Seed germination characteristics of *Halogeton glomeratus*

M. Ajmal Khan, Bilquees Gul, and Darrell J. Weber

Abstract: *Halogeton glomeratus* (Bieb.) C.A. Mey, an annual forb in the family Chenopodiaceae, is widely distributed in the inland salt deserts of western North America. Experiments were conducted to determine the effects of NaCl and temperature on seed germination and the recovery of germination responses after transfer to distilled water. Seeds of *H. glomeratus* were germinated at various temperature regimes (5–15°C, 10–20°C, 10–30°C, 15–25°C, 20–30°C, and 25–35°C), and salinities (0, 200, 400, 600, 800, and 1000 mM NaCl) in a 12 h dark : 12 h light photoperiod. Increases in NaCl concentration progressively inhibited seed germination, and this inhibition was more substantial in the dark than in the photoperiod treatment. Seed germination at concentrations higher than 800 mM NaCl was low (10%). Cooler temperatures significantly inhibited germination in all treatments. A temperature regime of high night (25°C) and high day (35°C) temperatures led to higher germination. Rate of germination decreased with an increase in salinity and was highest at 25–35°C and lowest at 5–15°C temperature regimes. Seeds were transferred from salt solution to distilled water after 20 days, and those from high salinities recovered quickly at all temperature regimes. Recovery germination percentages from the highest salinity treatment varied from 51 to 100% at various temperature regimes.

Key words: Great Basin desert, *Halogeton glomeratus*, halophyte, recovery of seed germination, salt deserts, temperature regime.

Résumé : L'*Halogeton glomeratus*, une herbacée annuelle de la famille des Chenopodiaceae, est largement distribuée dans les déserts salés continentaux de l'ouest de l'Amérique du Nord. Les auteurs ont effectué des expériences afin de déterminer les effets du NaCl et des températures sur la germination des graines et sur la reprise de germination après un transfert dans l'eau distillée. Les germinations des graines de l'*H. glomeratus* ont été conduites sous des régimes variés de température (5–15°C, 10–20°C, 10–30°C, 15–25°C, 20–30°C, et 25–35°C), et de salinité (0, 200, 400, 600, 800, et 1000 mM NaCl), avec une photopériode de 12 h de lumière et 12 h d'obscurité. Les augmentations de concentration en NaCl inhibent progressivement la germination des graines et cette inhibition est plus importante à l'obscurité qu'avec la photopériode utilisée. Aux concentrations plus élevées que 800 mM de NaCl, la germination des graines est faible (10%). Des températures plus fraîches inhibent significativement la germination avec tous les traitements. Un régime de température élevée la nuit (25°C) et élevée le jour (35°C) entraîne une plus forte germination. Le taux de germination diminue avec une augmentation de la salinité; il est le plus élevé et le plus faible respectivement avec des régimes de température de 25–35°C et 5–15°C. Lorsqu'on transfert les graines d'une solution saline à l'eau distillée après 20 j, celles provenant des solutions même les plus salines recouvrent rapidement sous tous les régimes de température. Les pourcentages de reprise de germination vont de 51 à 100% sous divers régimes de température.

Mots clés : désert de Grand Bassin, *Hologeton glomeratus*, halophyte, reprise de germination, déserts salés, régime de température.

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Introduction

Halogeton glomeratus (Bieb.) C.A. Mey is a succulent annual forb (Goodman 1973) with a taproot that can penetrate as deep as 51 cm. *Halogeton glomeratus* can produce about 450 kg of seeds per hectare (Cronin and Williams 1965). These seeds have dormancy, which allows *H. glomeratus* to survive in the seed bank for up to 10 years (Whitson 1987). *Halogeton glomeratus* is adapted to alkaline soils and semiarid environments (Harris 1990). It is distributed in disturbed sites along with *Kochia scoparia*, *Salsola iberica*, *Distichlis spicata*, mixed desert shrub, salt desert shrub, and pinyon–juniper communities. It is common at elevations of 1220 to 1985 m in most counties of Utah (Welsh et al. 1987). It occurs on soils that are heavy clays, clay loams, and loamy sands; and does best in soils where NaCl levels are around 5800 ppm (Cronin and Williams 1965). This plant was introduced from Eurasia into northern Nevada in the early 1930s. It spread quickly into the desert lands of Nevada and Utah. The plant is rich in oxalates and poses a serious threat to grazing animals, especially to sheep, which have suffered heavy losses for several decades (Welsh et al. 1987). *Halogeton glomeratus* seeds contain about 25% oil

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with 85% unsaturation, making it a first-rate edible oil (Weber et al. 2001).

Great Basin desert halophyte species are reported to be very highly tolerant to NaCl (Rivers and Weber 1971; Khan and Weber 1986; Gul and Weber 1999; Khan and Ungar 1999; Khan et al. 2000, 2001*a*, 2001*b*). Maximum halophyte seed germination occurs in distilled water or under reduced salinity stress (Khan et al. 2001*a*). Great Basin species that have a very high salt tolerance at the germination stage include *Kochia americana* (1700 mM NaCl, Clarke and West 1969), *Salicornia pacifica* (856 mM NaCl, Khan and Weber 1986), *Allenrolfea occidentalis* (800 mM NaCl, Gul and Weber 1999), *Salicornia rubra* (1000 mM NaCl, Khan et al. 2000), *Suaeda moquinii* (1000 mM NaCl, Khan et al. 2001*a*), *Kochia scoparia* (1000 mM NaCl, Khan et al. 2001*b*), and *Sarcobatus vermiculatus* (1000 mM NaCl, Khan et al. 2001*c*).

Variation in temperature under saline conditions has differential effects on the germination of halophytes (Ungar 1995). All halophytic species previously studied from the Great Basin desert modify their seed germination with changes in temperature (Khan et al. 2001*a*). Germination and rate of germination increased with an increase in temperature and optimal germination was obtained at a temperature regime of 25–35°C (Khan and Weber 1986; Gul and Weber 1999; Khan 1999; Khan et al. 2000, 2001*a*, 2001*b*, 2001*c*). Khan and Ungar (1999) reported that seeds of *Triglochin maritima* failed to germinate if the temperature was 5°C or lower.

Halophyte seeds have the ability to maintain seed viability for extended periods of time during exposure to hypersaline conditions and then commence germination when salinity stress is reduced (Woodell 1985; Keiffer and Ungar 1995). However, halophytes differ in their capacity to recover from salinity stress (Woodell 1985). This variation in recovery responses could be due to differences in the temperature regime to which they are exposed (Gul and Weber 1999). Recovery responses in Great Basin and other halophytes are significantly affected by temperature regimes (Khan and Ungar 1997; Khan and Gul 1998; Gul and Weber 1999; Khan et al. 2000, 2001*a*, 2001*b*, 2001*c*).

The primary objective of this investigation was to study the effects of temperature and salinity on the percent germination, rate of germination, and recovery responses of *H. glomeratus* seeds.

Materials and methods

Seeds of *H. glomeratus* were collected during the fall of 1996 from a salt flat located 2.5 miles (4.0 km) northwest of Faust, Utah, U.S.A. Seeds were collected randomly from the whole population to get an adequate representation of genetic diversity. The flowering spikes and seeds were stripped, and the materials were spread on tables at room temperature until thoroughly dried and then threshed by hand through screens. A small fanning mill was used to separate the seeds from chaff. Seeds were stored in sealed plastic jars at 4°C. Germination studies were started in the late fall of 1996. Seeds were surface sterilized with the fungicide Phygon (Phygon had no effect on seed germination). Seeds had 100% germination in distilled water in a viability test. Germination was carried out in 50 × 9 mm (Gelman no. 7232) tight-fitting plastic Petri dishes with 5 mL of test solution (0, 200, 400, 600, 800, and 1000 mM NaCl). Each dish was placed in a 10-cm diameter plastic Petri dish as an added precaution against loss of water by evaporation. Four replicates of 25 seeds each were used for each treatment. Seeds were considered to be germinated with emergence of the radicle.

The effect of temperature on germination was determined for six alternating temperature regimes of 5–15, 10–20, 10–30, 15–25, 20–30, and 25–35°C. A 24-h cycle was used, where the higher temperature (15, 20, 30, 35°C) coincided with the 12-h light period (Sylvania cool white fluorescent light, 110 µmol photons$\cdot m^{-2} \cdot s^{-1}$, 400–700 nm) and the lower temperature (5, 10, 15, 25°C) coincided with the 12-h dark period. Seeds were germinated in distilled water and 200, 400, 600, 800, and 1000 mM NaCl solutions under the above-mentioned temperature regimes. Percent germination was recorded on alternate days for 20 days. Ungerminated seeds from the 20-day NaCl treatments were transferred to distilled water to study the recovery of germination, which was also recorded at 2-day intervals for 20 days. The recovery percentage was determined by the following formula: $(a - b)/(c - b) \times 100$, where a is the total number of seeds germinated after being transferred to distilled water, b is the total number of seeds germinated in saline solution, and c is the total number of seeds. The rate of germination was estimated by using a modified Timson index of germination velocity $= \sum G/t$, where G is the percentage of seed germination at 2-day intervals and t is the total germination period (Khan and Ungar 1999). The maximum value possible using this index with our data was 50 (i.e., 1000/20). The higher the value, the more rapid the rate of germination.

Germination data (20 day and rate of germination) and recovery data (20 day and rate of recovery of germination) were transformed (arcsine) before statistical analysis to ensure homogeneity of variance before analysis. These data were analyzed using the procedures in SPSS, V.9.0 (SPSS Inc. 1999). Effect of salinity and temperature on seed germination was examined using two-way analysis of variance (ANOVA). A two-way ANOVA was used to demonstrate the significance of the main factors (salinity and temperature regime) and their interaction in affecting the rate and percent germination.

A linear regression analysis was used to determine the relationship between salt concentration and germination at different salinities.

Results

Germination of *H. glomeratus* significantly increased with increasing temperature, decreased with increasing salinity, and a significant interaction was found for the two factors (Table 1). Seeds of *H. glomeratus* germinated rapidly in nonsaline controls at all temperatures tested and reached final germination percentages in less than 4 days (Fig. 1). Seed germination was higher in distilled water than in any of the saline treatments (Fig. 2). Less than 10% of the seeds germinated in the 1000 mM NaCl treatment (Fig. 1). Change in temperature regimes significantly affected the germination of *H. glomeratus* seeds (Figs. 1 and 2). Germination at 5–15°C in the nonsaline control was only 58%. Seeds showed higher germination in all treatments at the highest temperature regime (25–35°C) with 100% germination in the nonsaline control (Figs. 1 and 2). A linear regression explains a high proportion of the germination response with R^2 values ranging from 0.73 to 0.91 in various temperature treatments (Fig. 2).

The index of germination velocity calculated by using a modified Timson's index showed that the rate decreased with an increase in salinity (Fig. 3). The rate of germination in-

Fig. 1. Mean germination percentages of *Halogeton glomeratus* in 0, 200, 400, 600, 800, and 1000 mM NaCl at different thermoperiods.

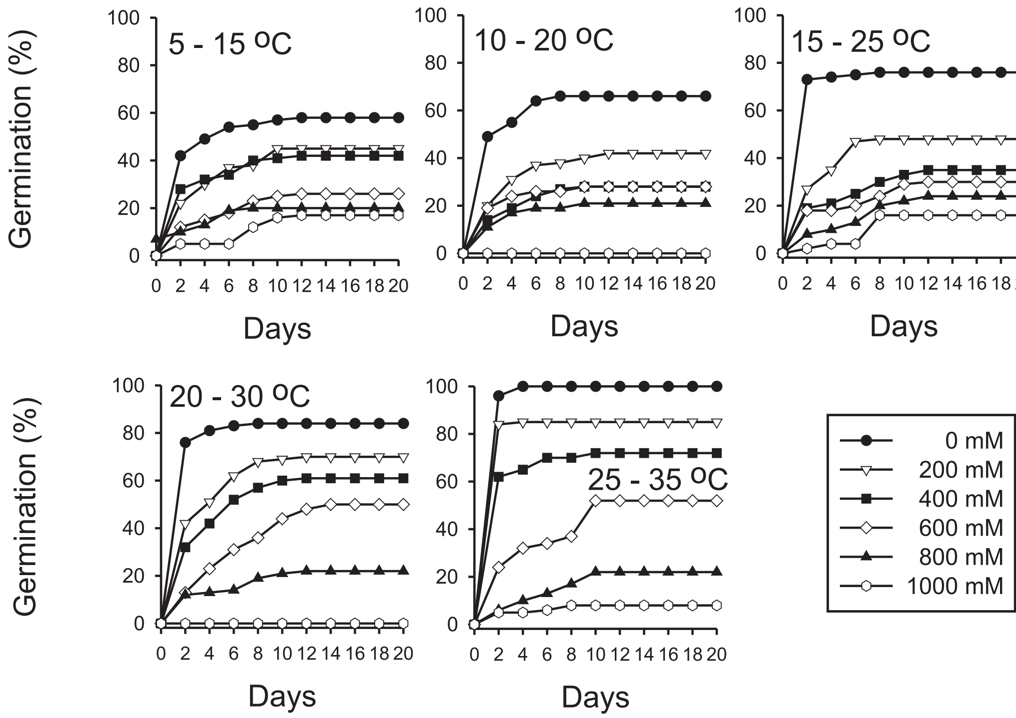
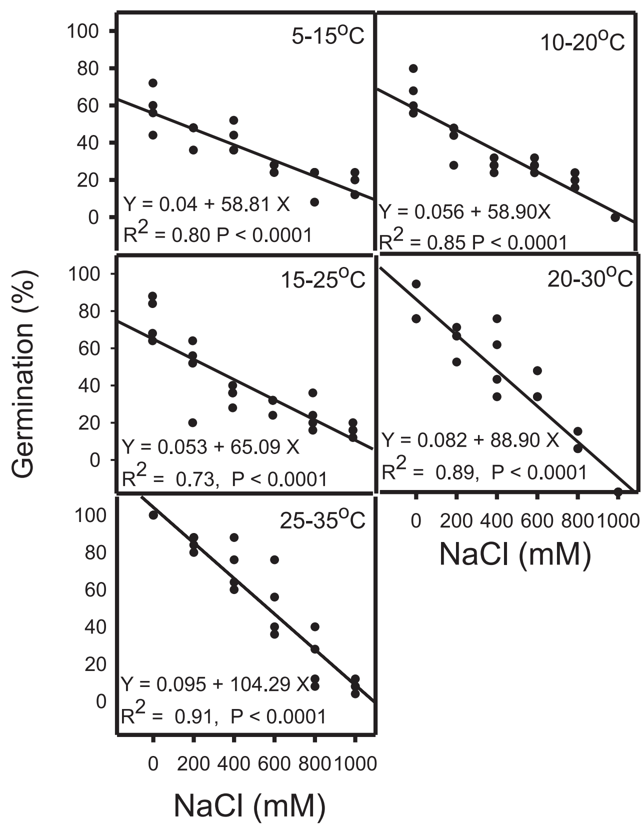


Table 1. Results of two-way ANOVA of characteristics by salinity, thermoperiods, and their interaction.

Independent variable	Salinity	Thermoperiod	Salinity × thermoperiod
Percent germination	154.75***	33.00***	5.33***
Rate of germination	223.99***	46.74***	7.64***
Percent recovery	16.73***	5.27***	3.23***
Rate of recovery	4.88***	0.87ns	2.09**

Note: Values represents *F*-values. ns, not significant.
$^{**}P < 0.01$.
$^{***}P < 0.001$.

Fig. 2. Final germination percentages of *Halogeton glomeratus* at different NaCl and thermoperiods.



creased with an increase in temperature and the highest rate of germination occurred in the 25–35°C temperature regime (Fig. 3). A two-way ANOVA of rate of germination indicated a significant effect of salinity and temperature and their interaction (Table 1).

After 20 days of salinity treatment, seeds were transferred to distilled water to determine the recovery of germination after salt inhibition. The results presented in Table 2 show that the recovery decreased with an increase in NaCl concentration at the temperature regimes tested. At lower salinities (0–600 mM NaCl), the recovery of germination progressively increased with an increase in temperature; however, at NaCl concentrations of 800 mM and above no significant effect of temperature was noted (Table 2). A two-way ANOVA of recovery percentages and rate of recovery indicated a significant effect of salinity and their salinity × temperature interaction, (Table 1) but temperature alone was not significant in affecting the rate of recovery of germination.

Fig. 3. Mean rate of germination of *Halogeton glomeratus* in various salinities and thermoperiods. Values at each temperature regime having the same letter are not significantly different ($P < 0.05$) from the control (Bonferonni test).

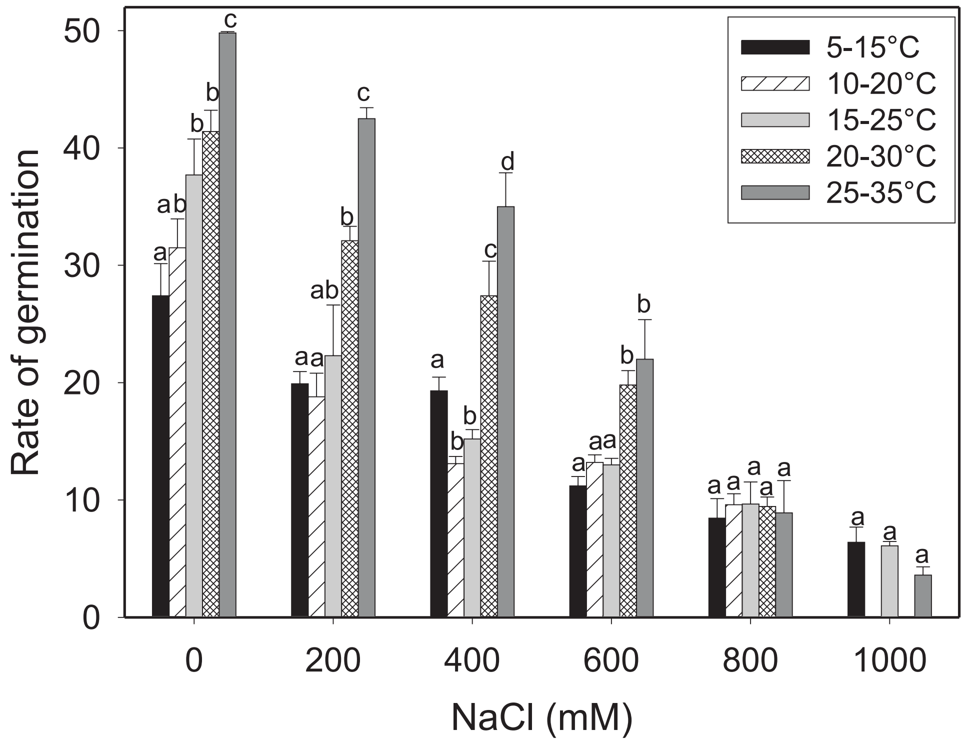


Table 2. Recovery percentage (mean ± SE) of germination of *Halogeton glomeratus* after they were transferred from 0, 200, 400, 600, 800, and 1000 mM NaC1 at thermoperiods of 5–15ºC, 10–20ºC, 15–25ºC, 20–30ºC, and 25–35ºC.

NaC1 (mM)	5–15ºC	10–20ºC	15–25ºC	20–30ºC	25–35ºC
0	58±5.7*a*	66±5.3*a*	76±5.9*a*	84±4.0*a*	100±0*a*
200	45±3.0*b*	42±5.3*b*	48±9.7*b*	70±3.5*b*	85±1.9*b*
400	42±3.8*b*	28±1.6*c*	35±2.5*b*	61±8.1*b*	72±6.9*c*
600	26±1.2*c*	28±1.6*c*	30±2.0*c*	50±3.4*b*	52±9.0*d*
800	20±4.0*c*	21±1.9*d*	24±4.3*c*	22±7.4*c*	22±7.6*e*
1000	7±3.0*d*	0±0*e*	6±1.6*d*	0±0*d*	8±1.6*f*

Note: Different letters represent significant ($P < 0.05$) differences between salinity treatments, based on ANOVA and Bonferroni tests.

Discussion

Vegetation growing in the Great Basin desert usually experiences a wide fluctuation in temperature and salinity during the growing season. It ranges from cold subfreezing (–7°C) spring temperatures to very hot (~37°C) summer temperatures. Hansen and Weber (1975) found that temperatures gradually increased from May to July and gradually decreased from August to September. Similarly, a moderate salinity level occurs because of the run-off water from mountains, which accumulates in the playas during early spring (Khan et al. 2001*a*), but the gradual evaporation of water in late spring and early summer causes a corresponding increase in salinity. Plant species that live in these habitats have to evolve a strategy to cope with these fluctuating environmental conditions.

Our results showed that *H. glomeratus*, a typical Great Basin desert halophyte, is highly tolerant to NaCl at the germination stage. All seeds germinated at optimal temperature (25–35°C) in distilled water and any increase in salinity inhibited germination. Less than 10% of the seeds germinated at 1000 mM NaCl. Ability of Great Basin desert halophytes to germinate under highly saline conditions has been reported (Khan and Weber 1986; Gul and Weber 1999; Khan and Ungar 1999; Khan et al. 2000, 2001*a*, 2001*b*, 2001*c*). Khan et al. (2000) reported that seeds of *Salicornia rubra*, a playa annual forb, germinated at 1000 mM NaCl under optimal temperature conditions. Similar results were reported for *Kochia scoparia* (Khan et al. 2001*b*); however, another annual from the Great Basin community, *Triglochin maritima*, could not germinate at 500 mM NaCl or above (Khan and Ungar 1999). Other perennial halophytes from the area such as *Salicornia utahensis*, *Suaeda moquinii*, *Allenrolfea occidentalis*, and *Sarcobatus vermiculatus* show some seed germination at 800 mM and above (Khan and Weber 1986; Gul and Weber 1999; Khan et al. 2001*a*, 2001*c*).

Seed germination of *H. glomeratus* was substantially affected by change in temperature. Cooler temperature regimes either delayed germination of the control under low salinity treatments or inhibited it at higher salinity concentrations. Seeds germinated quickly at warmer temperatures and in both nonsaline and saline conditions. A similar increase in germination under a higher temperature regime was reported for other Great Basin desert species, such as *Salicornia pacifica* var. *utahensis*, (Khan and Weber 1986), *Allenrolfea occidentalis* (Gul and Weber 1999), *Triglochin maritima* (Khan and Ungar 1999), *Salicornia rubra* (Khan et al. 2000), *Kochia scoparia* (Khan et al. 2001*a*), and *Suaeda* *moquinii* (Khan, et al. 2001*b*). However, halophytes from subtropical maritime deserts of Pakistan, e.g., *Haloxylon recurvum* (Khan and Ungar 1996), *Zygophyllum simplex* (Khan and Ungar 1997), *Suaeda fruticosa* (Khan and Ungar 1998), and *Arthrocnemum macrostachyum* (Gul and Khan 1998) showed better germination at a relatively cooler temperatures.

Seeds of *H. glomeratus* from the Faust, Utah, population, when transferred to distilled water after a 20-day treatment at various salinity concentrations, responded differentially under varying temperature regimes. Our data showed low recovery at the cooler temperature regime and a higher recovery at the warmer temperatures. Recovery was also inhibited in high salinity treatments at all temperatures. Gul and Weber (1999) reported that seeds of *Allenrolfea occidentalis* from high salinities recovered quickly (85 to 100%) at all temperature regimes. Khan and Ungar (1997) reported that the percentage of ungerminated seeds that recovered when they were transferred to distilled water differed significantly with variation in species and temperature regimes. *Zygophyllum simplex* had little recovery from all NaCl concentrations in all temperature regimes. *Haloxylon recurvum*, *Suaeda fruticosa*, and *Triglochin maritima* showed substantial recovery. Khan et al. (2000) showed that seeds of *Salicornia rubra* had a high recovery in high salt treatments, indicating that exposure to a high concentration of NaCl did not permanently inhibit germination. Similar results were reported for *Triglochin maritima* (Khan and Ungar 1998). Our results with *H. glomeratus* agreed with the recovery responses of annual forb *Zygophyllum simplex*, which failed to recover from higher salinity treatments (Khan and Ungar 1997).

Seeds of *H. glomeratus* are highly salt tolerant at germination and their response improved under warmer temperature regimes. This is consistent with previous reports on the degree of salt tolerance of other Great Basin halophytes, such as *Salicornia utahesis*, *S. rubra*, *Suaeda moquinii*, *Salicornia rubra, Kochia scoparia*, and *Allenrolfea occidentalis*. There was a significant difference in the recovery pattern. Although there was substantial recovery of germination at low salinity treatments (0–600 mM NaCl), exposure to high salinity substantially inhibited the recovery. This indicates that if seeds are exposed to high salinity during storage, it causes permanent damage to the seed. Although *H. glomeratus* seeds maintain a persistent seed bank, there will be little chance for those seeds germinating if they are exposed to highly saline conditions during the time they are in the soil. *Halogeton glomeratus* is considered to be a poisonous weed for grazing animals and particularly for sheep. The great loss in sheep occurs when sheep are starving and *H. glomeratus* is the only feed available. The risk of poisoning is low when *Halogeton glomeratus* is a minor part of the feed. However, *H. glomeratus* also produces 450 kg/ha of seeds (Cronin and Williams 1965), which contain a high quality edible oil (Weber et al. 2000). Because of this property, we believe that *H. glomeratus* could be used to reclaim desert sites, which are destroyed either by unsustainable irrigation practices or brine dumping during oil exploration. Simultaneously one could obtain seeds with high quality edible oils approaching that of canola or olive oils.

References

Clarke, L.D., and West, N.E. 1969. Germination of *Kochia americana* in relation to salinity. Agron. J. **20**: 286–287.

Cronin, E.H., and Williams, W.M. 1965. Principles for managing ranges infested with halogeton. J. Range Manag. **19**: 226–227

Goodman, P.J. 1973. Physiological and ecotypic adaptations of plants to salt desert conditions in Utah. J. Ecol. **61**: 473–494.

Gul, B., and Khan, M.A. 1998. Population characteristics of a coastal halophyte *Arthrocnemum macrostachyum*. Pak. J. Bot. **30**: 189–197.

Gul, B., and Weber, D.J. 1999. Effect of salinity, light, and thermoperiod on the seed germination of *Allenrolfea occidentalis*. Can. J. Bot. **77**: 1–7.

Hansen, D.J., and Weber, D.J. 1975. Environmental factors in relation to the salt content of *Salicornia pacifica* var. *utahensis*. Great Basin Nat. **35**: 86–96.

Harris, G.A. 1990. Cheat grass: invasion of potential and managerial implications. *In* Range weeds revisited: Proceeding of a symposium: a 1989 Pacific Northwest range management short course; 24–26 January 1989, Spokane, Wash. *Edited by* B.F. Roche and C.T. Roche. Washington State University, Department of Natural Resource Sciences, Cooperative Extension, Pullman, Wash. pp. 5–9.

Keiffer, C.W., and Ungar, I.A. 1995. Germination responses of halophyte seeds exposed to prolonged hypersaline conditions. *In* Biology of salt tolerant plants. *Edited by* M.A. Khan and I.A. Ungar. Department of Botany, University of Karachi, Pakistan. pp. 43–50.

Khan, M.A. 1999. Comparative influence of salinity and temperature on the germination of subtropical halophytes. Halophyte uses in different climates. I: Ecological and ecophysiological studies. Progress in biometeriology. Vol. 13. *Edited by* H. Lieth, M. Moschenko, M. Lohman, H.-W. Koyro, and A. Hamdy. Backhuys Publishers, Netherlands. pp. 77–88.

Khan, M.A., and Weber, D.J. 1986. Factors influencing seed germination in *Salicornia pacifica* var. *utahensis*. Am. J. Bot. **73**: 1163–1167.

Khan, M.A., and Ungar, I.A. 1996. Influence of salinity and temperature on the germination of *Haloxylon recurvum*. Ann. Bot. **78**: 647–551.

Khan, M.A., and Ungar, I.A. 1997. Effect of thermoperiod on recovery of seed germination of halophytes from saline conditions. Am. J. Bot. **84**: 279–283.

Khan, M.A., and Gul, B. 1998. Population characteristics of a coastal halophyte *Arthrocnemum macrostachyum*. Pak. J. Bot. **30**: 189–197.

Khan, M.A., and Ungar, I.A. 1998. Germination of salt tolerant shrub *Suaeda fruitcosa* from Pakistan: salinity and temperature responses. Seed Sci. Tech. **26**: 657–667.

Khan, M.A., and Ungar, I.A. 1999. Seed germination and recovery of *Triglochin maritima* from salt stress under different thermoperiods. Great Basin Nat. **59**: 144–150.

Khan, M.A., Gul, B., and D.J. Weber. 2000. Germination responses to *Salicornia rubra* to temperature and salinity. J. Arid Environ. **45**: 207–214.

Khan, M.A., Gul, B., and D.J. Weber. 2001*a*. Salinity and temperature effects on the germination of dimorphic seeds of *Suaeda moquinii*. Aust. J. Bot. **49**: 1–8.

Khan, M.A., Gul, B., and D.J. Weber. 2001*b*. Effect of salinity and temperature on the germination of *Kochia scoparia*. Wetland Manag. & Ecol. (in press).

Khan, M.A., Gul, B., and D.J. Weber. 2001*c*. Effect of temperature, and salinity on the germination of *Sarcobatus vermiculatus.* Biologia Plant. (in press).

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

SPSS. 1999. SPSS: SPSS 9.0 for Windows Update. SPSS Inc., Chicago, Ill.

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

Weber, D.J., Gul, B., Khan, M.A.,Williams, T., Wayman, P., and Warner, S. 2001. Composition of vegetable oil from seeds of native halophytic shrubs. *In* 2000. Proceedings: Shrubland Ecosystem Genetics and Biodiversity. 13–15 June 2000, Provo, Utah. Proceedings RMRS-P-000. *Edited by* E. D. McArthur, D.F. Fairbanks, J. Daniel. U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station, Ogden, Utah.

Welsh, S.L., Atwood, N.D., Goodrich, S., and Higgins, L.C. 1987. A Utah flora. Great Basin Nat. Mem. **9**: 1–894.

Whitson, T.D. 1987. ed. Weeds and poisonous plants of Wyoming and Utah. Res. Rep. 116-USU. University of Wyoming, College of Agriculture, Cooperative Extension Service. Laramie, Wyo.

Woodell, S.R.J. 1985. Salinity and seed germination patterns in coastal plants. Vegetatio, **61**: 223–229.