

Salt tolerance in *Salicornia rubra* from a salt playa of Great Basin Desert.

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Abstract: *Salicornia rubra* Nels. (Chenopodiaceae) is a stem succulent annual species widely distributed in the saline pans of Northern Utah playas. *Salicornia rubra* showed 98% germination in non-saline controls, at higher thermoperiod (25-35°C) compared to less than 50% germination at the lower thermoperiod (5-15°C). Seed germination was inhibited with the increases in salinity and few seed germinated at 1000 mM NaCl. Rate of germination also decreased with an increase in salinity. Exposure of the seeds to high salt concentration (800 and 1000 mM NaCl) had a priming effect on the seed germination. Optimal growth of *S. rubra* plants was recorded at 200 mM NaCl and the growth declined with a further increase in salinity. Most plants survived at 1000 mM NaCl treatment. Na⁺ and Cl⁻ contents of plants increased with an increase in salinity, while calcium (Ca²⁺), Magnesium (Mg²⁺) and Potassium (K⁺) content decreased. Water potential of plants become more negative with the increase in salinity.

Key Words: Germination, Growth, Ions, Recovery, Salinity.

Introduction

Salicornia rubra Nels. (Chenopodiaceae) is a highly salt tolerant annual species occurring in salt playas of the Great Basin desert (Ungar, 1965, 1974). It forms pure stands of a pioneer community in the most saline locations of inland salt playas at Goshen, Utah. It was associated with *Salicornia utahensis*, *Allenrolfea occidentalis*, and *Distichlis spicata* along a gradient of reduced salinity.

Annual *Salicornia* sp. are highly salt tolerant but vary in their response to salinity (Langlois, 1966; Ungar, 1977). *Salicornia europaea* showed a 10% germination at 5‰ (860 mM) NaCl (Ungar, 1967), *Salicornia bigelovii* had 63% germination at 8‰ (1376 mM) NaCl (Rivers and Weber, 1971), and *Salicornia stricta* was reported to have 10% germination at 10‰ (1720 mM) NaCl (Chapman, 1974). Germination of *Salicornia* sp is also substantially affected by the variation in the thermoperiod (Hogan, 1968; Rivers and Weber, 1971; Philippillai and Ungar, 1984; Berger, 1985; Khan and Ungar, 1996). Khan and Gul (1998) showed that germination of *Arthrocnemum indicum* (= *Arthrocnemum macrostachyum*) was

significantly higher at 15-25 °C thermoperiod at 600 and 800 mM NaCl. Halophyte seeds have the ability to maintain seed viability for extended periods of time during exposure to hypersaline conditions and then to commence germination when salinity stress is reduced (Ungar, 1982; Woodell, 1985; Keiffer & Ungar, 1995, Khan & Ungar 1996, 1997, Gul & Weber, 1999).

Growth of some halophytes is stimulated by low levels of salinity (Flowers and Yeo, 1986; Munns et al., 1993; Khan and Aziz, 1998, Khan et al. 1999, 2000a), while most species of halophytes are inhibited by high concentrations of salt with none showing optimal growth at seawater concentration (Ungar, 1991). Great Basin halophytes, however, showed a promotion of growth at salinities approaching seawater (400 to 600 mM NaCl) and a decline in growth at higher salinities (1000 mM, NaCl) (Gul et al., 2000). A similar result was also reported for a subtropical halophytic shrub *Suaeda fruticosa* (Khan et al. 2000b).

Salinity may cause a decrease in biomass production because increased soil salinity produce a lowering of plant water potentials, specific ion toxicities, or ionic imbalances (Neu-

man, 1997). Plants protect themselves from NaCl toxicity by minimizing Na⁺ uptake and transport to the shoots (Cramer et al., 1989). Osmotic adjustment under saline condition may be achieved by ion uptake, synthesis of osmolytes or both (Popp, 1994; Cheeseman, 1988). Halophytes differ widely in the extent to which they accumulate ions and overall degree of salt tolerance (Glenn et al., 1996). Stem and leaf-succulent Chenopods are commonly known as salt-accumulators and have high Na⁺ and Cl⁻ content (Breckle, 1975; Albert and Popp, 1997, Gorham et al., 1980; Neuman, 1997; Khan et al., 1999, 2000abc).

Little information is available on the salt tolerance of *Salicornia rubra* at different stages of growth. The purpose of this study is to determine the effect of salinity on, seed germination, growth, water relations and ion accumulation in *Salicornia rubra*.

Material and Methods

Seeds of *Salicornia rubra* were collected from salt flats situated near Goshen, Utah, USA. Seeds were surface sterilized using the fungicide Phygon. Four replicates of 25 seeds each were used for each treatment. Seeds were considered to be germinated with the emergence of the radicle.

To determine the effect of temperature on germination, alternating temperature regimes of 5-15 °C, 10-20 °C, 15-25 °C, 20-30 °C, and 25-35 °C, based on a 24-hr cycle were used, where the higher temperature (15, 20, 25, 30 and, 35 °C) coincided with the 12-hr light period (Sylvania cool white fluorescent lamps, 250 μM.m⁻².s⁻¹, 400 - 750 nM) and the lower temperature (5, 10, 15, 20, and 25 °C) coincided with the 12-hr dark period. NaCl concentration of 0, 200, 400, 600, 800 and 1000 mM NaCl solutions were used. After 20 days ungerminated seeds from the NaCl treatments were transferred to distilled water to study the recovery of germination, which was also recorded at 2-day intervals for 20 days. Percent germination was recorded every alternate day for 20 days. The rate of

germination was estimated by using a modified Timson index of germination velocity = $(\sum G/t)$, where G is percentage of seed germination at 2-days intervals, and t is total germination period (Khan and Ungar 1985).

For growth experiments seeds were grown into 5 inch diameter x 5 inch tall plastic pots containing nutrient free sand in a growth chamber at a thermoperiod of 25°C : 35°C (night : day). Five salinities (0, 200, 400, 600, 800, and 1000 mM NaCl) were used. Four pots were used for each treatment group and potted plants were grown in plastic trays containing half strength Hoagland's nutrient solution. Pots were sub-irrigated, and the water level was adjusted daily to correct for evaporation. Salt solutions were completely replaced once a week to avoid build-up of salinity in pots.

Fresh and dry weight of the plant shoots and roots were measured 90-d after the highest salt concentration was reached. Chloride, nitrate and sulfate ion contents were measured with a DX-100 ion chromatograph. Cation contents Na⁺, K⁺, Ca²⁺, and Mg²⁺ of the plant organs were analysed using a Perkin Elmer model 360 atomic absorption spectrophotometer. The water potential was measured using a plant moisture stress instrument (PMS Instrument Co.). Germination data were transformed (arcsine) before statistical analysis. An ANOVA analysis was used to determine if significant differences were present among means. A Bonferroni test was carried out to determine if significant (P < 0.05) differences occurred between individual treatments (SPSS 1999).

Results

Optimal germination in *S. rubra* occurred in distilled at warmer thermoperiods (20-30°C and 25-35°C) (Fig. 1). Seeds germination significantly (Table 1) decreased with the increase in the salinity of the medium and few seed germinated at 1000 mM NaCl (Fig. 1). At lower salinities (0 – 600 mM NaCl) optimal germination occurred at 20-30°C and 25-35°C, while at higher salinities no significant difference were

found among temperatures. The rate of germination was calculated using a modified Timson index showed that the rate decreased with an increase in salinity (Fig. 2). Highest rate of germination was obtained in the 25-35°C temperature regime and lowest in 5-15°C (Fig. 2). Seeds showed recovery from salinity stress at

all thermoperiods (Table 2). There was relatively lower recovery at lower temperatures in high salinity treatments. However, at higher temperature most seeds germinated when transferred from higher salinities to distilled water (Table 2).

Table 1. Results of Two-way ANOVA of characteristics by salinity (S), thermoperiods (T) and their interaction.

Independent variable	S	T	S x T
Percent germination	141.20***	21.81***	4.03***
Rate of germination	130.70***	32.91***	5.10***
Percent recovery	3.90**	4.22**	6.02***

Note. Number represents F-values. ** P<0.01; *** P<0.001.

Table 2. Recovery percentage (Mean \pm SE) of germination of *Salicornia rubra*. After they transferred from 0, 200, 400, 600, 800 and 1000 mM NaCl at thermoperiods of 5-15°C, 10-20°C, 15-25°C, 20-30°C and 25-35°C.

NaCl (mM)	5-15°C	10-20°C	15-25°C	20-30°C	25-35°C
0	81 \pm 15.7	54 \pm 21.3	45 \pm 7.3	0.0 \pm 0.0	2 \pm 2.0
200	35 \pm 3.5	43 \pm 7.1	17 \pm 9.6	0.0 \pm 0.0	2.5 \pm 2.5
400	58 \pm 7.5	33 \pm 6.9	15 \pm 5.2	54 \pm 12.3	22 \pm 9.0
600	48 \pm 7.0	48 \pm 4.2	36 \pm 3.4	48 \pm 8.4	34 \pm 5.6
800	48 \pm 7.7	46 \pm 3.1	45 \pm 2.7	32 \pm 7.4	59 \pm 12.1
1000	40 \pm 10.8	45 \pm 5.8	28 \pm 5.7	69 \pm 11.7	78 \pm 11.3

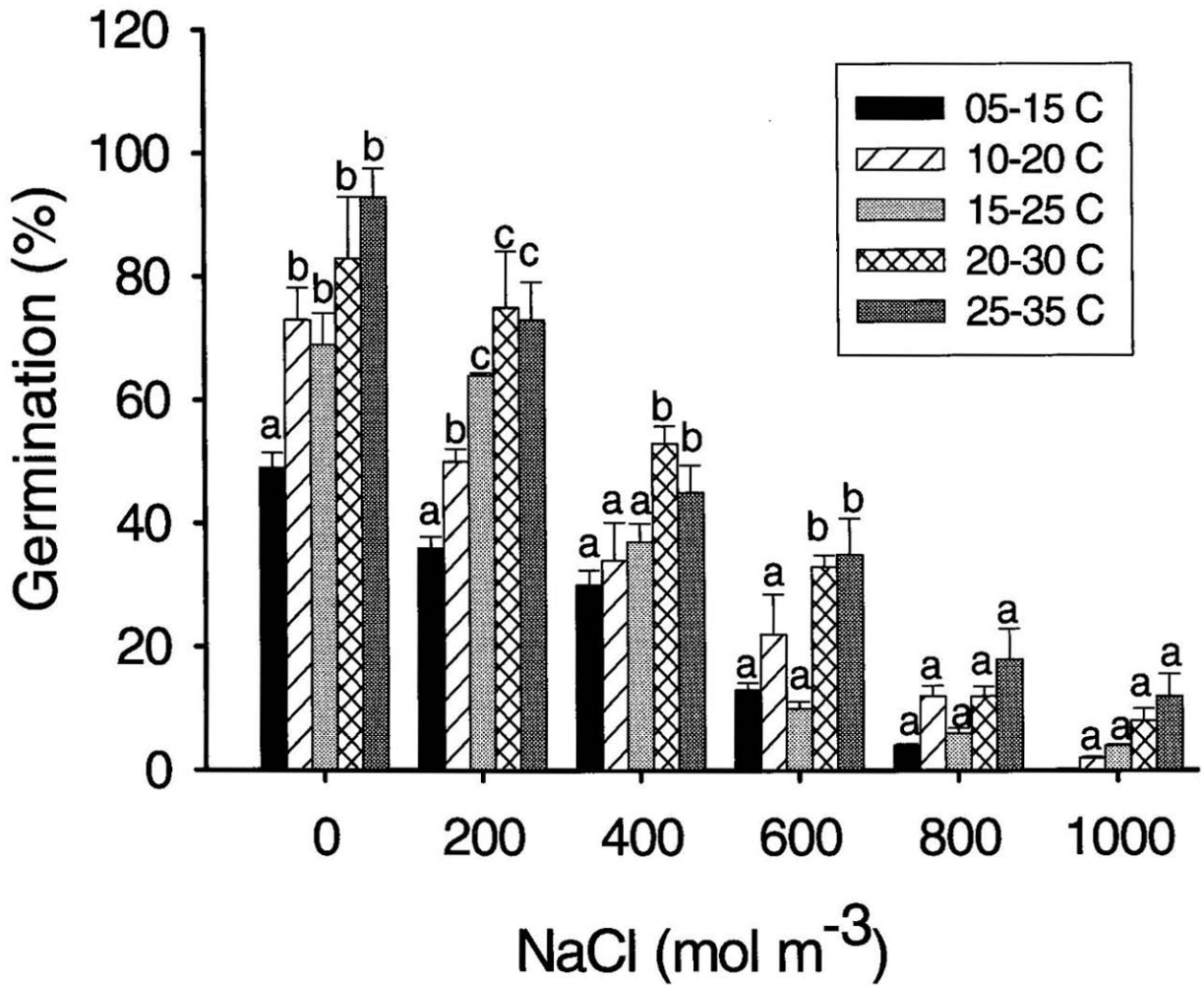


Fig.1. Mean (\pm SE) final germination percentages of *Salicornia rubra* seeds in various NaCl concentrations and thermoperiods. Values of the final germination percentages (Mean \pm SE) having the same letter are non significantly different at $P < 0.05$, Bonferroni test.

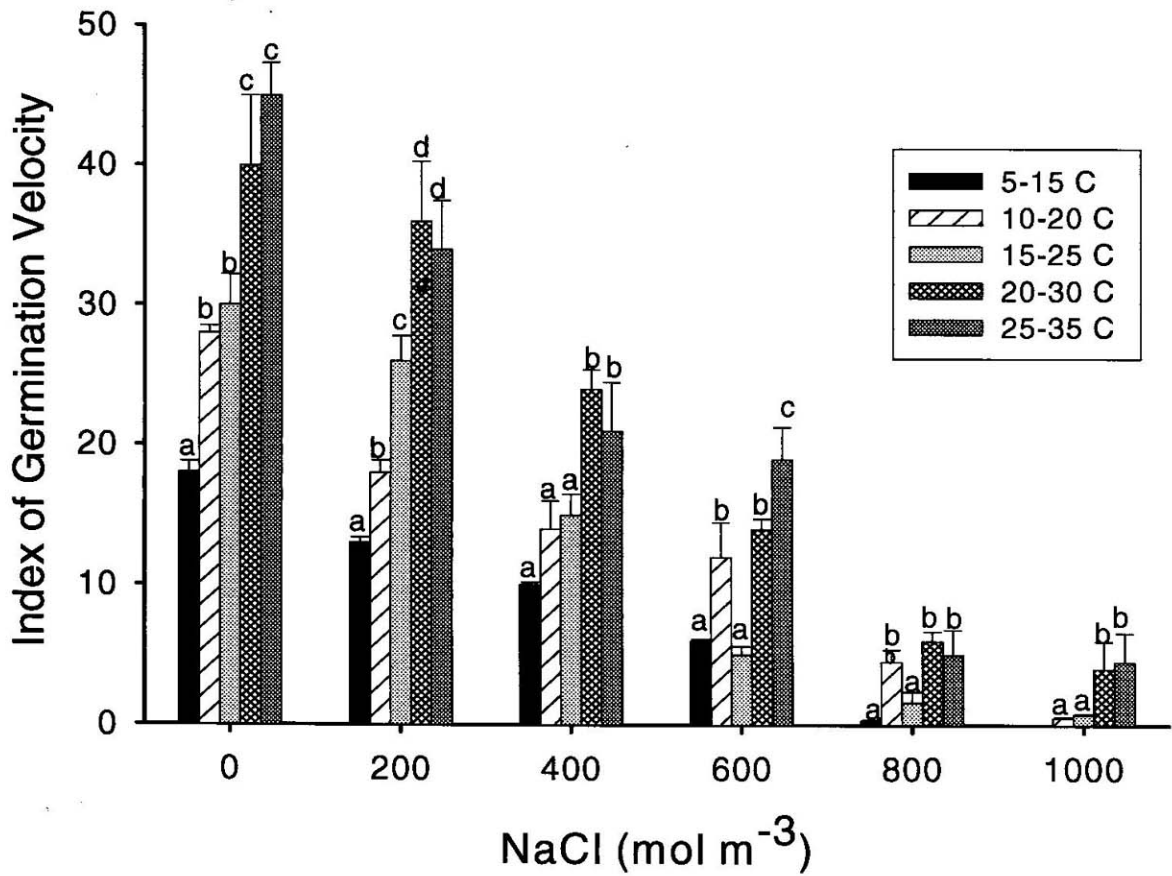


Fig.2. Index of germination velocity of *Salicornia rubra* seeds in various NaCl and thermoperiods. Values of the Index of germination velocity (Mean \pm SE) having the same letter are non significantly different at $P < 0.05$, Bonferroni test.

Optimal growth of *S. rubra* plants were recorded at 200 mM NaCl and the growth declined with a further increase in salinity (Fig. 3). A 50% growth reduction was obtained at 800 mM NaCl. Most plants survived at 1000 mM NaCl treatment. Root weight decreased at

low salinity and root weight was unchanged with a further increase in salinity (Fig. 3). Two way analysis of variance of fresh weight and dry weight showed significant ($p < 0.0001$) individual effect of salinity and plant parts but their interaction is not significant (Table 3).

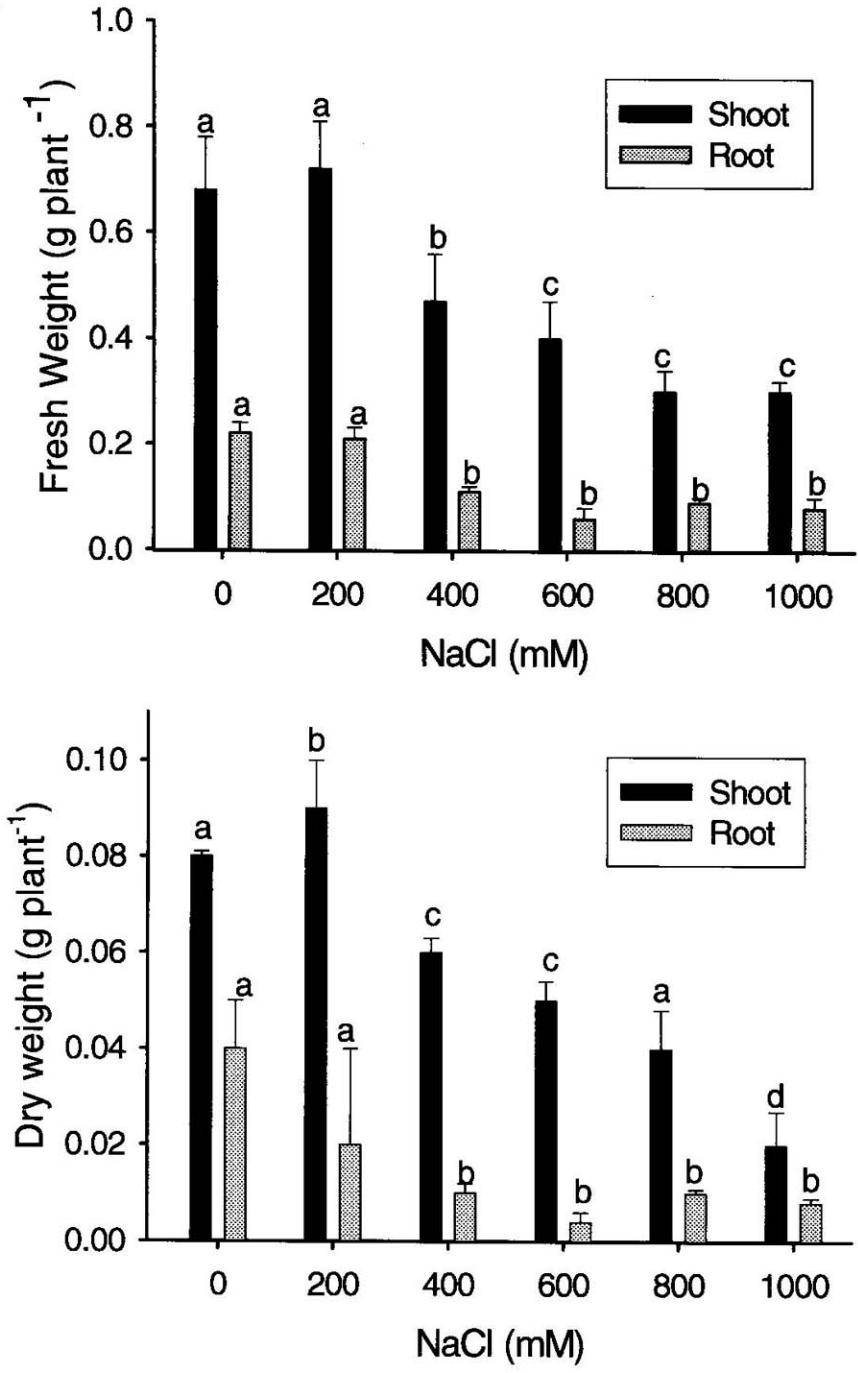


Fig.3. Effect of NaCl on the fresh and dry weights of *Salicornia rubra* plants. Bars represents (Mean \pm SE). Different letters above bars represent significant differences (P<0.05) among treatments.

Table 3. Results of two-way analysis of variance of characteristics by salinity (S) and Plant Part (P).

Dependent variables	Salinity (S)	Plant Part (P)	S x P
Fresh weight	11.1***	119.7***	2.6*
Dry weight	3.7**	34.4***	0.99 ^{n.s.}
Tissue water content	1.9 ^{n.s.}	0.6 ^{n.s.}	1.6 ^{n.s.}

Succulence of root and shoot both, when expressed as g tissue water g⁻¹ dry weight, increased at 400 – 600 mM NaCl and decreased with a further increase in salinity (Fig. 4). Water potential of *S. rubra* plants progressively

increased with an increase in salinity reaching – 5.8 MPa at 1000 mM NaCl. *Salicornia rubra* plants were progressively stressed with increase in salinity (Fig. 4).

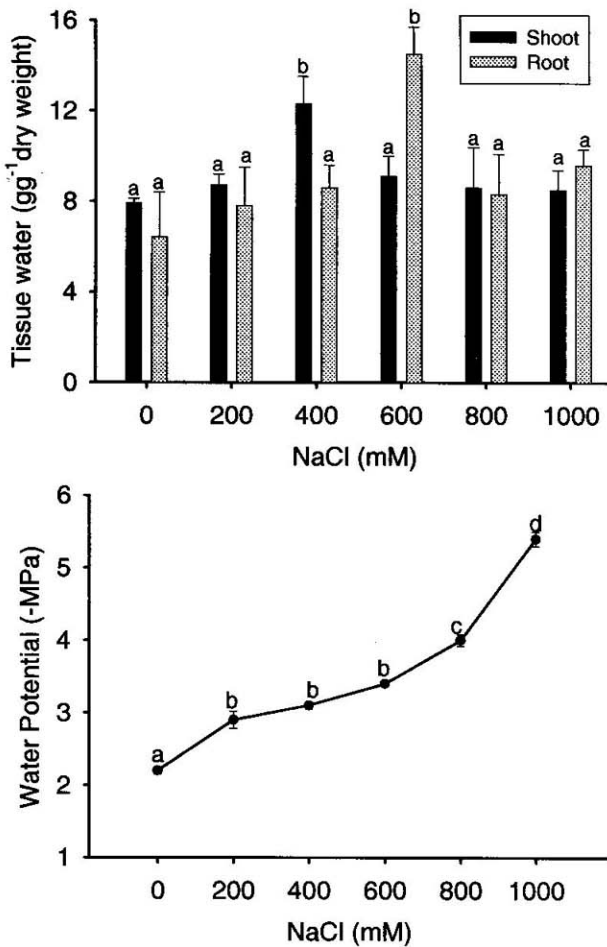


Fig.4. Effect of NaCl on the tissue water contents and water potential of *Salicornia rubra* plants. Bars represents (Mean ± SE). Different letters above bars represent significant differences (P<0.05) among treatments.

Total of cations (Na^+ , K^+ , Ca^{2+} , and Mg^{2+}) and the anion (Cl^-) content increased with increase in salinity (Table 4). At all NaCl concentrations, the increase in total inorganic ions resulted from increased Na^+ , and Cl^- while K^+ , Ca^{2+} , and Mg^{2+} concentrations decreased with an increase in salinity.

Table 4. Results of two-way analysis of variance of characteristics by salinity (S) and Plant Part (P).

Dependent variable	Salinity (S)	Plant Part (P)	S x P
Sodium	345.3***	1.9 ^{n.s.}	3.3*
Chloride	3.7**	34.4***	0.99 ^{n.s.}
Potassium	4.6**	31.3***	3.4*
Calcium	2.8*	68.4***	2.3*
Magnesium	9.4***	295.5***	27.2***
Nitrate	0.8 ^{n.s.}	1.1 ^{n.s.}	3.8**
Sulphate	2.8*	3.4*	6.5***

Note: Numbers represent F values, * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$,

^{n.s.} non-significant.

Discussion

Salicornia rubra grows in the most saline region of an inland salt playa at Goshen, Utah, and produced seeds during September and October. Seeds germinate during April when the snowmelt and the water from the surrounding mountains accumulates in the playa decreasing the salinity concentration of soil water. Field observation also showed that seeds continue to germinate until early summer when the temperature increases resulting into a corresponding increase in soil salinity due to rapid evaporation of water. Our laboratory studies indicated that *Salicornia rubra* germinated well under non-saline conditions. Cold temperatures delayed its germination and it increased substantially with increase in temperature. In addition the salinity tolerance of *S. rubra* seeds was also increased at higher day temperatures. Seeds of *S. rubra* showed 15% germination at 1000 mM NaCl.

Seed germination of *S. rubra* was affected by change in temperature. Seeds germinated quickly at warmer temperatures and showed best germination under both non-saline and saline conditions. Similar increase in germination under higher thermoperiod was reported for other Great Basin desert species like *Salicornia pacifica* var. *utahensis*, (Khan and Weber, 1986), *Allenrolfea occidentalis* (Gul and Weber, 1999), *Triglochin maritima* (Khan and Ungar, 1999) and *Suaeda moquinii* (Khan, Gul and Weber, unpublished data). Seeds of *S. rubra* from the Goshen, Utah population, when transferred to distilled water after 20-d treatment at various salinity concentrations responded differentially under different temperature regimes. The recovery was higher at higher thermoperiod and salinity regimes. This result is in agreement with other reports on recovery of seed germination in some Great Basin species (Khan and Gul, 1998; and Gul and Weber, 1999; Khan and Ungar, 1999).

Present study showed that growth of *Salicornia rubra* was significant promoted at 200 mM NaCl, while plants could also survive at 1000 mM NaCl. Earlier work on *Sarcocornia natalensis*, another stem succulent coastal halophyte from Chenopodiaceae showed that its shoot dry weight was greatest for plants grown at 300 mM NaCl and that exposure to 500 mM NaCl for 7 months resulted in only a moderate decrease in shoot weight (Naidoo and Rughunanan, 1990). Similarly *Halosarchia pergranulata* was assessed for plants exposed to NaCl treatment for 70 days with optimal shoot dry weights at 10-200 mM NaCl and only 20% of the maximum value at 800 mM NaCl (Short and Colmer, 1999). Another member of stem succulent halophytes family *Arthrocnemum macrostachyum* also showed optimal growth at 400 mM NaCl (Khan and Ungar, unpublished data). This shows that *S. rubra* is a very highly salt tolerant stem succulent species like all other in this group.

Succulence is thought to contribute to salt regulation by increasing the vacuolar volume available for ion accumulation (Greenway and

Munns, 1980; Albert, 1982; Ungar 1991). Salinity increased the water content of *Salsola kali* (Reimann and Breckle, 1995), *Arthrocnemum fruticosum* (Eddin and Doddema 1986) and *Arthrocnemum macrostachyum* (Khan and Ungar, unpublished data) and this increase in succulence were proposed to be caused by large salt accumulation. Our results showed that *S. rubra* showed a significant increase in succulence as well as salt accumulation at higher salinity (400 - 600 mM NaCl) both in root and shoot.

Measurement water potential through plant water status console showed that plant made their water potential increasingly more negative with the increase in salinity. It may be suggested therefore, that enhancement of dry mass production from 0 to 400 mol m⁻³ NaCl is due primarily to ion uptake.

The total concentration of inorganic ions increased with the increase in salinity and this increase is primarily due to increase in the concentration of Na and Cl. Na⁺ and Cl⁻ concentrations in tissue water exceed the medium salinity. Gorham and Wyn Jones (1983) reported that sodium content of *Suaeda maritima* tissues ranged from 218 mol m⁻³ g⁻¹ fresh weight in the apex to 433 mol m⁻³ g⁻¹ in flowers. Our results indicated that sodium and chloride concentration in shoots and roots increased with salinity. Magnesium, calcium, and potassium of the shoots of plants grown at optimal salinity represents levels adequate for growth (Epstein, 1972). Calcium and magnesium concentrations were extremely low in shoots of plants grown at high salinity agreeing with the results found for other halophytes (Flowers, 1972; Glenn and O'Leary, 1984; McNulty, 1985; Naidoo and Rughunanan, 1990, Ayala and O'Leary, 1995). Greenway et al. (1966) reported that growth of *Atriplex nummularia* was optimal at 100 to 200 mM NaCl. Leaf Na⁺ content increased from 0.9 to 5.0 mM⁻¹g dry weight and Cl⁻ increased from 0.4 to 3.6 mM⁻¹g in treatments with 1 and 300 mM NaCl. Potassium content of the leaves decreased over this NaCl range from 1.8 to 0.6 mM/g dry weight. At optimal growth conditions

plants accumulated from 4.1 to 6.4 mM Na/g and 2.0 to 3.0 mM Cl/g dry weight of leaf material. Greenway (1968) had shown that when *A. nummularia* was exposed to salinities ranging from 0 to 1% NaCl, resulting in an ion accumulation of Na⁺ at high salt concentrations and a reduction in potassium content in leaves.

In conclusion *Salicornia rubra* is a fast growing stem succulent halophyte, which is highly salt tolerant at germination stage. *Salicornia rubra* was found to complete its life cycle in 1000 mM NaCl and showed significant promotion in 200 mM NaCl. Growth enhancement at lower salinities indicates that this species is a obligate halophyte. The mechanism for salt tolerance in this species could involve striking a delicate balance between ion accumulation, osmotic adjustment, maintenance of water potential, and growth. Tissue water content increased at high salinity. The Na⁺ and Cl⁻ content of leaves increased while Ca²⁺, Mg²⁺, and K⁺ content decreased with increasing salinity indicating that nutrient deficiencies might occur in leaves when plants are exposed to high salinity.

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