Salicornia rubra Nels. (Chenopodiaceae) is a salt-tolerant annual species occurring in salt playas of the Great Basin desert of western United States (Ungar 1965, 1974). Salicornia rubra is found in pure stands on the most saline location of an inland salt playa at Goshen, Utah, and is associated with S. utahensis, Allenrolfea occidentalis, and Distichlis spicata (Khan et al. 2000). Salicornia rubra is capable of germinating at 1000 mM NaCl at 25–35°C alternating temperature regime. Dormancy-regulating chemicals were evaluated for their ability to alleviate the innate and salinity-enforced dormancy in seeds of Salicornia rubra. Betaine, GA3, kinetin, fusicoccin, ethephon, thiourea, proline, and nitrate had no effect in alleviating primary dormancy. Increases in NaCl concentration progressively inhibited germination of Salicornia rubra seeds. Ethephon, fusicoccin, GA3, kinetin, thiourea, and nitrate promoted germination under low saline conditions. At high salinity fusicoccin had no effect, whereas GA3, kinetin, and ethephon substantially alleviated salt effects. Application of these dormancy-regulating compounds could be of practical value in seeding a saline area for restoration purposes, particularly under high saline conditions.

Key words: gibberellic acid, ethephon, fusicoccin, halophytes, kinetin, seed dormancy, Salicornia rubra, thiourea.

Salicornia rubra Nels. (Chenopodiaceae) is a salt-tolerant annual species occurring in salt playas of the Great Basin desert in western United States. It forms pioneer communities on the most saline location of an inland salt playa at Goshen, Utah. Seeds of Salicornia rubra are capable of germinating at 1000 mM NaCl at 25–35°C alternating temperature regime. Dormancy-regulating chemicals were evaluated for their ability to alleviate the innate and salinity-enforced dormancy in seeds of Salicornia rubra. Betaine, GA3, kinetin, fusicoccin, ethephon, thiourea, proline, and nitrate had no effect in alleviating primary dormancy. Increases in NaCl concentration progressively inhibited germination of Salicornia rubra seeds. Ethephon, fusicoccin, GA3, kinetin, thiourea, and nitrate promoted germination under low saline conditions. At high salinity fusicoccin had no effect, whereas GA3, kinetin, and ethephon substantially alleviated salt effects. Application of these dormancy-regulating compounds could be of practical value in seeding a saline area for restoration purposes, particularly under high saline conditions.

Key words: gibberellic acid, ethephon, fusicoccin, halophytes, kinetin, seed dormancy, Salicornia rubra, thiourea.

1Department of Botany and Range Science, Brigham Young University, Provo, UT 84602 USA.
2Present address: Department of Botany, University of Karachi, Karachi-75270, Pakistan.
3Corresponding author.

Maintaining salt playa areas generally requires seed germination of the halophytes. Often this involves breaking dormancy in the presence of high salinity. It is of interest to evaluate the relationship between dormancy-regulating compounds and salinity in maintaining the salt playa or restoring saline areas with halophytes. The present study was designed to determine the role of dormancy-regulating chemicals in alleviating the innate and salinity-enforced dormancy in *Salicornia rubra*.

**METHODS**

During fall 1994 we collected seeds of *Salicornia rubra* from salt flats situated at Goshen, Utah, USA. Seeds were separated from the inflorescence and stored at 4°C. They were surface sterilized using the fungicide Phygon (2,3 dichloro-1,4-naphthoquinone). Germination was carried out in 50 × 9-mm tight-fitting plastic petri dishes with 5 mL of test solution. As an added precaution against loss of water by evaporation, we placed each dish in a 10-cm-diameter plastic petri dish. Four replicates of 25 seeds each were used for each treatment. When the radicle emerged (2 mm), we considered seeds to be germinated.

Seeds were germinated in a growth chamber at an alternating temperature regime of 25–35°C, where the higher temperature coincided with the 12-hour light period (cool white fluorescent lamps, 110 µmol photons m⁻² s⁻¹, 400–750 nm) and the lower temperature coincided with the 12-hour dark period. Nitrate concentrations of 20 mM, thiourea concentration of 10 mM, ethephon concentration of 10 mM, fusicoccin concentration of 5 µM, gibberellic acid concentration of 3 mM, kinetin concentration of 0.05 mM, and NaCl concentration of 0, 300 (–1.38 MPa), 600 (–2.76 MPa), and 900 (–4.14 MPa) mM were used.

Percent germination was recorded every alternate day for 20 days. We estimated the rate of germination by using a modified Timson index of germination velocity = ΣG/t, where G is percentage of seed germination at 2-day intervals, and t is the total germination period (Khan and Ungar 1985). 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 were transformed (arc-sine) before statistical analysis. We used an ANOVA analysis to determine if significant differences were present among means and a Bonferroni test to determine if significant (*P* < 0.05) differences occurred between individual treatments (SPSS 1996).

**RESULTS**

In distilled water, 66% of the seeds germinated. Proline, betaine, GA3, kinetin, thiourea, nitrate, fusicoccin, and ethephon had no effect in alleviating primary dormancy of the seeds (Table 1). Fusicoccin treatment increased the germination rate and produced up to 80% germination compared to 66% in distilled water (*P* > 0.05; Table 2).

Increase in NaCl concentration in the medium progressively inhibited germination of *Salicornia rubra* seeds. A maximum of 66% germination was obtained in distilled water, and no seed germinated at 900 mM NaCl (Table 1). Inclusion of ethephon partially alleviated (*P* < 0.01) salinity-enforced germination inhibition (Table 1). Fusicoccin alleviated
Table 1. Percentage of Salicornia rubra seeds that germinated under various salinities and germination-regulating chemicals. Values in the same column (i.e., each dormancy-regulating chemical) followed by the same letter are not significantly different (P > 0.05) from each other (Bonferroni test).

<table>
<thead>
<tr>
<th>NaCl (mM)</th>
<th>Water</th>
<th>Proline</th>
<th>Betaine</th>
<th>GA3</th>
<th>Kinetin</th>
<th>Thiourea</th>
<th>Nitrate</th>
<th>Fusicoccin</th>
<th>Ethephon</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>66 ± 4.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>62 ± 6.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>52 ± 3.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>63 ± 2.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>62 ± 4.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>74 ± 6.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>65 ± 4.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>80 ± 4.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>72 ± 5.9&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>300</td>
<td>22 ± 2.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>30 ± 3.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>25 ± 1.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>28 ± 2.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>41 ± 3.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>60 ± 3.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>36 ± 3.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>38 ± 3.0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>40 ± 7.1&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>600</td>
<td>4 ± 1.9&lt;sup&gt;c&lt;/sup&gt;</td>
<td>10 ± 3.2&lt;sup&gt;c&lt;/sup&gt;</td>
<td>5 ± 0.9&lt;sup&gt;c&lt;/sup&gt;</td>
<td>34 ± 6.4&lt;sup&gt;c&lt;/sup&gt;</td>
<td>33 ± 6.4&lt;sup&gt;c&lt;/sup&gt;</td>
<td>8 ± 2.0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>13 ± 4.0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>17 ± 5.6&lt;sup&gt;c&lt;/sup&gt;</td>
<td>16 ± 2.8&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>900</td>
<td>0 ± 0&lt;sup&gt;d&lt;/sup&gt;</td>
<td>4 ± 0.8&lt;sup&gt;d&lt;/sup&gt;</td>
<td>3 ± 0.8&lt;sup&gt;d&lt;/sup&gt;</td>
<td>8 ± 4.1&lt;sup&gt;d&lt;/sup&gt;</td>
<td>8 ± 4.1&lt;sup&gt;d&lt;/sup&gt;</td>
<td>7 ± 0.9&lt;sup&gt;d&lt;/sup&gt;</td>
<td>5 ± 2.7&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0 ± 0&lt;sup&gt;d&lt;/sup&gt;</td>
<td>14 ± 1.0&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Table 2. Rate of seed germination of Salicornia rubra seeds under various salinities and germination-regulating chemicals. Values in the same column (i.e., each dormancy-regulating chemical) followed by the same letter are not significantly different (P > 0.05) from each other (Bonferroni test).

<table>
<thead>
<tr>
<th>NaCl (mM)</th>
<th>Water</th>
<th>Proline</th>
<th>Betaine</th>
<th>GA3</th>
<th>Kinetin</th>
<th>Thiourea</th>
<th>Nitrate</th>
<th>Fusicoccin</th>
<th>Ethephon</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>27 ± 2.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>24 ± 3.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>29 ± 1.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>29 ± 1.52&lt;sup&gt;a&lt;/sup&gt;</td>
<td>32 ± 2.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>28 ± 1.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>36 ± 2.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>33 ± 3.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>29 ± 1.9&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>300</td>
<td>13 ± 2.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>12 ± 0.7&lt;sup&gt;b&lt;/sup&gt;</td>
<td>17 ± 0.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>18 ± 1.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>25 ± 1.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>17 ± 5.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>16 ± 1.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>18 ± 5.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10 ± 1.1&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>600</td>
<td>5 ± 1.4&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3 ± 0.5&lt;sup&gt;c&lt;/sup&gt;</td>
<td>15 ± 3.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>15 ± 3.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4 ± 0.7&lt;sup&gt;c&lt;/sup&gt;</td>
<td>6 ± 2.0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>8 ± 2.4&lt;sup&gt;c&lt;/sup&gt;</td>
<td>8 ± 1.3&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.9 ± 0.7&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>900</td>
<td>2 ± 0.7&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2 ± 0.5&lt;sup&gt;d&lt;/sup&gt;</td>
<td>4 ± 1.8&lt;sup&gt;d&lt;/sup&gt;</td>
<td>4 ± 1.5&lt;sup&gt;d&lt;/sup&gt;</td>
<td>3 ± 0.3&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2 ± 1.2&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0 ± 0&lt;sup&gt;d&lt;/sup&gt;</td>
<td>7 ± 0.6&lt;sup&gt;e&lt;/sup&gt;</td>
<td>0 ± 0&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

(P < 0.01) seed germination at low NaCl treatment (Table 1). Gibberellic acid and kinetin both were ineffective in promoting germination in nonsaline treatments, while both compounds significantly (P < 0.01) alleviated salinity effects on germination (Table 1). Nitrogenous compounds (thiourea and nitrate) promoted germination under low saline conditions. At 300 mM NaCl treatment, application of thiourea substantially alleviated germination from 22% in control to about 60%. In the presence of nitrate and thiourea, some germination was reported at 900 mM NaCl (Table 1). Proline and betaine did not alter germination under saline and nonsaline conditions (Table 1). At low salinity (300 mM NaCl) all the chemicals promoted the rate of germination as compared to high salinity (Table 2).

**DISCUSSION**

Salicornia rubra grows in the most saline region of inland salt playas, but seed germination in natural conditions takes place during the early spring when spring rains and runoff from mountains considerably reduce playa salinity. Salinity progressively increases during late spring and early summer, and few seeds germinate during these periods. Seeds of S. rubra showed a partial dormancy (66% germination) in nonsaline control under laboratory conditions. This dormancy could not be alleviated with the application of proline, betaine, gibberellic acid, kinetin, ethylene, thiourea, and nitrate, while fusicoccin had some promoting effect. Seed germination in S. rubra was inhibited with an increase in salinity, and no seed germinated at 900 mM NaCl. Fusicoccin, ethephon, GA3, kinetin, nitrate, and thiourea partially alleviated the inhibitory effects of salinity on germination whereas proline or betaine showed little effect.

Compatible osmotica-like proline and betaine are reported to partially alleviate innate dormancy in Zygophyllum simplex, Atriplex griffithii, Halopyrum mucronatum, and Arthrocenum indicum (Khan and Ungar 1997, Khan et al. 1998, Khan and Ungar unpublished data). Khan et al. (1998) showed that proline and betaine did not relieve salinity-induced dormancy in Arthrocenum indicum. Similar results are reported for Kosteletzkya virginica and Halopyrum mucronatum (Poljakoff-Mayber et al. 1994). Both proline and betaine alleviated the innate dormancy of Zygophyllum simplex seeds, but neither was effective at high salinities (Khan and Ungar 1996). Gul (1998), however, reported that proline and
betaine both alleviated high salinity effects in *Allenrollea occidentalis*. Our results with *S. rubra* showed that proline and betaine failed to alleviate both innate and salinity-induced dormancy.

Seed dormancy enforced by low salinity was partially alleviated by fusicoccin in *S. rubra*, and there was no significant effect on high salinity treatments. This alleviation may be due to the stimulation of ATPase during the early phases of germination to facilitate proton extrusion and K\(^+\) uptake (Marre 1979, Stout). A stimulation of germination by fusicoccin in various kinds of seeds has been observed (Lado et al. 1974, Ismail 1990, Gul and Weber 1998). Fusicoccin has the ability to remove the inhibitory effect of abscisic acid on germination of normal seeds and on embryo growth of decoated seeds (Lado et al. 1975). It is more likely that abscisic acid production due to salinity stress could be counteracted by fusicoccin and thus alleviate the inhibitory effect of salinity.

Dormancy in seeds of numerous species is reported to be relieved by applying ethylene (Ketring 1977, Bewley and Black 1985), which reverses the inhibitory effect of abscisic acid and osmotic stress (Karssen 1976, Schonbeck and Egley 1981). Applying ethylene to *S. rubra* seeds stimulated germination under nonsaline and saline conditions.

Thiourea and nitrate both stimulated the germination of *S. rubra* seeds under saline conditions. The alleviating effect of thiourea on osmoinhibition gradually decreases with an increase in salinity. *Salicornia rubra* showed a full recovery from the low salinity effects and partial alleviation of the inhibitory effect of high salinities. GA3 and kinetin both alleviated the salinity effect on the germination of *S. rubra* seeds. GA3 and kinetin are known to alleviate the salinity effect in some halophytic seeds (Khan and Ungar 1996, 2000, Khan et al. 1998), while it was ineffective in other halophytes such as *Suaeda fruticosa* and *Haloxylon recurvum* (Khan and Ungar unpublished data).

*Salicornia rubra* produces numerous seeds at the end of autumn and beginning of winter. Most of the seeds (65%) readily germinate if proper conditions are provided. Seeds in their natural environment are prevented from germinating due to very cold temperatures. Seeds begin germinating very early during spring, but germination decreases with increased salinity. For restoration of saline areas, seeds of *S. Rubra* could be scattered prior to spring rains. In highly saline soil areas, treatment of the seeds with GA3 or kinetin prior to scattering would increase the germination rate.

**Literature Cited**


SPSS, INC. 1996. SPSS: SPSS 7.0 for Windows update. SPSS Inc., USA.


Received 6 March 2000
Accepted 1 November 2000