

ORIGINAL ARTICLE

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## The effect of plant growth regulators, nitric oxide, nitrate, nitrite and light on the germination of dimorphic seeds of *Suaeda salsa* under saline conditions

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**Abstract** *Suaeda salsa*, a leaf succulent shrub in the family Chenopodiaceae, is one of the most important halophytes in China. *Suaeda salsa* produces dimorphic seeds (soft brown seeds and hard black seeds). Seeds of *S. salsa* were collected from the coastal salt flats near Huanghua City, China. Experiments were conducted to determine the salinity-alleviating effect of plant growth regulators, nitric oxide, nitrate, nitrite and light on the germination of dimorphic seeds of *S. salsa*. Brown seeds had a higher germination rate than black seeds in all experiments. Black seeds were more sensitive to salt in the absence of light in comparison to brown seeds. Brown seeds absorbed water more quickly in comparison to black seeds and were found to be more tolerant of salt stress. Our results showed that 1-aminocyclopropane-1-carboxylate (ACC, the immediate precursor of ethylene), nitrite, GA<sub>4</sub> and BA improved seed germination in the presence of salt. However, nitrate, GA<sub>1</sub>, GA<sub>3</sub> failed to alleviate salt stress. ABA inhibited seed germination and seedling growth. Possible mechanisms involved in the alleviation of salt stress in *S. salsa* seeds and the ecological adaptation of the seeds to the environment are discussed.

**Key words** Dimorphic seed · Germination · Plant growth regulator · *Suaeda salsa*

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### Introduction

About 9.5 billion hectares of the world's soil are saline, not including large areas of secondarily salinized soil in cultivated land. In addition, freshwater resources are becoming increasingly limited. It has become imperative under these conditions to look for plants with economic value that can grow under saline conditions (Zhao et al. 2002). Salt marsh and salt desert environments vary both spatially and temporally, showing environmental gradients and unpredictable seasonal and annual conditions (Ungar 1995). Small microtopographic changes can lead to significant differences in water-table and surface-soil salinities. Seed dimorphism and polymorphism have been reported for a number of halophytic taxa including *Arthrocnemum*, *Atriplex*, *Chenopodium*, *Cakile*, *Salicornia*, *Salsola*, *Spergularia*, *Suaeda* and *Trianthema* (Ungar 1977; Galinato and van der Valk 1986; Mohammad and Sen 1988; Ungar 1988; Morgan and Myers 1989; Khan and Gul 1998). The change may enable halophytes to respond to varying salt-marsh or desert environments and could provide multiple opportunities for seedling establishment and survival in the salt environment (Philipupillai and Ungar 1984). Similar polymorphism has also been shown in other *Suaeda* species, such as *S. depressa* (Ungar and Capilupo 1969; Williams and Ungar 1972), *S. fruticosa* (Jhamb and Sen 1984; Khan and Ungar 1998), *S. maritima* (Boucaud and Ungar 1973, 1976), *S. japonica* (Yokoishi and Tanimoto 1994) and *S. moquinii* (Khan et al. 2001).

The limit of salt tolerance varies among halophytes (Khan 2002), and this variation could be due to a number of factors such as variation in morphology and distribution (Baskin and Baskin 1998). The limit of salt tolerance for *Suaeda* species varies from 400–1,000 mM NaCl (Ungar 1962; Ungar and Capilupo 1969; Clarke and Hannon 1970; Okusanya 1979; Yokoishi and Tanimoto 1994; Khan and Ungar 1998; Khan et al. 2001).

Plant growth regulators such as gibberellic acid (GA<sub>3</sub>), abscisic acid (ABA), kinetin and ethylene are known to influence the dormancy status of seeds (Karssen 1995). The

effect of dormancy-regulating chemicals on the germination of halophytes has been studied in relation to their response to salinity (Ungar 1991). Change in growth regulator balance induced by salt stress may be a mechanism that induces dormancy in seeds (Ungar 1978, 1984). The application of GA<sub>3</sub> (Khan and Ungar 1997, 1998), kinetin (Khan and Ungar 1997), fusicoccin (FC) (Ismail 1990; Gul and Weber 1998), and ethylene (Kepczynski and Karssen 1985; Kepczynski 1986; Ismail 1990) have been shown to alleviate salinity-enforced dormancy. Nitrogenous compounds such as nitrate and thiourea are also reported to promote germination (Bewley and Black 1994). Recent reports have demonstrated the involvement of nitric oxide in plants in hormonal signaling (Guo et al. 2003.) and many other biological processes; for example, nitric oxide (SNP as donor) may stimulate germination of lettuce seeds in the dark (Beligni and Lamattina 2000) or may stimulate dormant *Arabidopsis* and barley seeds (Bethke et al. 2004a, b). Boucaud and Ungar (1976) have found that 0.85 M NaCl strongly reduced the endogenous cytokinin concentration in *Suaeda* seeds.

*Suaeda salsa*, a leaf succulent shrub in the family Chenopodiaceae, is one of the most important halophytes in China with potential economic values for food and oil (Wang et al. 2001; Zhao et al. 2002). *Suaeda salsa* produces dimorphic seeds (brown inner seed coat with soft half-transparent outer testa and brown inner seed coat with hard black outer testa) on the same plant. These morphological seed variations are also linked to ecological strategies of various *Suaeda* species. There is little information available on germination of dimorphic seeds of *S. salsa*. Seed germination under saline conditions is poor, and our objective was to develop technology to improve germination and recruitment of this species under saline conditions. The present investigation is designed to determine if the application of plant growth regulators and dormancy-relieving nitrogenous compounds could alleviate the effects of salinity on the germination of dimorphic seeds of *S. salsa* under both light and dark conditions.

## Materials and methods

Seeds of *S. salsa* were collected during the fall of 2002 in the coastal saline soils of Huanghua City, Hebei Province of China. Seeds were dried for a few days and, after cleaning, stored in paper bags at approximately 20°C with relative humidity 30–40% in the laboratory. *S. salsa* produces two distinct types of seeds. The first has a brown inner seed coat and a soft, semi-transparent outer seed coat, and the second has a brown inner seed coat and a hard, non-transparent (black and smooth) outer seed coat. Seeds were scored as germinated when radicle protrusion was visible with microscope (inner seed coat was broken). Black seeds and brown seeds were separated from the inflorescence.

Seeds were washed with 0.02% Triton X solution and rinsed with distilled water, and 50–100 seeds were placed on single-layer wet filter paper within closed, plastic Petri

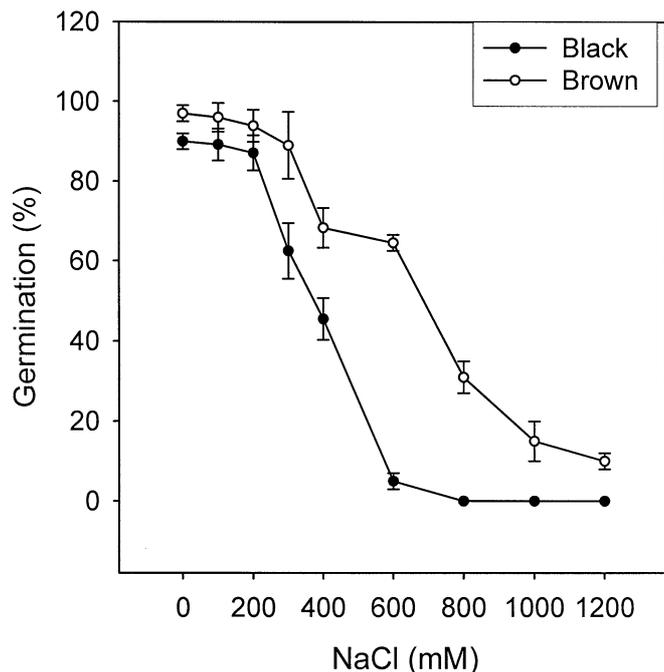
dishes. For measuring the water-uptake process, seeds were also weighed for 10 h every 20–60 min after imbibition. A centrifuge was used for 2 min at 12,000 rpm to remove seed surface water before scaling. To determine the effects of salt and light on germination of the dimorphic seeds, seeds were germinated in 0, 100, 200, 300, 400, 600, 800, 1,000, and 1,200 mM NaCl at 23°C using triplicate samples under continuous light or dark conditions.

Following the experiments on seed germination, tests were performed on triplicate samples at 23°C with continuous light (fluorescent lamp, intensity approximately 100 mmol m<sup>-2</sup> s<sup>-1</sup>). The percent germination was recorded everyday for 6 or 10 days. To determine the effects of plant growth regulators on seed germination, GA<sub>1</sub>, GA<sub>3</sub>, and GA<sub>4</sub> were used at 0.1, 1, and 10 μM, and cytokinin (6-benzyladenine, BA) at 0.1, 1, and 10 μM for seeds under saline stress (NaCl concentration for black seeds: 400 mM, brown seeds: 800 mM). ABA was used at 0.1, 1, 10, and 100 μM for inhibiting seed germination under different salinity stresses. ACC [the immediate precursor of ethylene, which changes to ethylene in the present of ACC oxidase in seeds, Yang and Hoffman (1984)] was used at 2.5 μM–2.5 mM for germination of seeds under saline stress (NaCl concentration for black seeds: 500 mM; for brown seeds: 800 mM). The pH of all solutions was neutral, ranging from 6.5–7.2. In order to control the wetness of the filter paper, the Petri dishes were sealed with Parafilm laboratory film. The weight of all Petri dishes (including wet paper and seeds) was measured every 2 days when checking germination and additional distilled water was added.

NaNO<sub>3</sub> was used at 0.1–50 mM, NaNO<sub>2</sub> at 0.1–5 mM and sodium nitroprusside (SNP; Merck, Darmstadt, Germany), as a nitric oxide donor, was used at 5–200 mM to test seed germination under saline stress (NaCl concentration for black seeds: 400 mM; for brown seeds: 800 mM). Statistical analysis was done using Microsoft Excel statistical packages. Triton X, ABA, ACC, NaCl, NaNO<sub>3</sub> and NaNO<sub>2</sub> were purchased from Wako Pure Chemicals (Tokyo, Japan); GAs were purchased from Prof. Lewis Mander (Australian National University, Australia).

## Results

Germination of both black and brown seeds was inhibited with an increase in salinity. Black seeds failed to germinate beyond 600 mM NaCl, while brown seeds were able to germinate in concentrations up to 1,200 mM NaCl (Fig. 1). The 50% inhibition of germination was achieved for black seeds between 300 and 400 mM NaCl and between 600 and 800 mM NaCl for brown seeds (Fig. 1). Brown seeds absorbed water more quickly than black seeds (Fig. 2) at all salinity levels. Water absorption in brown seeds decreased with an increase in salinity but salinity had little effect on water absorption in the case of black seeds (Fig. 2). The first brown seed germinated after 120 min and the first black seed after 360 min. This was the point at which relative water content for both seed types approached 30%.

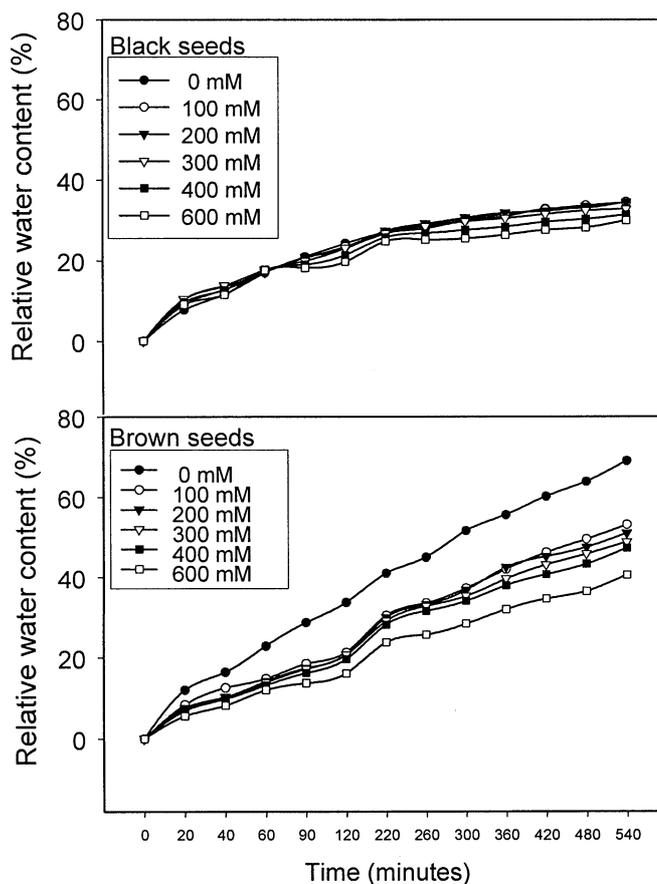


**Fig. 1.** Percent germination of brown and black seeds of *Suaeda salsa* in NaCl solution. The brown and black seeds were sown in 0, 100, 200, 300, 400, 600, 800, 1,000, or 1,200 mM NaCl with continuous light. After 10 days of cultivation, the germinated seeds were counted. To calculate the average rate of germination, more than 100 seeds were used for each treatment. The experiments were repeated three times and SE was calculated (error bars)

Light had little effect on the germination of brown seeds in both nonsaline and saline conditions (Fig. 3). Likewise, light did not affect the germination of black seeds under nonsaline and low saline (200 mM NaCl) conditions. However, under increasing salinity stress, light appear to promote more germination in comparison to darkness (Fig. 3). At 400 mM NaCl, about 10% of black seeds germinated in the dark in comparison to 78% germination in the light.

Generally, ACC, BA and GA<sub>4</sub> promoted *Suaeda salsa* seed germination under conditions of salt stress (Fig. 4). GA<sub>1</sub> and GA<sub>3</sub> at 10 μM, however, could not promote seed germination in brown seeds in 800 mM NaCl or in black seeds in 400 mM or 500 mM NaCl (data not shown). ABA inhibited seed germination of *S. salsa* in salt stress, especially for the black seeds (Fig. 5). ABA at concentrations of 10 and 1 μM significantly inhibited black seed germination in 200 and 300 mM NaCl solution, but brown seeds were not inhibited even in 600 mM NaCl solution (Fig. 5).

Nitrite improved the germination rate of both black and brown seeds under saline conditions (Fig. 5). Nitrite at 5 mM showed maximum improvement in brown seeds but caused inhibition in black seeds. Nitrate, however, had little effect on the seed germination of *Suaeda salsa* (data not shown). SNP also significantly promoted germination for both black and brown seeds under salt stress (Fig. 5).



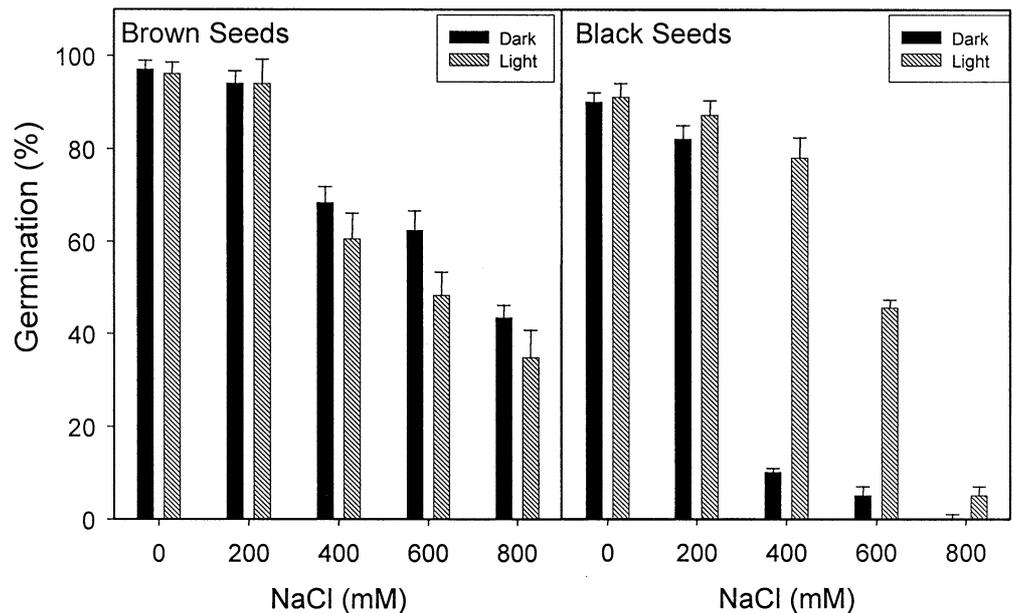
**Fig. 2.** Water uptake of brown and black seeds of *Suaeda salsa* in NaCl solution. The brown and black seeds were weighed at regular intervals for 600 min. A centrifuge was used for 2 min at 12,000 rpm to remove the surface water before weighing. The experiments were repeated three times and SE was calculated. Relative water content (%) was based on the weight of initial dry seeds and calculated according to the following equation:  $RWC = [(W_w - D_w)/D_w] \times 100$ . RWC relative water content,  $W_w$  wet weight of seeds,  $D_w$  initial dry weight of seeds

## Discussion

Fifteen percent of brown seeds of *Suaeda salsa* germinated at 1,200 mM NaCl. The limits of salt tolerance vary somewhat among species of succulent halophytes (Khan 2002) with some seeds of the leaf succulents *S. moquinii* (30% germination at 100 mM NaCl; Khan et al. 2001), and *S. linearis* (1% germination at 100 mM NaCl) germinating in up to 849 mM NaCl (Ungar 1962, 1967) while others like *Arthrocnemum indicum* (3% germination at 100 mM NaCl) can germinate in 1,000 mM NaCl (Khan and Gul 1998). There are reports of other species (*Salicornia bigeloviae*, *S. europaea*, *S. pacifica*) indicating some germination at NaCl concentrations above 800 mM (Rivers and Weber 1971; Ungar 1979; Khan and Weber 1986).

The limit of salt tolerance for *Suaeda* species varies from 400–1,000 mM NaCl (Ungar 1962; Ungar and Capiluppo 1969; Clarke and Hannon 1970; Okusanya 1979; Yokoishi and Tanimoto 1994; Khan and Ungar 1998; Khan et al.

**Fig. 3.** Percent germination of brown and black seeds of *Suaeda salsa* in NaCl solution. The brown and black seeds were sown in 0, 100, 200, 300, 400, 600, 800, 1,000, or 1,200 mM NaCl with both continuous light or dark conditions. After 10 days of cultivation, the germinated seeds were counted. To calculate the average rate of germination more than 100 seeds were used for each treatment. The experiments were repeated three times and SE was calculated (error bars)



2004). Brown seeds of *S. salsa* were among the most salt tolerant seeds at the germination stage. *S. salsa* seeds were collected from the Bohai coast salt marshes of Huanghua, China. Plants surviving in such a high saline environment require a higher degree of salt tolerance during seed germination. Black seeds of *S. salsa* on the other hand were not very tolerant to salinity. No seed germinated at concentrations higher than 600 mM NaCl.

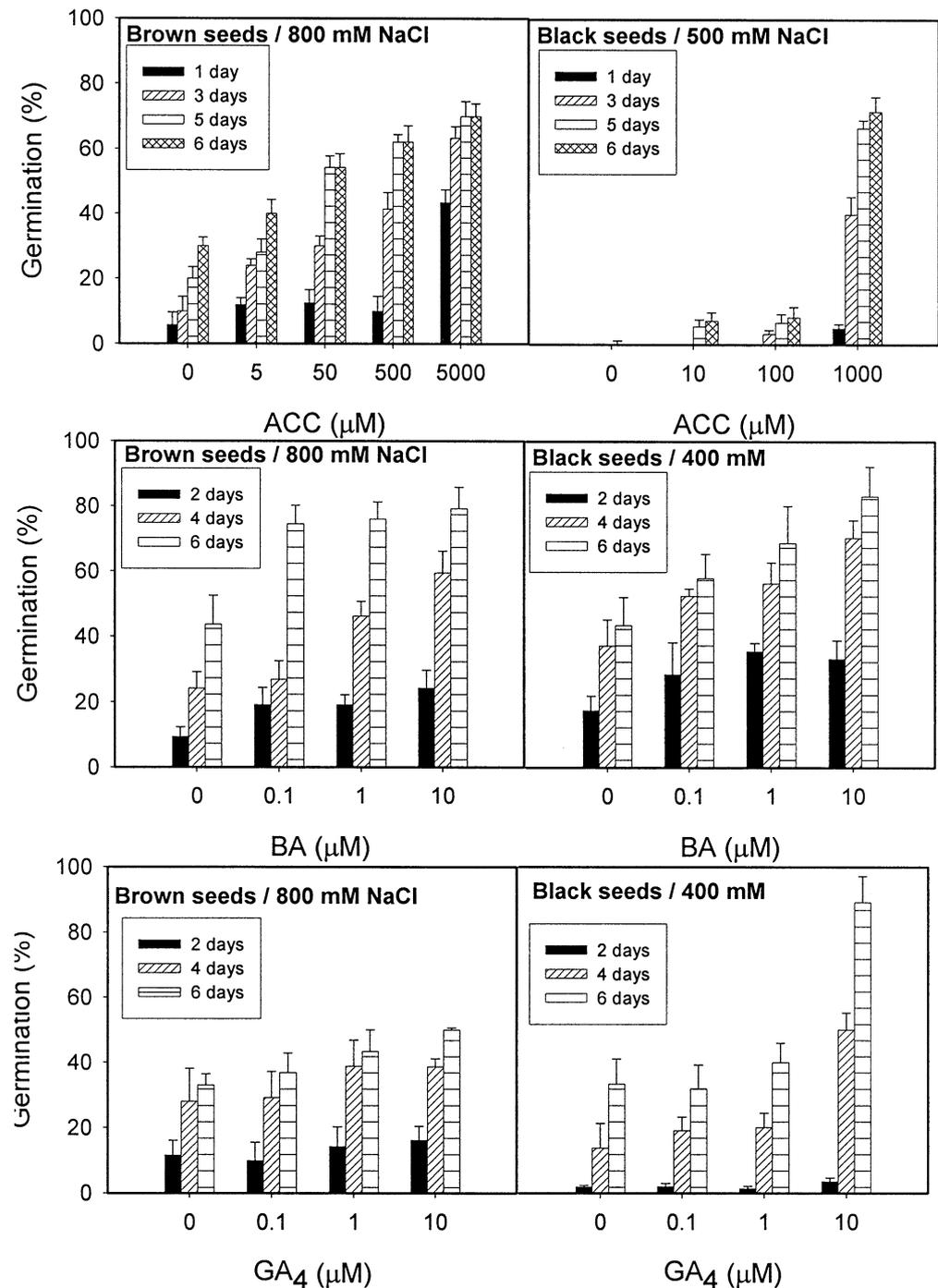
Seed dimorphism and polymorphism are reported in many halophytic species including *Arthrocnemum*, *Chenopodium*, *Atriplex*, *Cakile*, *Salicornia*, *Salsola*, *Spergularia*, and *Suaeda* growing under saline conditions (Khan and Ungar 1984a, b; Mohammad and Sen 1988; Myers and Morgan 1989; Ungar 1991; Khan et al. 2001, 2004; Khan 2002). *S. salsa* produces brown and black seeds on the same plant; this appears to a useful strategy to increase chances for population establishment under variable temperatures and soil salinities (Ungar 1995). Brown seeds, for example, are more tolerant of salt stress and could germinate in spring when soil salinity is high, while during late spring and summer *S. salsa* may build up its population in low salinity through black seeds.

The germination response to light was related to seed size. Many small seeds were light sensitive, implying that light acts as a depth-sensing mechanism, thereby avoiding possible fatal germination of seeds buried too deep in soil (Schutz et al. 2002). Light control of seed germination or dormancy through phytochromes has been well documented (Yamaguchi and Kamiya 2002). For light sensitivity, there are two mechanisms: light may promote gibberellin biosynthesis or increase seed sensitivity to gibberellins by phytochromes (Yamaguchi and Kamiya 2000), or light (through phytochromes) or GA may affect ABA content through ABA biosynthesis or catabolism enzymes (Toyomasu et al. 1994). Light is another factor having profound effects on the seed germination of many species along

with salinity (Khan and Ungar 2000). Germination of many halophytes occurs when there is an optimal combination of day length, thermoperiod and salinity (Young et al. 1980; Khan and Weber 1986; Naidoo and Naicker 1992; Gutterman et al. 1995; Khan and Ungar 1997). Black seeds of *Suaeda salsa* were sensitive to light in higher saline conditions, while brown seeds were not. This may lead to a seed bank dominated by black seeds.

Effects of salinity on the germination of black seeds of *Suaeda salsa* were almost completely alleviated when ACC was present in the medium; there was a partial alleviation in brown seeds. It is suggested that ethylene regulates seed dormancy by inhibiting ABA signaling (Beaudoin et al. 2000). Plant responses to salt stress were modulated by changes in the expression level of ethylene receptors (Zhao and Schaller 2004), and increasing ethylene content may enhance ethylene signal transduction. Application of ethylene relieves dormancy in seeds of several species (Abeles and Lonski 1969; Ketring 1977; Adkins and Ross 1981; Corbineau et al. 1989; Whitehead and Nelson 1992; Bewley and Black 1994) and reverses the inhibitory effect of abscisic acid and osmotic stress (Karssen 1976; Schonbeck and Egley 1981). Ethylene may act by stimulating the germination of nondormant seeds or by breaking dormancy in seeds that exhibit an embryo dormancy (Ketring and Morgan 1969; Egley and Dale 1970; Whitehead and Nelson 1992; Sutcliffe and Whitehead 1995). However, seeds of many plants do not respond to ethylene (Ismail 1982) or some of the alleviating effects on salinity are not substantial. Alleviation of salinity effects on the germination of halophytes by ethylene is quite variable. Ethylene completely alleviated the effect of salinity in *Aeluropus lagopoides*, *Allenrolfea occidentalis*, *Ceratoides lanata*, *Kochia scoparia*, *Limonium stocksii* and *Suaeda fruticosa* (Gul and Weber 1998; Gulzar and Khan 2002; Khan et al. 2004); partially alleviated salinity effects on germination in *Arthrocnemum*

**Fig. 4.** Percent germination of brown and black seeds of *Suaeda salsa* in NaCl solution. The brown seeds were germinated in 800 mM NaCl while black seeds were germinated in 500 mM NaCl. ACC (5, 10, 50, 100, 500, and 1,000  $\mu\text{M}$ ), BA (0.1, 1, and 10  $\mu\text{M}$ ) and GA<sub>4</sub> (0.1, 1, and 10  $\mu\text{M}$ ) were used in continuous light with and without salinity with both black and brown seeds. After 2, 4 and 6 days of cultivation, the germinated seeds were counted. To calculate the average rate of germination more than 100 seeds were used for each treatment. The experiments were repeated three times and SE was calculated

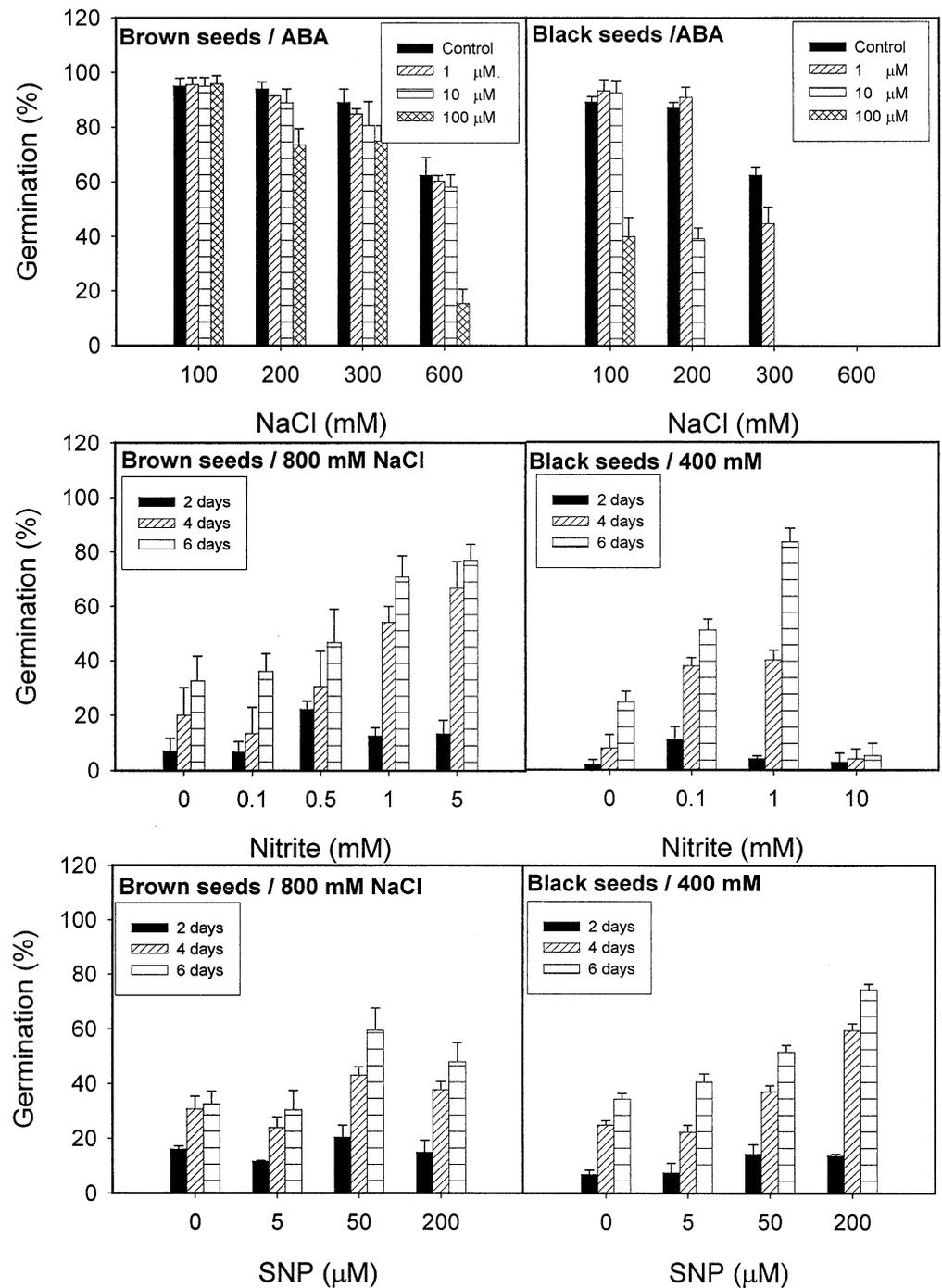


*indicum*, *Salicornia rubra*, *Suaeda moquinii*, *Halogeton glomeratus*, *Salicornia utahensis*, *Salsola iberica*, *Sporobolus ioclados*, *Zygophyllum simplex*, and *Atriplex rosea* (Khan et al. 2000; Khan and Ungar 2001a, 2002; M.A. Khan, unpublished data); and in some species, ethylene did not have any effect, such as in *Triglochin maritima*, *Urochondra setulosa*, *Sarcobatus vermiculatus*, *Cressa cretica*, *Atriplex stocksii*, and *Atriplex prostrata* (Gulzar and Khan 2001; Khan and Ungar 2001a, b; M.A. Khan, unpublished data).

Kinetin substantially improved seed germination of *Suaeda salsa* in salinities tested. Kinetin also had a similar

response in *Atriplex stocksii*, *Ceratoides lanata*, *Zygophyllum simplex* (Khan and Rizvi 1994; Khan and Ungar 1998; Khan et al. 2004); had some effect in alleviating the salinity effect in *Salicornia utahensis*, *Zygophyllum simplex*, *Arthrocnemum macrostachyum*, *Allenrolfea occidentalis*, *Triglochin maritima* and *Salicornia rubra* (Khan and Weber 1986; Khan and Ungar 1998, 2001b, 2002; Khan et al. 1998); and had no effect on the germination of *Sporobolus ioclados*, *Urochondra setulosa*, *Suaeda fruticosa*, *Salsola imbricata* and *Haloxylon stocksii* (Gulzar and Khan 2002; M.A. Khan, unpublished data).

**Fig. 5.** Percent germination of brown and black seeds of *Suaeda salsa* in NaCl solution. The brown seeds were germinated in 800 mM NaCl while black seeds were germinated in 400 mM NaCl. Nitrite (0, 0.1, 0.5, 1 or 5 mM), and SNP (0, 5, 50 or 200  $\mu$ M) were used in continuous light with and without salinity with both black and brown seeds. ABA (0, 1, 10 and 100 mM) was used with 100, 200, 300 and 600 mM NaCl for both black and brown seeds. After 2, 4 and 6 days of cultivation, the germinated seeds were counted. To calculate the average rate of germination more than 100 seeds were used for each treatment. The experiments were repeated three times and SE was calculated



GA<sub>4</sub>, but not GA<sub>3</sub>, at 10  $\mu$ M alleviated *S. salsa* seed dormancy induced by high salt concentration. The results suggest that GA<sub>4</sub> is perhaps an active form of gibberellin in *S. salsa* seeds, or that the activity of GA<sub>4</sub> is stronger than GA<sub>3</sub> in promoting seed germination, or that the two promote seed germination at different stages (Karssen 1976). The mechanisms through which gibberellins promote seed germination may alleviate the inhibitory effect of ABA which is induced by salt stress (Xiong and Zhu 2003). Gibberellic acid has been reported to have different effects on the germination of halophytes. Seed germination under saline con-

ditions was almost completely alleviated in *Atriplex stocksii* and *Zygophyllum simplex* (Khan and Rizvi 1994; Khan and Ungar 1997). Some positive effects were reported for *Atriplex triangularis*, *Salicornia utahensis*, *Allenrolfea occidentalis*, *Arthrocnemum macrostachyum*, *Polygonum aviculare* and *Salicornia rubra* (Khan and Weber 1986; Gul and Weber 1998; Khan and Ungar 1998, 2002; M.A. Khan, unpublished data), while species like *Triglochin maritima*, *Sporobolus ioclados*, *Urochondra setulosa*, *Suaeda fruticosa*, *Salsola imbricata* and *Haloxylon stocksii* failed to respond to any gibberellic acid treatment (Khan and Ungar

2000; Gulzar and Khan 2002; M.A. Khan, unpublished data).

Both nitrite and SNP stimulated the germination of *Suaeda salsa* seeds while nitrate had little effect. Others have reported a stimulatory action of nitrogenous compounds on seed germination (Bewley and Black 1994). Khan and Ungar (2002) 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. Seed germination of *Allenrolfea occidentalis* and *Halopyrum mucronatum*, however, is promoted by thiourea in NaCl treatments (Gul and Weber 1998; Khan and Ungar 2001c). Some nitrogenous compounds such as SNP, nitrate, nitrite, and thiourea are known to stimulate the germination of seeds (Esashi et al. 1979; Aldosaro et al. 1981; Yoshiyama et al. 1996; Beligni and Lamattina 2000; Batak et al. 2002). Batak et al. (2002) showed that the nitrate and/or nitrite effect on seed germination is mediated through phytochrome. Our results suggest nitric oxide played a more important role in stimulating seed germination under conditions of salt stress than nitrate in *S. salsa* seeds.

*Suaeda salsa* produces numerous seeds at the end of autumn. The present study has determined that dimorphic seeds produced by this plant also differ physiologically in their response to light and salinity during germination. Black seeds are not very salt tolerant and germinate better in light and may become the part of the seed bank and start germinating when soil salinity is reduced. Brown seeds, on the other hand, are more salt tolerant during germination, and changes in light have little effect on germination. Recruitment may occur from brown seeds from early spring through early summer. Salt marshes usually experience unpredictable drought during some growing seasons. Any such drought incidence early in spring could destroy the entire population of seedlings recruited either from black or brown seeds. At early stages under more saline conditions, brown seeds could germinate and maintain the fitness of the species. Seeds start germinating very early during spring, and germination decreased with the increase in salinity. This decrease in germination appears to be mediated through reduction in germination-regulating chemicals such as ethylene, gibberellin (GA<sub>4</sub>) and kinetin. Our objective was to determine the physiological properties of the dimorphic seeds, and it would be interesting to do field studies to determine the ecological role of seed dimorphism in maintaining *S. salsa* populations.

## References

- Abeles FB, Lonski J (1969) Stimulation of lettuce seed germination by ethylene. *Plant Physiol* 44:277–280
- Adkins SW, Ross JD (1981) Studies in wild oat seed dormancy. 1 – The role of ethylene in dormancy breakage and germination of wild oat seeds (*Avena fatua* L.). *Plant Physiol* 67:358–362
- Aldosaro J, Mantilla A, Nicholas G (1981) Effect of ABA, fusicoccin, and thiourea on germination and K<sup>+</sup> and glucose uptake in chickpea seeds of different temperatures. *Physiol Plant* 52:353–362
- Baskin CC, Baskin JM (1998) Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic, San Diego
- Batak I, Devic M, Giba Z, Grubisic D, Poff K, Konjevic R (2002) The effects of potassium nitrate and NO-donors on phytochrome A- and phytochrome B- specific induced germination of *Arabidopsis thaliana* seeds. *Seed Sci Res* 12:253–259
- Beaudoin N, Serizet C, Gosti F, Giraudat J (2000) Interactions between abscisic acid and ethylene signaling cascades. *Plant Cell* 12:1103–1116
- Beligni MV, Lamattina L (2000) Nitric oxide stimulates seed germination and de-etiolation, and inhibits hypocotyl elongation, three light-inducible responses in plants. *Planta* 210:215–221
- Bethke PC, Badger MR, Jones RL (2004a) Apoplastic synthesis of nitric oxide by plant tissues. *Plant Cell* 16:332–341
- Bethke PC, Gubler F, Jacobsen JV, Jones RL (2004b) Dormancy of *Arabidopsis* seeds and barley grains can be broken by nitric oxide. *Planta* 219(5):847–855
- Bewley JD, Black M (1994) Seeds: physiology of development and germination. Plenum, New York
- Boucaud J, Ungar IA (1973) The role of hormones in controlling the mechanically induced dormancy of *Suaeda* spp. *Physiol Plant* 29:97–102
- Boucaud J, Ungar IA (1976) Hormonal control of germination under saline conditions of three halophytic taxa in the genus *Suaeda*. *Physiol Plant* 37:143–148
- Clarke LD, Hannon JD (1970) The mangrove swamp and salt marsh communities of the Sydney district. III. Plant growth in relation to salinity and water logging. *J Ecol* 58:351–369
- Corbineau F, Rudnicki RM, Come D (1989) ACC conversion by sunflower seeds in relation to maturation, germination and thermodormancy. *Plant Growth Regul* 8:105–115
- Egley GH, Dale JE (1970) Ethylene, 2-chloroethylphosphonic acid and witchweed germination. *Weed Sci* 18:586–589
- Esashi Y, Ohara Y, Okazaki M, Hishinuma K (1979) Control of cocklebur seed germination by nitrogenous compounds: nitrite, nitrate, hydroxylamine, thiourea, azide, and cyanide. *Plant Cell Physiol* 20:349–361
- Galatino MI, Van der Valk AG (1986) Seed germination traits of annuals and emergents recruited during drawdowns in the Delta marsh, Manitoba, Canada. *Aquat Bot* 26:89–102
- Gul B, Weber DJ (1998) Effect of dormancy compounds on the seed germination of non-dormant *Allenrolfea occidentalis* under salinity stress. *Ann Bot* 82:555–560
- Gulzar S, Khan MA (2001) Effect of temperature and salinity on the germination of *Urochondra setulosa*. *Seed Sci Technol* 29:21–29
- Gulzar S, Khan MA (2002) Alleviation of salinity-induced dormancy in perennial grasses. *Biol Plant* 45:617–619
- Guo FQ, Okamoto M, Crawford NM (2003) Identification of a plant nitric oxide synthase gene involved in hormonal signaling. *Science* 302:100–103
- Gutterman Y, Kamenetsky R, Van Rooyen M (1995) A comparative study of seed germination of two *Allium* species from different habitats in the Negev desert highlands. *J Arid Environ* 29:305–315
- Ismail AMA (1982) Effect of strigol analogue and etrel on the germination capacity of the seeds *Cistanche phelypaea*. *Phytomorphology* 32:241–245
- Ismail AMA (1990) Germination ecophysiology in populations of *Zygophyllum qatarense* Hadidi from contrasting habitats: effect of temperature, salinity and growth regulators with special reference to fusicoccin. *J Arid Environ* 18:185–194
- Jhamb RB, Sen DN (1984) Seed germination behaviour of halophyte in Indian desert: 1, *Suaeda fruticosa* (Linn.) Forssk. *Curr Sci* 53:100–101
- Karsen CM (1976) Uptake and effect of abscisic acid during induction and progress of radicle growth in seeds of *Chenopodium album*. *Physiol Plant* 36:259–263
- Karsen CM (1995) Hormonal regulation of seed development, dormancy, and germination studied by genetic control. In Kigel J, Galili G (eds) Seed development and germination. Marcel Dekker, New York, pp 333–350
- Kepeczynski J (1986) Inhibition of *Amaranthus caudatus* seed germination by polyethylene glycol-6000 and abscisic acid and its reversal by ethephon or 1-aminocyclopropane-1-carboxylic acid. *Physiol Plant* 67:588–591

- Kepczynski J, Karssen CM (1985) Requirement for the action of endogenous ethylene during germination of non-dormant seeds of *Amaranthus caudatus*. *Physiol Plant* 63:49–52
- Ketring DL (1977) Ethylene and seed germination. In: Khan AA (ed) *The physiology and biochemistry of seed dormancy and germination*. North Holland, Amsterdam, pp 157–158
- Ketring DL, Morgan PW (1969) Ethylene as a component of the emanations from germinating peanut seeds and its effect on dormant Virginia-type seeds. *Plant Physiol* 44:326–330
- Khan MA (2002) Halophyte seed germination: success and pitfalls. In: Hegazi AM, El-Shaer HM, El-Demerdashe S, Guirgis RA, Abdel Salam Metwally A, Hasan FA, Khashaba HE (eds) *International symposium on optimum resource utilization in salt affected ecosystems in arid and semi arid regions*. Desert Research Centre, Cairo, pp 346–358
- Khan MA, Gul B (1998) High salt tolerance in germinating dimorphic seeds of *Arthrocnemum indicum*. *Int J Plant Sci* 159:826–832
- Khan MA, Rizvi Y (1994) Effect of salinity, temperature, and growth regulators on the germination and early seedling growth of *Atriplex griffithii* var. *stocksii*. *Can J Bot* 72:475–479
- Khan MA, Ungar IA (1984a) The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. *Amer J Bot* 71:481–489
- Khan MA, Ungar IA (1984b) Seed polymorphism and germination responses to salinity stress *Atriplex triangularis* Willd. *Bot Gaz* 145:487–494
- Khan MA, Ungar IA (1997) Alleviation of seed dormancy in the desert forb *Zygophyllum simplex* L. from Pakistan. *Ann Bot* 80:395–400
- Khan MA, Ungar IA (1998) Germination of the salt tolerant shrub *Suaeda fruticosa* from Pakistan: salinity and temperature responses. *Seed Sci Technol* 26:657–667
- Khan MA, Ungar IA (2000) Alleviation of salinity-enforced dormancy in *Atriplex griffithii* Moq var *stocksii* Boiss. *Seed Sci Technol* 28:29–37
- Khan MA, Ungar IA (2001a) Role of dormancy regulating chemicals in release of innate and salinity-induced dormancy in *Sporobolus arabicus*. *Seed Sci Technol* 29:299–306
- Khan MA, Ungar IA (2001b) Effect of dormancy regulating chemicals on the germination of *Triglochin maritima*. *Biol Plant* 44:301–303
- Khan MA, Ungar IA (2001c) Alleviation of salinity stress and the response to temperature in two seed morphs of *Halopyrum mucronatum* (Poaceae). *Aust J Bot* 49:777–783
- Khan MA, Ungar IA (2002) Role of dormancy-relieving compounds and salinity on the germination of *Zygophyllum simplex* L. *Seed Sci Technol* 30:507–514
- Khan MA, Weber DJ (1986) Factors influencing seed germination in *Salicornia pacifica* var *utahensis*. *Am J Bot* 73:1163–1167
- Khan MA, Ungar IA, Gul B (1998) Action of compatible osmotic and growth regulators in alleviating the effect of salinity on the germination of dimorphic seeds of *Arthrocnemum indicum* L. *Int J Plant Sci* 159:313–317
- Khan MA, Gul B, Weber DJ (2000) Improving seed germination of *Salicornia rubra* (Chenopodiaceae) under saline conditions using germination regulating chemicals. *West N Am Nat* 62:101–105
- Khan MA, Gul B, Weber DJ (2001) Germination of dimorphic seeds of *Suaeda moquinii* under high salinity stress. *Aust J Bot* 49:185–192
- Khan MA, Gul B, Weber DJ (2004) Action of plant growth regulators and salinity on the seed germination of *Ceratoides lanata*. *Can J Bot* 82:37–42
- Mohammad S, Sen DN (1988) A report on polymorphic seeds in halophytes. I. *Trianthema triquetra* L. in Indian desert. *Curr Sci* 57:616–617
- Morgan WC, Myers BA (1989) Germination of salt-tolerant grass *Diplachne fusca*. I. Dormancy and temperature responses. *Aust J Bot* 37:225–237
- Myers BA, Morgan WC (1989) Germination of the salt-tolerant grass *Diplachne fusca*. II. Salinity responses. *Aust J Bot* 37:239–251
- Naidoo G, Naicker K (1992) Seed germination in the coastal halophytes *Triglochin bulbosa* and *Triglochin striata*. *Aquat Bot* 42:217–229
- Okusanya OT (1979) An experimental investigation into the ecology of some maritime cliff species. II. Germination studies. *J Ecol* 67:293–304
- Philippupillai J, Ungar IA (1984) The effect of seed dimorphism on the germination and survival of *Salicornia europaea* L. populations. *Am J Bot* 71:542–549
- Rivers WG, Weber DJ (1971) The influence of salinity and temperature on the seed germination in *Salicornia bigelovii*. *Physiol Plant* 24:73–75
- Schonbeck MW, Egle GH (1981) Phase-sequence of redroot pigweed seed germination responses to ethylene and other stimuli. *Plant Physiol* 68:175–179
- Schutz W, Milberg P, Lamont BB (2002) Seed dormancy, after-ripening and light requirements of four annual *Asteraceae* in south-western Australia. *Ann Bot* 90:707–711
- Sutcliffe MA, Whitehead CS (1995) Role of ethylene and short chain saturated fatty acids in the smoke-stimulated germination of *Cyclopa* seeds. *J Plant Physiol* 145:271–271
- Toyomasu T, Yamane H, Murofushi N, Inoue Y (1994) Effects of exogenously applied gibberellin and red light on the endogenous levels of abscisic acid in photoblastic lettuce seeds. *Plant Cell Physiol* 35:127–129
- Ungar IA (1962) Influence of salinity on seed germination in succulent halophytes. *Ecology* 43:763–764
- Ungar IA (1967) Vegetation-soil relationships on saline soils in northern Kansas. *Am Midl Nat* 78:98–120
- Ungar IA (1977) Salinity, temperature, and growth regulator effects on seed germination of *Salicornia europaea* L. *Aquat Bot* 3:329–335
- Ungar IA (1978) Halophyte seed germination. *Bot Rev* 44:233–246
- Ungar IA (1979) Seed dimorphism in *Salicornia europaea*. *Bot Gaz* 140:102–108
- Ungar IA (1984) Alleviation of seed dormancy in *Spergularia marina*. *Bot Gaz* 145:33–36
- Ungar IA (1988) Effects of the parental environment on the temperature requirements and salinity tolerance of *Spergularia marina* seeds. *Bot Gaz* 149:432–436
- Ungar IA (1991) *Ecophysiology of vascular halophytes*. CRC Press, Boca Raton
- Ungar IA (1995) Seed germination and seed-bank ecology of halophytes. In: Kigel J, Galili G (eds) *Seed development and germination*. Marcel and Dekker, New York, pp 599–628
- Ungar IA, Capilupo F (1969) An ecological life history study of *Suaeda depressa* (Pursh) Wats. *Adv Front Plant Sci* 23:137–158
- Wang B, Lüttge U, Ratajczak R (2001) Effects of salt treatment and osmotic stress on V-ATPase and V-PPase in leaves of the halophyte *Suaeda salsa*. *J Exp Bot* 52:2355–2365
- Whitehead CS, Nelson RM (1992) Ethylene sensitivity in germinating peanut seeds. The effect of short-chain saturated fatty acids. *J Plant Physiol* 138:479–483
- Williams MD, Ungar IA (1972) The effect of environmental parameters on the germination, growth, and development of *Suaeda depressa* (Pursh) Wats. *Am J Bot* 59:912–918
- Xiong L, Zhu JK (2003) Regulation of abscisic acid biosynthesis. *Plant Physiol* 133:29–36
- Yamaguchi S, Kamiya Y (2000) Gibberellin biosynthesis: its regulation by endogenous and environmental signals. *Plant Cell Physiol* 41:251–257
- Yamaguchi S, Kamiya Y (2002) Gibberellins and light-stimulated seed germination. *J Plant Growth Regul* 20:369–376
- Yang SF, Hoffman NE (1984) Ethylene biosynthesis and its regulation in higher plants. *Annu Rev Plant Physiol* 33:155–189
- Yokoishi T, Tanimoto S (1994) Seed germination of the halophyte *Suaeda japonica* under salt stress. *J Plant Res* 107:385–388
- Yoshiyama M, Maruyama A, Atsumi T, Esashi Y (1996) Mechanism of action of C<sub>2</sub>H<sub>2</sub> in promoting the germination of cocklebur seeds. III. A further enhancement of priming effect with nitrogenous compounds and C<sub>2</sub>H<sub>2</sub> responsiveness of seeds. *Aust J Plant Physiol* 23:519–525
- Young JA, Kay BL, George H, Evans RA (1980) Germination of three species of *Atriplex*. *Agron J* 72:705–709
- Zhao XC, Schaller GE (2004) Effect of salt and osmotic stress upon expression of the ethylene receptor ETR1 in *Arabidopsis thaliana*. *FEBS Lett* 562:189–192
- Zhao K, Fan H, Ungar IA (2002) Survey of halophyte species in China. *Plant Sci* 163:491–498