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Seed germination of a halophyte, *Halostachys caspica*

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ABSTRACT

Halostachys caspica (Chenopodiaceae) is a halophytic shrub commonly found in saline areas of the western deserts in China that produces small-sized seeds (0.07 mg). Effects of temperature, light, NaCl, and polyethylene glycol-6000 on seed germination were investigated by incubating seeds in Petri dishes in controlled environments. Seed germination was promoted by both light and temperature alternation. Seed dormancy was not detected. Temperature dependence of seed germination indicated that *H. caspica* seeds are able to germinate at any time between spring and autumn in their habitats in China. Seed germination was almost completely withheld when seeds were moistened with 500 mmol kg^{-1} NaCl, but seeds remained viable after moistening with 3000 mmol kg^{-1} NaCl for 41 d. Opportunities for seed germination were expected to be very limited in the field because for photoblastic *H. caspica* seeds to germinate, the seeds need to be almost exposed to the soil surface, where they are likely to suffer severe water deficiency and high salinity. It was suggested that germination of *H. caspica* seeds in the field is facilitated by a supply of a large amount of water from melting snow in early spring.

Keywords: China, desert, light, salinity, shrub, temperature alternation

INTRODUCTION

Halostachys caspica (M.B.) C.A. Mey. (Chenopodiaceae) is a deciduous halophytic shrub distributed in the western deserts of China. The distribution of this species is restricted to highly salinized locations where the groundwater table is located about 0.5 m below the soil surface. The mature plants of this species produce a large number of small-sized seeds (0.07 mg) each year. Omasa et al. (1995) reported that the saplings of *H. caspica* grew favorably on addition of 0–690 mM NaCl solution (1 mM ≈ 1 mmol kg^{-1}) to the root medium; the most favorable concentration for growth was 230 mM NaCl. This result indicated that *H. caspica* saplings can adapt to environments with high NaCl concentrations. However, there is little information regarding the seed germination responses of this species to salinity and other environmental factors.

Seed germination characteristics can be an important factor that determines the adaptation of species to saline environments (Ungar, 1995). Most seeds are located near the soil surface where salt accumulates in salinized locations. The salt concentration at the surface of salinized soil changes over time: continuous evaporation of groundwater gradually deposits salt on the soil surface, but rainfall or melting snow can rapidly leach salt from the surface and supply water to the seeds. Thus, germination responses of seeds to the environments are expected to be crucial for the successful establishment of plants in saline environments.

The present study was undertaken to understand the seed germination characteristics of *H. caspica*. In this study we investigated the interactive effects of tem-

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perature and light on seed germination, the interactive effects of temperature and NaCl on seed germination, and the effects of high NaCl concentration on seed viability. Additionally, in order to investigate the action of NaCl on the germination of the seeds of this species, we compared the germination response to NaCl with that to isotonic polyethylene glycol (PEG)-6000, which cannot permeate plant cell walls and acts solely as an osmoticum on seeds (Hardegree and Emmerich, 1990). Since NaCl is the most abundant salt in many salinized locations in deserts in China (Wang et al., 1993), we used it to examine the effects of salinity on seed germination.

MATERIALS AND METHODS

Seeds

Seeds of *H. caspica* (mean seed weight: 0.070 mg) were collected from plants growing on saline soil in Fukang, China (44°18'N, 87°55'E), soon after seed maturation in November 1996. Annual precipitation and annual mean temperature in Fukang are 172 mm and 6.1 °C, respectively (means from 1958 to 1980). The monthly mean temperature is <0 °C from November to March, 16–26 °C from May to September, and about 10 °C in April and October. The diurnal temperature difference is 10–20 °C. Precipitation from November to March is about 36 mm (means from 1958 to 1980, 31% of annual precipitation) and usually falls as snow, which covers the ground during winter and melts in early spring. Between April and October, the highest monthly precipitation was observed in June (28 mm) and the lowest was observed in August (11 mm) (means from 1958 to 1980). When the total soluble salt content at a soil depth range of 0–10 cm in a typical habitat of *H. caspica* in Fukang was measured in late May, late August, and mid-October in 1992, it ranged between 16 and 54 g per kg dry soil (Xiaoming Li, unpublished results).

The collected seeds were initially stored at room temperature until being transported to Japan in March 1997, where they were stored at ca. −18 °C; however, some seeds were stored in a refrigerator (ca. 0 °C) or in an air-conditioned room (ca. 23 °C) to test their longevity at these temperatures. The germination experiments were carried out from May 1997 to August 1998. Additionally, germinability of seeds stored in different temperature conditions was occasionally checked until May 2004.

METHODS

In all the experiments, 25 seeds were sown on three layers of filter paper (Toyo, No. 1) in a 50-mm glass Petri dish. The filter paper was moistened with about 5 mL of deionized water or a solution of NaCl or PEG-6000. The Petri dishes were covered with glass lids and placed in an incubator or an environment-controlled cabinet in which temperature and light conditions were controlled. In all the treatments, the seeds were observed daily through a magnifying glass; a seed was considered to have germinated when the radicle protruded, and germinating seeds were discarded. About two-thirds of the volume of the fluid in each Petri dish was replaced daily. After each experiment, the final percentage germination (G_F) was determined. Each treatment was replicated four or five times.

Experiment 1: Effects of temperature, light, and NaCl on seed germination

Seeds in Petri dishes were maintained at a constant or diurnally alternating temperature regime in continuous dark or in 12-h light/12-h dark in an incubator. When the temperature was alternated in light/dark treatment, the seeds were exposed to a lower temperature for 12 h in the dark and to a higher temperature for 12 h in the light. In the light, the seeds were illuminated with fluorescent lamps (photon flux density at wavelengths 400–700 nm at the surface of the seeds (PFD): 50–90 μmol m^{-2} s^{-1}; photon density irradiated to the seeds per day (PD/d): 2.2–3.9 mol m^{-2} d^{-1}). During the exposure to light, the temperature of the fluid in the Petri dishes was ca. 2 °C higher than that in the incubator. For continuous dark treatments, the Petri dishes were put in a light-proof metal box and maintained at a different temperature regime in the incubator. For continuous dark treatments, daily seed observation was performed under dim light (PFD: ca. 2 μmol m^{-2} s^{-1}); during each day's observation, seeds were usually illuminated for 1–2 min. For either treatment, G_F was determined after 15 d of incubation.

In order to examine the effects of temperature and light on seed germination, seeds were incubated with deionized water, and their germination was examined under 14 different constant or alternating temperature regimes. For each temperature regime, examination was carried out under light/dark or dark.

In order to examine the effects of temperature and NaCl on seed germination, seeds in Petri dishes were maintained at any of the 12 different constant or alternating temperature regimes in light/dark and moistened with a NaCl solution (0, 100, 200, 300, 400, or 500 mmol kg^{-1} NaCl).

Experiment 2: Effects of moistening seeds with a high-concentration NaCl on seed viability

Seeds were incubated with 3000 mmol kg^{-1} NaCl solution (49% saturation at 20 °C) in Petri dishes at 20 °C in the dark in an incubator for 41 d; subsequently, the seeds were rinsed several times with deionized water, transferred to other Petri dishes, and incubated with deionized water at 12 h 10 °C (dark)/12 h 30 °C (light) in an incubator, as described in Experiment 1.

Experiment 3: Comparison of the effects of NaCl and PEG of known water potential on seed germination

Seeds in Petri dishes were maintained in an environment-controlled cabinet at a constant temperature of 20 °C, moistened with deionized water or a solution of NaCl or PEG-6000 of known water potential (Ψ_w), and continuously illuminated with fluorescent lamps (PFD: 270–300 μmol m^{-2} s^{-1}; PD/d: 23–26 mol m^{-2} d^{-1}—PD/d in this experiment was 7–11 times larger than that in Experiment 1). Since a preliminary experiment showed that during light exposure the temperature of the fluid in the Petri dishes was ca. 2 °C higher than that in the cabinet, the temperature in the cabinet was set at 18 °C in order to maintain the temperature of the seeds at 20 °C. The NaCl solutions of known Ψ_w (from 0 to –4.2 MPa) were prepared according to Lang (1967), and the PEG-6000 solutions of known Ψ_w (from 0 to –4.3 MPa) were prepared according to a calibration curve that was determined from isopiestic psychrometer measurements (Boyer and Knipling, 1965) at 20 °C using NaCl solutions of known Ψ_w as standards. Twenty days after incubation with each solution, G_F was determined.

Statistical analysis

Student's *t*-test was used to statistically test the difference between the two mean values. Tukey's test following one-way ANOVA was used for comparison of multiple means. Percentage values were arcsine transformed prior to statistical analysis.

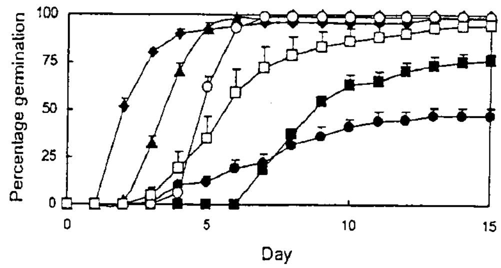

Fig. 1. Changes over time in percentage germination of *H. caspica* seeds in light/dark (PD/d: 2.2–3.9 mol m^{-2} d^{-1}) when the seeds were moistened with deionized water in a temperature regime of 20 °C (constant) (●), 10 °C/15 °C (■), 20 °C/25 °C (▲), 30 °C/35 °C (◆), 5 °C/20 °C (○), or 25 °C/40 °C (□). Each point represents the mean of four replications; error bars indicating SE are shown only where SE was larger than point size.

RESULTS

Seed longevity, seed dormancy, and effects of temperature and light on seed germination

For seeds stored in either of three different temperature conditions, we did not detect seed dormancy during the storage period of 7.2 years. For seeds stored at ca. 0 °C or ca. 23 °C for 7.2 years (7.7 years after maturation), the germination percentages were 96 ± 2.0% and 86 ± 3.5% (mean ± SE; n = 4), respectively (when examined by incubating seeds with water for 10 d in 10 °C (dark)/30 °C (light)).

Figure 1 and Table 1 show the effects of temperature and light on seed germination. Seeds began to germinate 2–7 d after incubation (Fig. 1). Seed germination was

Table 1

Final percentage germination (G_F) of *H. caspica* seeds in constant temperature regimes (A) and alternating temperature regimes (B) in light/dark (PD/d: 2.2–3.9 mol m^{-2} d^{-1}) or continuous dark. Data are the means of four replications. Values with the same superscript letter are not significantly different from each other ($p < 0.05$; Tukey's test)

A. Constant temperature							
Temperature	10 °C	15 °C	20 °C	25 °C	30 °C	35 °C	40 °C
Light/dark	0^{h}	11^{efg}	47^{c}	56^{bc}	42^{cd}	17^{ef}	0^{h}
Continuous dark	0^{h}	0^{h}	1^{h}	1^{h}	0^{h}	0^{h}	0^{h}
B. Alternating temperature							
Temperature	10 °C/15 °C	20 °C/25 °C	30 °C/35 °C	5 °C/20 °C	25 °C/40 °C	10 °C/30 °C	5 °C/35 °C
Light/dark	76^{b}	100^{a}	98^{a}	99^{a}	95^{a}	98^{a}	99^{a}
Continuous dark	0^{h}	1^{h}	2^{gh}	4^{fgh}	2^{h}	20^{de}	19^{de}

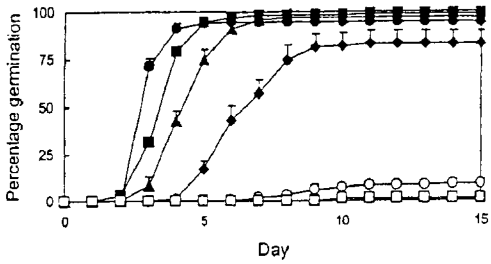

Fig. 2. Changes over time in percentage germination of *H. caspica* seeds at 10 °C/30 °C in light/dark (PD/d: 2.2–3.9 mol m^{-2} d^{-1}) when the seeds were moistened with deionized water (●), or a solution of 100 (■), 200 (▲), 300 (◆), 400 (○), or 500 (□) mmol kg^{-1} NaCl. Each point represents the mean of four replications; error bars indicating SE are shown only where SE was larger than point size.

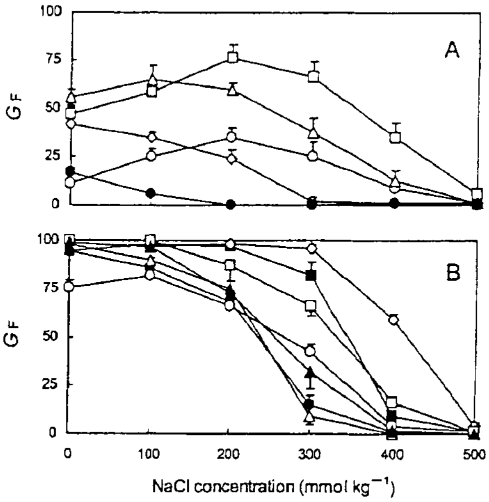

Fig. 3. Final percentage germination (G_F) of *H. caspica* seeds when the seeds were moistened with NaCl solutions of different NaCl concentrations at different temperature regimes in light/dark (PD/d: 2.2-3.9 mol m^{-2} d^{-1}). A: constant temperature regimes, ○: 15 °C, □: 20 °C, △: 25 °C, ◇: 30 °C, ●: 35 °C. B: diurnally alternating temperature regimes, ○: 10 °C/15 °C, □: 20 °C/25 °C, △: 30 °C/35 °C, ◇: 5 °C/20 °C, ●: 25 °C/40 °C, ■: 10 °C/30 °C, ▲: 5 °C/35 °C. Each point represents the mean of four replications; error bars indicating SE are shown only where SE was larger than point size.

retarded more in all the constant temperature regimes and the alternating temperature regime of 10 °C/15 °C than in other alternating temperature regimes. In all temperature regimes, seed germination was markedly suppressed in the continuous dark in comparison to that in light/dark (Table 1). G_F was higher in the alternating temperature regimes compared to those at constant temperature regimes (Table 1). When the difference between the higher and lower temperatures was large (temperature difference: 20 °C and 30 °C) in alternating temperature regimes (10 °C/30 °C and 5 °C/35 °C), G_F in the continuous dark was fairly higher (Table 1).

Effects of temperature and NaCl on seed germination

Seed germination was retarded more as the NaCl concentration increased (Fig. 2). G_F was generally decreased with increasing NaCl concentration; however, at constant temperature regimes of 15 °C and 20 °C, G_F was highest at 200 mmol kg^{-1} NaCl (Fig. 3). G_F was almost zero at 500 mmol kg^{-1} NaCl in all the temperature regimes. At lower NaCl concentrations (0, 100, and 200 mmol kg^{-1}), diurnal alternation of temperature markedly increased G_F, whereas at higher NaCl concentrations (400 and 500 mmol kg^{-1}), no conspicuous effects of diurnal alternation of temperature on G_F were evident. At 400 mmol kg^{-1} NaCl, G_F was higher in treatments in which the temperature in the light was 20 °C (20 °C and 5 °C/20 °C) than in the other treatments.

Effects of moistening seeds with high concentration NaCl on seed viability

While moistening seeds with 3000 mmol kg^{-1} NaCl solution for 41 d, no seed germination was observed. When the seeds were transferred to deionized water, the seeds began to germinate 3 d after the transfer, and germination percentage 4 d after the transfer was 99 ± 0.8% (mean ± SE; n = 5), indicating that *H. caspica* seeds exposed to high concentrations of NaCl remained ungerminated, but viable and nondormant.

Comparison of the effects of NaCl and PEG on seed germination

At most Ψ_w values, no conspicuous difference was found in G_F between the isotonic NaCl and PEG treatments (Fig. 4). For both NaCl and PEG treatments, G_F at −1 to −2 MPa was higher than that at 0 MPa: for example, G_F at 0 MPa was significantly lower than that at −1.5 MPa NaCl ($p < 0.001$) and significantly lower than that at −1.4 MPa PEG ($p < 0.001$). G_F at higher NaCl concentrations in this experiment was considerably higher than that in the 20 °C light/dark treatment in the above experiment (Fig. 3): for example, in the above experiment, at 20 °C, G_F at 400 and 500 mmol kg^{-1} NaCl was 35% and 6%, respectively, whereas in this experiment, G_F at −2.1 MPa NaCl (469 mmol kg^{-1} NaCl) and −3.0 MPa NaCl (667 mmol kg^{-1} NaCl) was 85% and 24%, respectively. This was interpreted to be

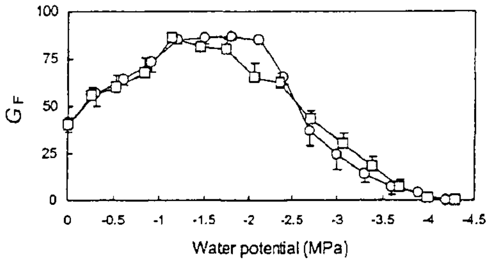

Fig. 4. Final percentage germination (G_F) of *H. caspica* seeds when the seeds were moistened with a PEG (□) or NaCl (○) solution of known water potential at 20 °C in continuous light (PD/d: 23–26 mol m^{-2} d^{-1}). Each point represents the mean of four replications; error bars indicating SE are shown only where SE was larger than point size.

the result of a higher PD/d in this experiment than in the experiment above, and it indicated that when seeds were irradiated with a larger number of photons, the seeds germinated at lower Ψ_w.

DISCUSSION

Seed germination of *H. caspica* was promoted by both light and diurnal temperature alternation. While diurnal temperature alternation increased G_F at higher Ψ_w (Fig. 3), an increase in light intensity increased G_F at lower Ψ_w (Fig. 3 vs. Fig. 4). Seeds can be enabled to germinate by multiple processes that alleviate germination-inhibitory effects. For example, cell wall loosening of the embryo (Schopfer and Plachy, 1993), softening of emdosperm cells constraining extension growth of the embryo (de Miguel and Sánchez, 1992), and an increase in solute concentration in the cytosol of the embryo (Mc Donough, 1975) have been included in the processes that initiate seed germination. Our result suggests that light and diurnal temperature alternation facilitate seed germination by different modes of actions.

At a constant temperature of 20 °C, G_F was higher for seeds treated with NaCl or PEG solutions of intermediate Ψ_w than for seeds treated with solutions of higher Ψ_w (Fig. 4). Higher seed germination percentages in intermediate concentrations of NaCl than in water have been reported in some halophytes (Rivers and Weber, 1971; Okusanya, 1977). One hypothesis that could explain our result would be as follows: (1) light released one germination-inhibitory effect, but another germination-inhibitory effect was not released because of the absence of temperature alternation; (2) seeds treated with solutions with higher Ψ_w rapidly imbibed water, but because they were withheld to germinate, some of them died due to excessive imbibition (Hegarty, 1978); (3) seeds treated with solutions with intermediary Ψ_w imbibed water more slowly and stayed alive for longer periods; (4) the second germination-inhibitory effect was slowly released even in the absence of temperature alternation; however, since higher percentages of seeds had died in treatments with higher Ψ_w due to excessive imbibition when it was released, G_F of seeds treated with intermediate Ψ_w was higher than that of seeds treated with higher Ψ_w. As far as *H. caspica* is concerned, the higher G_F at intermediate Ψ_w would not be of ecological significance since it is unlikely that the temperature of seeds irradiated with light would be maintained constant under field conditions.

The similar responses of G_F of *H. caspica* seeds to Ψ_w obtained in NaCl and PEG treatments (Fig. 4) suggest that the effect of NaCl on *H. caspica* seeds was mainly osmotic. NaCl would not permeate through the testa of *H. caspica* seeds and would not cause either toxic effects on the embryos, or favorable effects on seed water uptake. Similar responses of seed germination have been reported for some other species (Cluff et al., 1983; Myers and Morgan, 1989; Naidoo and Naicker, 1992). The maintenance of viability of *H. caspica* seeds moistened with a high concentration of NaCl would have resulted because the embryos were protected from entrance of external NaCl. The Ψ_w of the NaCl solution that prevented germination of *H. caspica* seeds was not very different from those that prevented germination in other halophytes (Macke and Ungar, 1971; Williams and Ungar, 1972; Khan and Ungar, 1996; Ungar, 1996).

As long as light and temperature alternation were provided, *H. caspica* seeds germinated favorably under a wide range of temperature regimes. Moreover, seed dormancy was not found in *H. caspica*. These indicate that *H. caspica* seeds are able to germinate at any time between spring and autumn in their habitats in China, although they will never germinate during the cold winter.

Promotion of seed germination by light or temperature alternation has been detected in many species that produce small-sized seeds and it was reported to be effective in avoiding futile germination in deep soil or under the vegetative cover of mature plants (Probert, 1992; Fenner, 1995). Compared to some photosensitive seeds (Koller et al., 1964; Dixit and Amritphale, 1996), *H. caspica* seeds appeared to require fairly high fluence of light for their germination because daily short-time illumination with dim light for observation in the continuous dark treatment did not result in appreciable seed germination. This indicates that for germination of *H. caspica* seeds, the seeds need to be almost exposed to the soil surface.

However, in saline and water-deficient environments, where there is severe water evaporation and salt accumulation on the soil surface, the opportunities for seed germination will be limited. Indeed, monthly measurement of salt contents in soil of salinized locations in desert regions (Blank et al., 1994; Pujol et al., 2000) indicated that the salt content in soil is usually higher than the concentration that enables seed germination of species distributed in those areas. Moreover, in desert environments, seed germination at the soil surface occurs only after the supply of a large amount of water (Mott, 1972, 1974). Nevertheless, *H. caspica* seeds remained viable even after they were exposed to very high salinity, and the longevity of its seeds appeared to be fairly good as compared to some other desert plants (Kigel, 1995; Tobe et al., 2005). In this regard, *H. caspica* seeds have the advantage of exploiting rare opportunities for seed germination in the harsh environment.

Monthly precipitation from April to October in Fukang (see Materials and Methods) appears to be generally insufficient to cause leaching of salt from the soil surface and seed germination. On the other hand, water supply from melting snow in early spring appears to be more promising to result in seed germination because it releases a larger amount of water in a short period. Although seed germination may be retarded at lower temperatures, low temperatures in the early spring would also reduce evaporation and salt accumulation at the soil surface, and thus, would favor seed germination of *H. caspica*. Supply of a larger amount of water from melting snow in a short period will result in greater amounts of runoff, and unevenness of soil surface will cause spatial heterogeneity in the distribution of water (Mott, 1972, 1974); hence, water flows and accumulates in depressions where salinity will be substantially reduced and the surface will be kept moistened for a relatively longer period, thus facilitating the germination of seeds. Since mature plants of *H. caspica* produce and disperse a large number of seeds every year, seedling establishment from a very low proportion of seeds would suffice to enable the recruitment of this species.

REFERENCES

Blank, R.R., Young, J.A., Martens, E., Palmquist, D.E. 1994. Influence of temperature and osmotic potential on germination of *Allenrolfea occidentalis* seeds. J. Arid Environ. 26: 339–347.

Boyer, J.S., Knipling, E.B. 1965. Isopiestic technique for measuring leaf water potentials with a thermocouple psychrometer. Proc. Nat. Acad. Sci. U.S.A. 54: 1044–1051.

Cluff, G.J., Evans, R.A., Young, J.A. 1983. Desert saltgrass seed germination and seedbed ecology. J. Range Manage. 36: 419–422.

de Miguel, L., Sánchez, R.A. 1992. Phytochrome-induced germination, endosperm softening and embryo growth potential in *Datura ferox* seeds: sensitivity to low water potential and time to escape to FR reversal. J. Exp. Bot. 43: 969–974.

Dixit, S., Amritphale, D. 1996. Very low fluence response in the induction and inhibition of seed germination in *Celosia argentea*. Seed Sci. Res. 6: 43–48.

Fenner, M. 1995. Ecology of seed banks. In: Kigel, J., Galili, G., eds. Seed development and germination. Marcel Dekker, New York, USA, pp. 507–528.

Hardegree, S.P., Emmerich, W.E. 1990. Partitioning water potential and specific salt effect on seed germination of four grasses. Ann. Bot. 66: 587–585.

Hegarty, T.W. 1978. The physiology of seed hydration and dehydration, and the relation between water stress and the control of germination: a review. Plant Cell Environ. 1: 101–119.

Khan, M.A., Ungar, I.A. 1996. Influence of salinity and temperature on the germination of *Haloxylon recurvum* Bunge ex. Boiss. Ann. Bot. 78: 547–551.

Kigel, J. 1995. Seed germination in arid and semiarid regions. In: Kigel, J., Galili, G., eds. Seed development and germination. Marcel Dekker, New York, USA, pp. 645–697.

Koller, D., Sachs, M., Negbi, M. 1964. Germination-regulating mechanisms in some desert seeds. VIII. *Artemisia monosperma*. Plant Cell Physiol. 5: 85–100.

Lang, A.G.R. 1967. Osmotic coefficients and water potentials of sodium chloride solutions from 0 to 40 °C. Aust. J. Chem. 20: 2017–2023.

Macke, A.J., Ungar, I.A. 1971. The effects of salinity on germination and early growth of *Puccinellia nuttalliana*. Can. J. Bot. 49: 515–520.

Mc Donough, W.T. 1975. Water potential of germinating seeds. Bot. Gaz. 136: 106–108.

Mott, J.J. 1972. Germination studies on some annual species from an arid region of Western Australia. J. Ecol. 60: 293–304.

Mott, J.J. 1974. Factors affecting seed germination in three annual species from an arid region of Western Australia. J. Ecol. 62: 699–709.

Myers, B.A., Morgan, W.C. 1989. Germination of the salt-tolerant grass *Diplachne fusca*. III. Salinity responses. Aust. J. Bot. 37: 239–251.

Naidoo, G., Naiker, K. 1992. Seed germination in the coastal halophytes *Triglochin bulbosa* and *Triglochin striata*. Aquat. Bot. 42: 217–229.

Okusanya, O.T. 1977. The effect of sea water and temperature on the germination behaviour of *Crithmum maritimum*. Physiol. Plant. 41: 265–267.

Omasa, K., Natori, T., Tobe, K., Tanaka, K. 1995. Physioecological studies on drought and salt resistance of plants under controlled environments. In: Japan-China joint study on desertification, phase II report. Science and Technology Agency, Tokyo, Japan, pp. 355–366 (in Japanese, English abstr.).

Probert, R.J. 1992. The role of temperature in germination ecophysiology. In: Fenner, M., ed. Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, UK, pp. 285–325.

Pujol, J.A., Calvo, J.F., Ramírez-Díaz, L. 2000. Recovery of germination from different osmotic conditions by four halophytes from southeastern Spain. Ann. Bot. 85: 279–286.

Rivers, W.G., Weber, D.J. 1971. The influence of salinity and temperature on seed germination in *Salicornia bigelovii*. Physiol. Plant. 24: 73–75.

Schopfer, P., Plachy, C. 1993. Photoinhibition of radish (*Raphanus sativus* L.) seed germination: control of growth potential by cell-wall yielding in the embryo. Plant Cell Environ. 16: 223–229.

Tobe, K., Zhang, L., Omasa, K. 2005. Seed germination and seedling emergence of three annuals growing on desert sand dunes in China. Ann. Bot. 95: 649–659.

Ungar, I.A. 1995. Seed germination and seed-bank ecology in halophytes. In: Kigel, J., Galili, G., eds. Seed development and germination. Marcel Dekker, New York, USA, pp. 599–628.

Ungar, I.A. 1996. Effect of salinity on seed germination, growth, and ion accumulation of *Atriplex patula* (Chenopodiaceae). Am. J. Bot. 83: 604–607.

Wang, Z., Zhu, S., Shu, R., Li, L., Dan, G., You, W., Zeng, X., Zhang, C., Zhang, L., Song, R. 1993. Saline soils in China. Science Press, Beijing, China (in Chinese).

Williams, M.D., Ungar, I.A. 1972. The effect of environmental parameters on the germination, growth, and development of *Suaeda depressa* (Pursh) Wats. Am. J. Bot. 59: 912–918.