, elongation recovery and survival of seedlings decreased significantly with increase of pretreatment salinity (Fig. 4b, c).

Table 2 Three-way ANOVA for effects of temperature, light, cold stratification and their interactions on germination percentage of *Kalidium caspicum* seeds

Source of variance	df	SS	MS	F-value	P-value
Temperature	4	1,920.65	480.16	18.07	<0.001
Light	1	285.24	285.24	10.74	0.002
Cold stratification	1	2,943.32	2,943.32	110.77	<0.001
Temperature × light	4	550.76	137.69	5.18	0.001
Temperature × cold stratification	4	663.44	165.86	6.24	<0.001
Light × cold stratification	1	206.95	206.95	7.79	0.007
Temperature × light × cold stratification	4	500.52	125.13	4.71	0.002

**Fig. 2** Germination of nonstratified and of 4-week cold-stratified *Kalidium caspicum* seeds in NaCl solutions during 20 days incubation at 25°C in light. Different lowercase letters indicate significant difference of germination percentages among different treatments after 20 days of incubation. S, stratified seeds; N, nonstratified seeds

Discussion

For many species, cold stratification increases germination percentage and rate and widens the temperature and light conditions for germination (Baskin and Baskin 1998, 2004a, b; Bewley and Black 1982; Huang et al. 2004a, b; Leadem 1986; Thanos and Skordilis 1987). Ungar and Binet (1975)

reported that the germination percentage of seeds of the coastal halophyte *Spergularia media* (Caryophyllaceae) cold stratified for 10 days was higher in light than that in darkness, whereas seeds stratified for 30 days germinated equally well in light and in darkness. Likewise, cold stratification also changed the light requirement for germination of *K. caspicum* seeds. Nonstratified seeds germinated to significantly higher percentages in continuous darkness than in continuous light at 15°C, whereas seeds stratified for 4 weeks germinated to equally high percentages in light and darkness. Further, after cold stratification, the minimum temperature at which a high percentage (>85%) of *K. caspicum* seeds germinated decreased from 20 to 15°C. At all temperatures tested, germination percentages were considerably higher and TG_{50} lower for stratified than for nonstratified seeds.

Thus, freshly matured seeds of *K. caspicum* exhibit some physiological dormancy (sensu Baskin and Baskin 1998). Tobe et al. (2000) and Li and Zhang (2007) stated that the seeds of *K. caspicum* are nondormant. However, Fig. 1 of Tobe et al.'s (2000) study shows that at 20°C in darkness (but see below) germination rate of cold stratified seeds is much higher than that of nonstratified seeds, which agrees with our results that seeds of *K. caspicum* exhibited some degree of non-deep physiological dormancy.

In our study, both rate and percentage of germination of stratified seeds in distilled water and in NaCl solutions were significantly higher than those

Table 3 Two-way ANOVA for effects of cold stratification, salinity and their interactions on seed germination percentage of *Kalidium caspicum* in NaCl solutions

Source of variance	df	SS	MS	F-value	P-value
Cold stratification	1	1,242.25	1,242.25	30.50	<0.001
Salinity	2	15,393.34	7,696.67	188.95	<0.001
Cold stratification × salinity	2	16.36	8.18	0.20	0.820

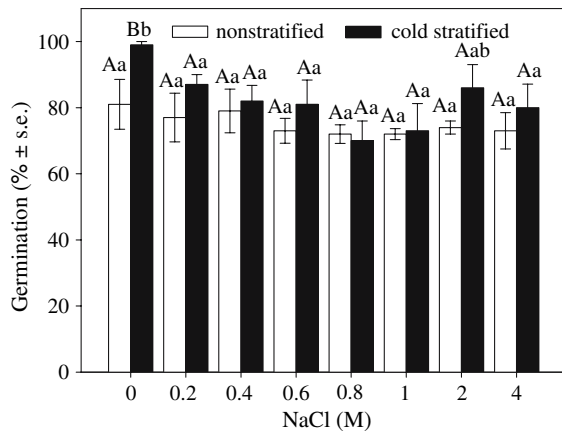


Fig. 3 Effect of NaCl concentration and of cold stratification on percentage of seeds of *Kalidium caspicum* that germinated in NaCl solutions plus those that germinated after transfer to distilled water, after 40 days of incubation at 25°C in light. Different uppercase letters indicate significant differences in germination percentages among different treatments in the same concentration of NaCl. Different lowercase letters indicate significant differences in germination percentages of seeds with the same treatment (cold stratified or nonstratified) across all concentrations of NaCl

that had not been stratified. However, germination is quite high in non-saline conditions regardless of stratification but very low in saline conditions if not subjected to cold stratification (and relatively low in saline conditions in any case). Thus, cold stratification of *K. caspicum* is of relatively greater importance in saline than in non-saline conditions. Similar results were reported for *Salicornia europaea* (Chenopodiaceae) (Philipupillai and Ungar 1984). Large seeds of this species cold stratified for 4 weeks germinated to 82 and 43% in 0.52 and 0.85 M NaCl solutions, respectively, whereas nonstratified seeds germinated to 4 and 0%, respectively. Cold stratification also greatly increased seed germination percentages of *Spergularia marina* in 0.17 and 2.6 M NaCl (Ungar 1984).

Young radicles of *K. caspicum* elongated very quickly in distilled water, and their mean length had reached 5 cm in 12 h incubation. Radicles also had high salinity tolerance (up to 0.4 M), but when they were transferred back to distilled water their ability to resume elongating and to survive decreased significantly with increase in pretreatment salinity. All seedlings pretreated with ≥ 0.6 M NaCl lost the ability to elongate, and they died after 10 days incubation in distilled water. Thus, for successful

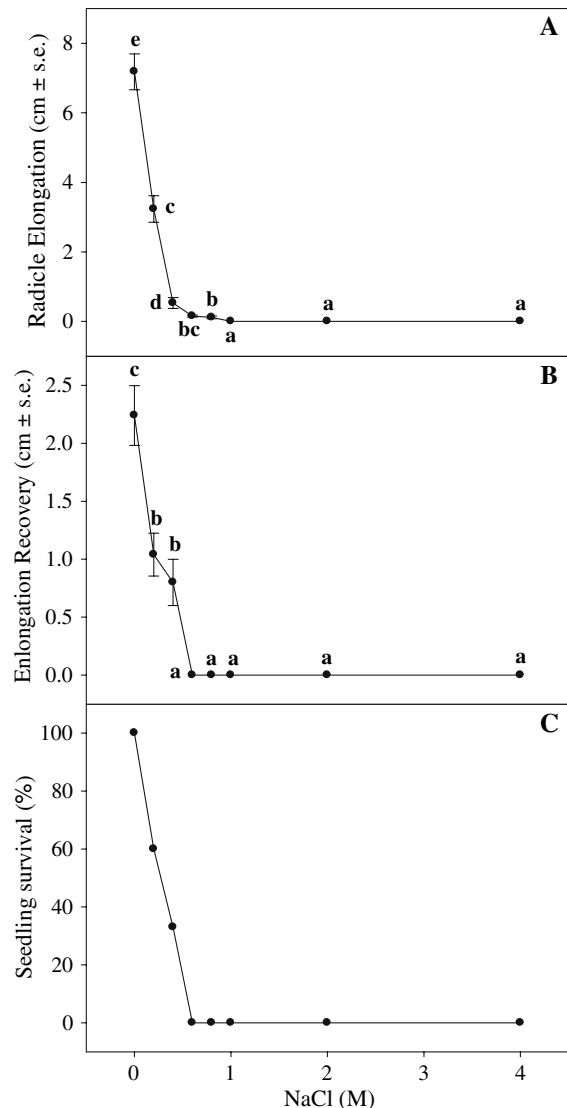


Fig. 4 (a) Effect of NaCl concentration on radicle elongation of *Kalidium caspicum* seedlings incubated for 10 days at 25°C in light. (b) Radicle elongation recovery in *Kalidium caspicum* after transfer from different concentrations of NaCl to distilled water. Radicle length recovery was recorded after incubation for 10 days at 25°C in light. (c) Survival of radicles of *Kalidium caspicum* incubated in light at 25°C for 10 days after transfer from different concentrations of NaCl to distilled water. Values with the same lowercase letter are not significantly different from each other

establishment of *K. caspicum* seedlings salt concentration at the soil surface and at shallow soil depths needs to be diluted by precipitation and/or by melt-water from snow. During the rainy season in spring and summer, salinity on the soil surface would be decreased by precipitation, and then seeds could

germinate and seedlings become established (Qu et al. 2007). For *K. gracile*, seedling radicle growth decreased with increase of NaCl concentration. However, after seedlings were transferred to distilled water and recovered elongation, total length of radicles pretreated with 0.445 M NaCl was similar to that in the control (Shen et al. 2003). Zeng et al. (2006) reported that radicles of *K. foliatum* can tolerate 0.4 M NaCl and the difference between radicle growth in distilled water control and 0.3 M NaCl was not significant. Thus, the ability of seedlings of *K. gracile* and *K. foliatum* to tolerate salinity is greater than that of *K. caspicum*.

Germination of a high percentage of both nonstratified and stratified seeds of *K. caspicum* in our study was inhibited by 0.2 M NaCl (−0.91 MPa). Further, only about 10% of cold-stratified seeds and 2% of nonstratified seeds germinated in 0.4 M NaCl (−1.82 MPa), and 0.6 M NaCl (−2.74 MPa) completely inhibited germination. Similarly, Tobe et al. (2000) showed that germination of *K. caspicum* seeds was significantly inhibited by −0.8 MPa, and only 10% of the nonstratified seeds germinated at 10 and at 20°C at −1.6 MPa, which was the lowest water potential of NaCl solutions in their study. In our study, germination percentages in NaCl solutions (0.2–4.0 M) plus those after transfer to distilled water were 72–77% for nonstratified seeds and 70–87% for cold-stratified seeds. This indicates that high salinities delay germination in this species but do not cause seeds to lose viability.

There are some similarities and differences among the germination characteristics of the three *Kalidium* spp. that have been studied. Germination percentage of seeds of *K. caspicum* (this study), *K. gracile* (Shen et al. 2003) and *K. foliatum* (Song et al. 2006; Qu 2006, Zeng et al. 2006) decreased with increase in salinity. Song et al. (2006) tested germination of *K. foliatum* only in distilled water and at 0.1 M and 0.5 M NaCl. In their study, germination percentage of *K. foliatum* was not decreased by 0.1 M NaCl, whereas it was drastically decreased by 0.5 M NaCl (<5% germination) (Song et al. 2006). Zeng et al. (2006) reported that seed germination of *K. foliatum* in 0.0–0.3 M NaCl solutions were higher than 80% and 0.6 M NaCl solution completely inhibited seed germination of this species. Further, seeds of all three *Kalidium* species exhibited germination recovery after transfer from NaCl solutions to distilled water.

Total germination percentages for nonstratified and stratified seeds were 72–77% and 70–87%, respectively, for *K. caspicum* (this study) and ≤69% (Song et al. 2006) and 72–86% (Qu 2006), respectively, for *K. foliatum*. Total germination of nonstratified seeds (stratified seeds not tested) of *K. gracile* was 90–93% (Shen et al. 2003).

In northwest China, seeds of *K. caspicum* mature in November, when the average air temperature is <0°C (Li 1990) and thus too low for germination. In the field, seeds germinate primarily from April to July. In April, the temperature is about 10°C (Li 1990; Zhao et al. 2004), and soil moisture increases due to snow melt. It seems likely that seeds of *K. caspicum* would be cold stratified in early spring after soil temperatures increase to >0°C and before they become high enough for germination. From May to July, temperatures in the natural habitat of *K. caspicum* are 16–25.6°C (Zhao et al. 2004). Further, during this spring season melting snow and rainfall (Li 1990) dilute salts on the soil surface and at shallow depths. Thus, stratified seeds of *K. caspicum*, which germinated to about 90% at 15–30°C, can germinate to high percentages under this optimal combination of high soil moisture, high temperatures and decreased salinity. Even though salinity in the desert habitat is high in the dry season, seeds remain viable and then germinate after salinity is diluted by precipitation.

Delay of germination until spring, and germination recovery when salinity has been decreased in its natural habitat, is part of the adaptive strategy of *K. caspicum* to the harsh desert environment of northwest China. This adaptation allows seedlings to grow successfully at a time of year when temperature, soil moisture and salinity are most suitable for plant establishment from seeds. Radicles of *K. caspicum* elongate quickly in distilled water and can tolerate up to 0.8 M (−3.68 MPa) NaCl, and no seedlings died during 10 days incubation in 0.0–0.8 M NaCl. Root elongation recovered in 60% of seedlings pretreated in 0.2 M NaCl and in 33% of those pretreated in 0.4 M, after they were transferred to distilled water (Fig. 4). Thus, when soil salinity decreases to a low level, seeds germinate, and roots of seedlings of *K. caspicum* may grow quickly to a sufficient soil depth and become established. Clearly, then, the seed germination and early seedling growth stages of the life cycle of *K. caspicum* are parts of the adaptive

strategy of this species that allows it to inhabit the harsh saline desert conditions in northwest China and other areas of central Asia.

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