



Effect of Dormancy Relieving Compounds on the Seed Germination of Non-dormant *Allenrolfea occidentalis* under Salinity Stress

BILQUEES GUL* and DARRELL J. WEBER

Department of Botany and Range Sciences, Brigham Young University, Provo, Utah 84602-5181, USA

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Allenrolfea occidentalis (Chenopodiaceae) is a highly salt tolerant plant species that is widely distributed in inland salt marshes and salt playas of the western United States. We investigated the influence of dormancy-relieving compounds (fusicochin, ethephon, nitrate and thiourea) in alleviating salinity stress on the seed germination of *A. occidentalis*. Seed germination decreased with an increase in salinity and no seed germinated at 800 mM NaCl. Fusicochin (5 μ M), ethephon (10 mM) and nitrogenous compounds (20 mM nitrate and 10 mM thiourea) were able to counteract the inhibition produced by salinity treatments. All dormancy relieving compounds significantly ($P < 0.0001$) promoted germination at all salinity concentrations. Fusicochin completely reversed the inhibitory effects of salinity on seed germination of *A. occidentalis*. Ethephon application significantly promoted germination at all salinities. Nitrate and thiourea were relatively less effective in alleviating the effects of high salinity on germination.

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Key words: *Allenrolfea occidentalis*, ethephon, fusicochin, halophyte, dormancy, nitrate, salinity, seed germination, thiourea.

INTRODUCTION

Allenrolfea occidentalis (S. Wats.) Kuntze (iodine bush) is a perennial halophytic shrub native to the salt deserts of western United States and north western Mexico (Flowers, 1934; Ungar, 1974; Jansen and Parfitt, 1977). It is one of the most salt tolerant succulent shrub species occurring in salt pans and is found growing in soils containing more than 6.0% NaCl. It grows in the bottom of internally drained basins at the margins of salt playas in the Great Basin (Billings, 1945) where the majority of the salt is NaCl (Hansen and Weber, 1975). The plants produce seeds by autumn and most are dispersed onto saline soil around the parent plant. Wind and water, upon which they readily float, often disperse the seeds. *Allenrolfea occidentalis* seeds are highly tolerant to salinity during germination, but no seeds germinate at 800 mM NaCl (Gul and Weber, 1998). Cool thermoperiods (5–15 °C) inhibit germination, and optimal germination is obtained at a warm thermoperiod (25–35 °C). High salinity-inhibited-germination is completely alleviated when seeds are transferred to distilled water (Gul and Weber, 1998).

There is little information available on the seed germination of *A. occidentalis*. Gold (1939) determined that seeds could germinate in up to 700 mM NaCl. He concluded that germination tends to decrease with increasing concentrations of salt, and that temperature conditions influence the effect of salinity upon seed germination.

Fusicochin (FC), a diterpene glycoside and major phytotoxic substance in culture filtrates of the plant pathogen *Fusicoccin amygdali* markedly stimulates germination,

and several physiological processes in plant tissues (Marre, 1979; Ballio *et al.*, 1968; Ballio and Scalorbi, 1981). FC reproduces the effect of cytokinins on cell enlargement, on the extrusion of hydrogen ions, and on the transmembrane potential in isolated cotyledons (Marre, Lado and Rasi-Caldogno, 1974). This suggests that FC, like cytokinins and perhaps gibberellins, might affect seed germination. If so, FC could be employed as a tool to understand the mechanism of the hormonal control of dormancy (Marre, 1979). Fusicochin completely reversed the effects of all salinity treatments on the germination of *Zygophyllum quatarensis* and *Z. simplex* seeds (Ismail, 1990; Khan and Ungar, 1998).

Ethephon (2-chloroethylphosphonic acid) was highly effective in reversing the inhibitory effect of PEG and ABA or a combination of these on the germination of *Amaranthus caudatus* seeds (Kepczynski, 1986). Seeds of several species show a substantial response to ethylene in the breaking of dormancy and studies have also shown that ethylene produced by seeds has a regulatory role in determining germination (Esashi and Leopold, 1969). These authors also reported that ethylene is formed by the seed soon after the start of imbibition and is capable of stimulating germination. There are numerous reports on the breakage of seed dormancy by ethylene. These reports raise the possibility that the production of ethylene may contribute to the breaking of dormancy in imbibed seeds (Toole, Bailey and Toole, 1964; Ketring and Morgan, 1969). Seeds of *Cyclopia intermedia* and *C. subternata* exhibit both a seed-coat-imposed dormancy and an embryo dormancy, which is broken by exposure to ethylene (Sutcliffe and Whitehead, 1995). Salt enforced-dormancy in *Zygophyllum simplex* is partially alleviated by ethephon (Khan and Ungar, 1998).

* For correspondence.

Nitrate is known to stimulate the germination of seeds (Stokes, 1965; Mayer and Poljakoff-Mayber, 1975) and it received considerable attention as a possible regulator of seed germination in the soil (Egely, 1995). The mixture of 67 mM nitrate and 0.14 mM ethephon stimulated germination of *Chenopodium album* seeds (Karssen, 1976; Carmona and Murdoch, 1995). Nitrate ions enhance germination in controlled experiments, usually when combined with other factors such as alternating temperatures, chilling, light, or plant growth regulators (Vincent and Roberts, 1977; Bewley and Black, 1994). Thiourea has been shown to be effective in alleviating the inhibition of germination by salt or high temperature stress (Esashi *et al.*, 1979; Bewley and Black, 1994; Noor and Khan, 1995; Khan and Ungar, 1998).

This paper determines the effect of salinity and the role of four dormancy alleviating compounds (FC, ethephon, nitrate and thiourea) on the germination of *A. occidentalis* seeds under salinity stress. Chemicals were selected because of their dormancy relieving action in other species (Roberts and Smith, 1977; Ismail, 1982; Ismail, 1990; Carmona and Murdoch, 1995; Khan and Ungar, 1998).

MATERIALS AND METHODS

Seeds of *A. occidentalis* were collected during autumn 1995 from a salt playa located 1 km east of Goshen, northwest Utah. Seeds were randomly collected from the whole population to represent the genetic diversity of the population. The flowering spikes and seeds were stripped as the seeds matured and the inflorescence dried. Seeds were air dried and threshed by hand through screens. A small fanning mill was used to separate seeds from chaff. Seeds were stored in sealed plastic jars at 4 °C. Germination studies began in the spring of 1996. Seeds were surface sterilized with the fungicide, Phygon; this had no effect on seed germination. Seeds showed 100% germination in distilled water in a viability test before germination. Four 25-seed replicates were placed directly in 50 × 9 mm (Gelman No. 7232) tight-fitting plastic Petri dishes and submerged in 5 ml of test solution. Each dish was placed in a 10 cm diameter plastic Petri dish as an added precaution against loss of water by evaporation. Seeds were considered to have germinated when the radicle emerged. Each experiment was conducted at least twice.

Seeds were germinated in a chamber at an alternating temperature regime of 25–35 °C, where the higher temperature coincided with the 12 h light period (Sylvania cool white fluorescent light, 110 μmol photons m⁻² s⁻¹, 400–700 nm) and the lower temperature coincided with the 12 h dark period. FC (5 μM), ethephon (10 mM), nitrate (20 mM), thiourea (10 mM) and NaCl (0, 200, 400, 600 and 800 mM) solutions were used to enhance germination in salinity treatments. Preliminary experiments showed that the concentrations used were optimal. Percent germination was recorded on alternate days for 20 d. The rate of germination was estimated using a modified Timson index of germination velocity = $\Sigma G/t$, where G is the percentage of seed germination at 2 d intervals and t is the total germination period (Khan and Ungar, 1984). The maximum value

possible using this index with our data was 1000/20 = 50. The higher the value, the more rapid the rate of germination.

Germination data (20 d and rate of germination) were transformed (arcsine) before statistical analysis. These data were analysed using SPSS, V.7 (SPSS Inc., 1996). Two way analysis of variance was used to demonstrate the significance of main factors (growth regulators × salinity treatments) and their interaction in affecting the rate and percentage germination. A Bonferonni test was used to determine if differences among means were significant ($P < 0.05$).

RESULTS

Two way ANOVA indicated a significant ($P < 0.0001$) effect of both salinity and dormancy relieving compounds and their interaction on the percent and velocity of seed germination (Table 1). All seeds germinated in non-saline control. Germination of *A. occidentalis* seeds was inhibited with an increase in salinity and 7% germination was recorded at 800 mM NaCl (Fig. 1). Fusicoccin, ethephon, nitrate and thiourea all significantly alleviated the inhibitory effect of NaCl on germination at all salinities (Fig. 1).

Fusicoccin (5 μM) completely reversed the inhibitory effect of salinity in all treatments in only 96 h (Fig. 2). At the highest salinity (800 mM NaCl) the FC treatment stimulated 98% germination (Fig. 1). Germination velocity was high (47) in all treatments (Table 2).

Ethephon took 10 d to completely alleviate the inhibitory effect of 800 mM NaCl (Fig. 2). At the highest salinity, 90% germination was obtained in ethephon-treated seeds in comparison to 7% in non-treated seeds (Fig. 1).

Nitrate took longer to alleviate the salinity effect (Fig. 2). However, after 20 d it completely overcame the effect of salinity. Seed germination at 800 mM NaCl was promoted from 7% in the control to 85% in nitrate-treated seeds (Fig. 1). Thiourea stimulated germination in 400 mM NaCl (Fig. 1). Seed germination was promoted from 30 and 7% at 600 and 800 mM NaCl to 70 and 77%, respectively (Fig. 1).

The rate of germination increased with the application of fusicoccin at all salinities (Table 2). The highest rate of germination was obtained in fusicoccin at 800 mM NaCl, and lowest in distilled water (Table 2). Rate of germination gradually decreased with an increase in NaCl concentration in ethephon, nitrate and thiourea (Table 2).

TABLE 1. Results of two way analysis of variance of characteristics by regulators (nitrate, thiourea, ethephon and fusicoccin) and salinity treatments

Dependent variable	Independent variable		
	Regulators (R)	Salinity (S)	R × S
Germination %	10.6***	14.8***	4.4***
Germination velocity	83.8***	64.2***	9.2***

Numbers represent F values. *** $P < 0.0001$.

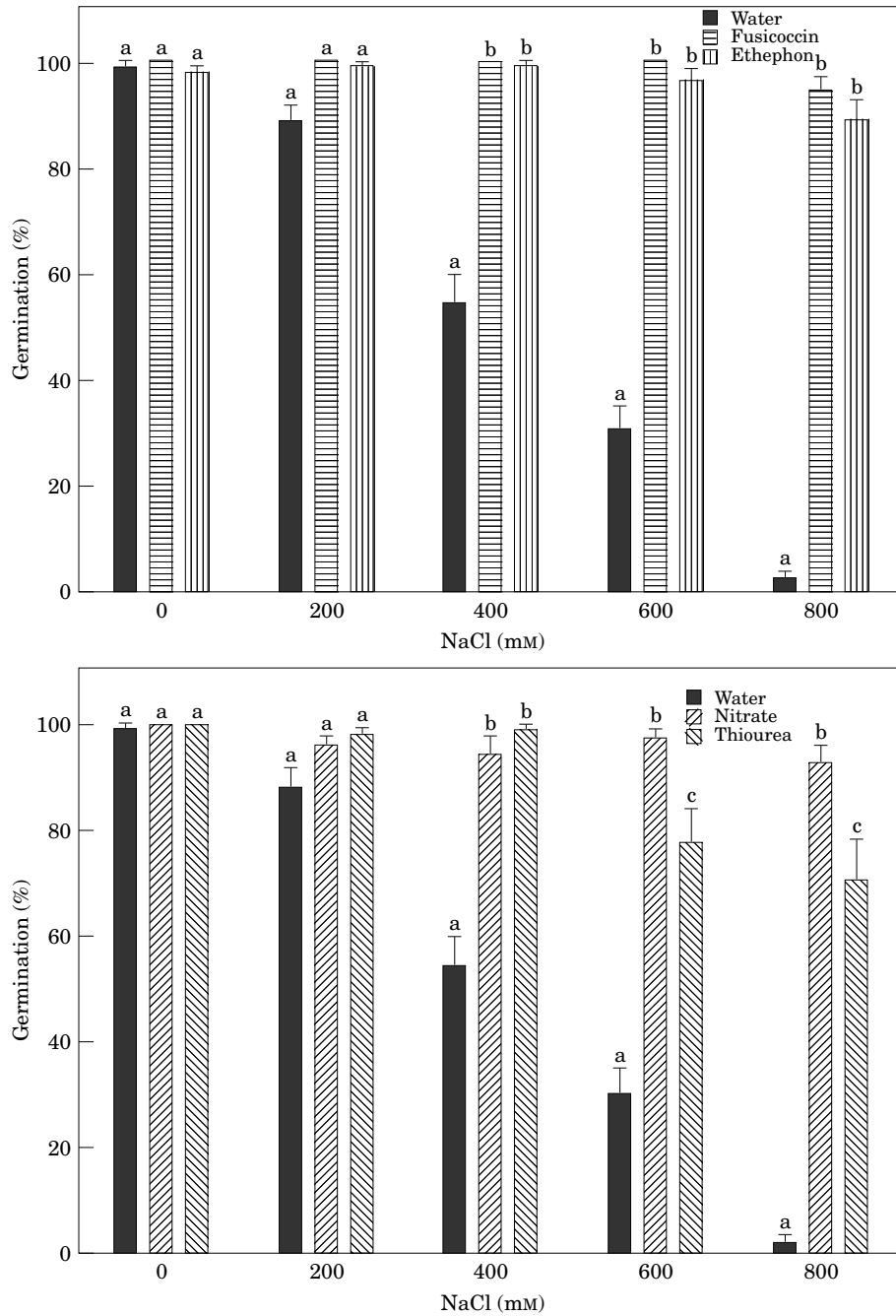


FIG. 1. Final germination percentages of *Allenrolfea occidentalis* seeds in 0, 200, 400, 600 and 800 mM NaCl and fusicoccin (5 mM), ethephon (10 mM), nitrate (20 mM) and thiourea (10 mM). Values for each salinity concentration having the same letter are not significantly different ($P > 0.05$).

TABLE 2. Index of germination velocity, using a modified Timson index

Salinity (mM)	Water	Thiourea (mM)	Nitrate (mM)	Ethephon (mM)	Fusicoccin (μ M)
0	48.2 ± 9.3 ^a	46.2 ± 1.2 ^a	46.2 ± 0.8 ^a	42.7 ± 0.9 ^a	47.6 ± 0.6 ^a
200	38.2 ± 2.3 ^a	40.8 ± 0.9 ^a	41.2 ± 0.9 ^a	43.8 ± 0.5 ^a	47.5 ± 0.2 ^a
400	20.6 ± 1.6 ^b	34.8 ± 1.2 ^a	38.3 ± 1.5 ^a	43.4 ± 0.8 ^a	47.8 ± 0.4 ^a
600	9.7 ± 2.1 ^b	26.9 ± 2.6 ^b	34.5 ± 1.8 ^a	40.4 ± 1.2 ^a	46.4 ± 0.6 ^a
800	0.7 ± 0.4 ^b	23.5 ± 2.2 ^b	29.9 ± 1.2 ^b	35.6 ± 1.7 ^a	43.3 ± 1.1 ^a

Values in each column with the same superscript are not significantly different at $P > 0.05$, Bonferroni test.

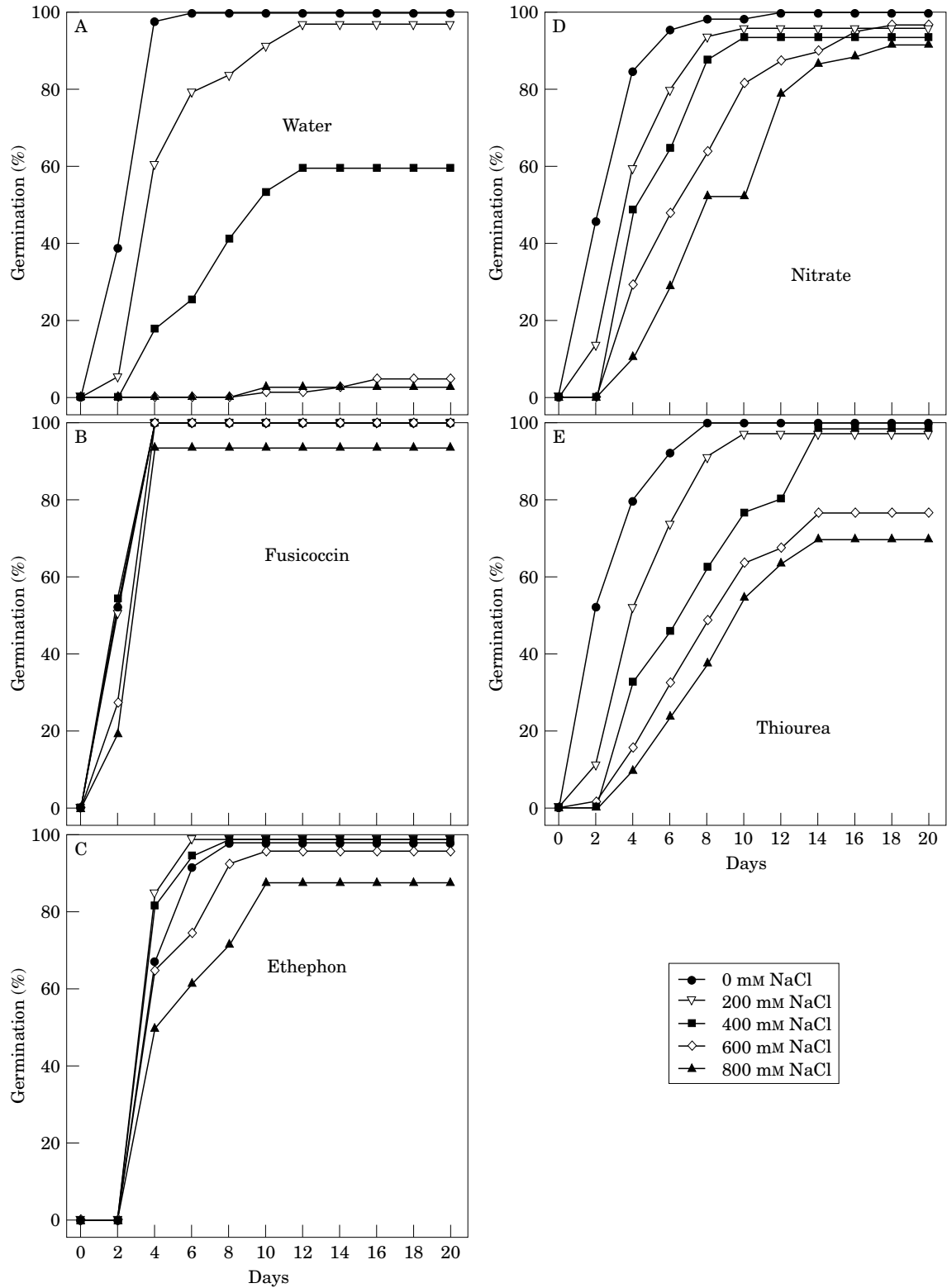


FIG. 2. Germination percentages of *Allenrolfea occidentalis* seeds in 0 (●), 200 (▽), 400 (■), 600 (◇) and 800 (▲) mM NaCl and water (A), fusicoccin (5 mM) (B), ethephon (10 mM) (C), nitrate (20 mM) (D) and thiourea (10 mM) (E).

DISCUSSION

Seed germination in *A. occidentalis* was inhibited with an increase in salinity, and only 7% of seeds germinated at 800 mM NaCl. Fusicoccin completely alleviated the inhibitory effects of salinity on the germination of *A. occidentalis* seeds, whereas other compounds showed partial or complete alleviation of the effect of salinity. The alleviation of salinity-enforced seed dormancy by FC may be due to stimulation of ATPase production which rapidly increases during the early phases of germination to facilitate proton extrusion and K⁺ uptake (Marre, 1979; Stout, 1988). A stimulation of germination by FC in various kinds of seeds has been observed (Ismail, 1990; Lado, Rasi-Caldogno and Colombo, 1974; Khan and Ungar, 1998). FC has the ability to remove the inhibitory effect of ABA on germination of normal seeds and on embryo growth of decoated seeds (Lado, Rasi-Caldogno and Colombo, 1975). It is more likely that ABA production due to salinity stress could be counteracted by FC thus alleviating the inhibitory effect of salinity. FC strongly influences a number of important processes in particular those of cell enlargement, acidification of the medium, potassium uptake and stomatal opening; its mechanism of action depends on the direct activation of a single central transport system present in all higher plants. It appears, therefore, that the action of FC (like that of auxin and other natural plant hormones) involves some very general system, together with the ability to respond to plant hormones, at a relatively advanced stage of plant evolution (Marre, 1979).

Ethephon completely alleviated the germination inhibition in *A. occidentalis* caused by salinity. Seed germination is promoted by ethylene in many species (Abeles and Lonski, 1969; Adkins and Ross, 1981; Corbineau, Rudnicki and Come, 1989; Whitehead and Nelson, 1992; Khan and Ungar, 1998). Ethylene may act by stimulating the germination of non-dormant seeds or by breaking dormancy in seeds that exhibit an embryo dormancy; in many species the inhibition of seed germination due to dormancy or stress conditions can be completely or partially reversed by ethylene or ethephon (Ketring and Morgan, 1969; Egley and Dale, 1970; Whitehead and Nelson, 1992; Sutcliffe and Whitehead, 1995; Kepczynski and Kepczynska, 1997). This indicates that seeds have an ethylene-response mechanism. It has been reported that non-dormant chick-pea (Gallardo *et al.*, 1991) and *Amaranthus caudatus* (Kepczynski and Karssen, 1985) seeds subjected to high temperature, osmoticum or salinity stress inhibit endogenous ethylene production. However, seeds of many plants do not respond to ethylene (Ismail, 1982) and some of the promotive effects are not substantial. Ethylene may be loosely associated with a site required for phytochrome action (Suzuki and Taylorson, 1981). Light may be required for synthesis of growth promoting substances to initiate germination (Okusanya and Ungar, 1983) and *A. occidentalis* did not germinate well in the dark (Gul and Weber, 1998) indicating light sensitive seeds. Ethylene is reported to promote germination in light sensitive seeds (Esashi *et al.*, 1989; Kepczynski and Kepczynska, 1997).

Thiourea and nitrate stimulated the germination of *A.*

occidentalis seeds. Others have reported the promotive action of nitrogenous compounds on seed germination (Stokes, 1965; Esashi *et al.*, 1979; Bewley and Black, 1994; Khan and Ungar, 1998). The alleviating effect of thiourea on osmoinhibition gradually decreased with an increase in salinity. Khan and Ungar (1998) reported that nitrate and thiourea promoted the germination of *Zygophyllum simplex* seeds at the lowest (25 mM NaCl) salinity but did not promote germination at higher (125 mM NaCl) salinities. However *A. occidentalis* showed a partial alleviation of the inhibitory effect of salinity on germination at all salinities. Some nitrogenous compounds such as nitrate, nitrite and thiourea are known to stimulate the germination of seeds (Esashi *et al.*, 1979; Aldasaro, Matilla and Nicholas, 1981; Yoshiyama *et al.*, 1996). Thiourea counteracts the effect of ABA and reduces the level of cytokinins in plant tissues (Kabar and Baltepe, 1989). These adverse hormonal changes occur when plant tissues are subjected to water stress induced by drought, salinity or high temperatures (Kabar and Baltepe, 1989). Treatment with thiourea is highly effective in alleviating the inhibition of germination by salinity or high temperatures (Esashi *et al.*, 1979). Thiourea overcomes the inhibitory effect of salinity in *A. occidentalis*. It is also known to break dormancy and overcome the negative effect of temperature on seed germination (Esashi *et al.*, 1979; Aldasaro *et al.*, 1981).

All of the dormancy relieving compounds studied were able to alleviate seed dormancy enforced by salinity in *A. occidentalis*. Alleviation ranged from a complete reversal of the inhibitory effect of salinity by FC, to partial alleviation by thiourea. The inhibition of germination in *A. occidentalis* seeds was eliminated by application of exogenous ethephon and FC. It could be that high salinity caused a deficiency in available nitrogen and increased the production of inhibitors such as ABA. These harmful effects of salinity were overcome by application of nitrate, thiourea, ethephon or fusicoccin.

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