

# Assessing Seed Germination Responses of Great Basin Halophytes to Various Exogenous Chemical Treatments Under Saline Conditions

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## Abstract

Salinity causes imbalances in endogenous level of different dormancy regulating chemicals (DRCs) of seeds, resulting in germination inhibition and/or viability loss. Exogenous application of DRCs could therefore be an effective means to mitigate salinity effects on seed germination. In this study, we compared (1) salt tolerance and (2) variability and efficacy of various DRCs on seed germination of Great Basin halophytes under controlled laboratory conditions. Optimal seed germination of all test species was observed in distilled water and increases in salinity generally decreased seed germination. Exogenous application of all DRCs enhanced seed germination at all salinities, with more alleviations under high salinity. Ethephon, fusicoccin and kinetin treatments were generally most effective than others. While, *Salicornia rubra* and *Sarcocornia utahensis* responded to nearly all DRCs in comparison to other species. Our results thus indicate that effectiveness of DRC treatments could be salinity, species and chemical specific.

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## 1 Introduction

Soil salinity is the key factor that determines both the timing and the magnitude of seed germination, thereby population establishment of most halophytes in temperate saline habitats (Ungar 1978; Gul et al. 2013). Salinity tolerance of halophyte seeds from temperate dry cold habitats varies considerably among species (Khan and Gul. 2006; Easton and Kleindorfer 2008). For instance, seeds of some succulent halophytes such as

*Salicornia herbacea* (1700 mM NaCl, Chapman 1960), *Suaeda aralocapsica* (1.5 M NaCl, Wang et al. 2008), *Sarcocornia perennis* (1.3 M NaCl, Redondo et al. 2004) and *Haloxylon ammodendron* (1.3 M NaCl, Huang et al. 2003) could germinate in about twice the salinity as in seawater. While, seed germination of many dicot forbs such as *Tanacetum cinerariifolium* (260 mM NaCl; Li et al. 2011), *Limonium iconicum* (300 mM NaCl, Yildiz et al. 2008), *Limonium lilacinum* (300 mM NaCl, Yildiz et al. 2008) and *Chenopodium album* (300 mM NaCl; Yao et al. 2010) reduced substantially ( $\leq 10\%$ ) even under moderately ( $\leq 300$  mM NaCl) saline conditions.

Seed germination responses of halophytes to salinity can generally be divided into three types, i.e. (1) delayed seed germination under salinity (Ahmed and Khan 2010; Hameed et al. 2013, 2014), (2) prevention of seed germination due to osmotic constraint (Zia and Khan 2004; Liu et al. 2006) and (3) loss of seed viability due to ionic toxicity under (Khan and Gul 2006; Khan et al. 2006; Rasheed et al. 2015). Exposure of seeds to 300 mM NaCl for example led to marginal inhibition of seed germination in *Haloxylon salicornicum* (El-Keblawy and Al-Shamsi 2008), substantial germination inhibition in *Panicum turgidum* (El-Keblawy 2004), while high seeds mortality in *Suaeda heterophylla* (Hameed et al. 2013). Hence, it appears that the seed germination responses of halophytes to increasing salinity are quite complex.

A growing body of evidence suggests that the salinity upsets the balances of various chemical regulators such as phyto-hormones and protective compounds in the seeds, which leads to germination inhibition and/or viability loss of the seeds (Atia et al. 2009; Gul et al. 2013; Li et al. 2015). For instance, decline in endogenous gibberellic acid ( $GA_3$ ) levels is often ascribed to the seed germination inhibition under saline conditions (Kabar and Baltepe 1989; Bewley and Black 1994; Khan and Gul. 2006), which is further supported by the ameliorative effects of exogenous GA on seed germination of halophytes (Atia et al. 2009). Similarly exogenous supply of many other chemicals such as kinetin (Ahmed et al. 2014; El-Keblawy et al. 2011), eth-

ylene (Khan et al. 2009), fusicoccin (El-Keblawy et al. 2011; Rasheed et al. 2015) and nitrogenous compounds (Gul and Weber 1998; Khan and Ungar 2001a, b, Li et al. 2005; Atia et al. 2009) is also known to have positive effects on seed germination of halophytes under saline conditions. However, germination responses to these chemicals may vary among species and habitats (Ahmed et al. 2014; Gulzar and Khan 2002; Khan and Gul. 2006; El-Keblawy et al. 2011).

Seed germination inhibition under saline conditions is generally associated with changes in seeds' chemical environment (Khan and Gul 2006; Debez et al. 2001; Atia et al. 2009). The understanding of the action of various dormancy regulating chemicals (DRCs) on seed germination thus appears important. The aim of this research work was therefore to investigate the role of different DRCs in improving seed germination of some Great Basin halophytes under increasing salinity. Specifically, we addressed following questions:

- (a) How variable are the seed germination responses of halophytes to increasing salinity?
- (b) Can exogenous application of different DRCs enhance seed germination of halophytes in both non-saline and saline conditions?
- (c) Whether the effects of different DRCs to alleviate seed germination under saline are similar?

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## 2 Materials and Methods

### 2.1 Seed Collection and Study Site

Seeds of eight halophytes *Atriplex rosea*, *Suaeda nigra*, *Sarcobatus vermiculatus*, *Sarcocornia utahensis*, *Salicornia rubra*, *Bassia scoparia*, *Halogeton glomeratus* and *Krascheninnikovia ceratoides* were collected from their healthy populations growing in vicinity and inland sabkhas around Great Salt Lake, Utah, United State of America (Table 6.1). More specifically, seed collection sites were situated at the area which

**Table 6.1** Common name(s), life cycle, habit, distribution and habitat (seed collection site) of the test species

Species	Common name	Life cycle	Habit	Distribution	Habitat
<i>Atriplex rosea</i> L.	Tumbling saltbush, red orach	Annual	Herb	Disturbed sites, often in riparian habitats and barnyards in Eurasia and North America (Billings 1945; Welsh et al. 1987)	Salt marsh near Faust, Utah, USA
<i>Bassia scoparia</i> (L.) A.J.Scott (Syn. <i>Kochia scoparia</i> (L.) Schrader)	Mexican fireweed, Summer cypress	Annual	Herb	Saline areas in Southern and Eastern Russia, Europe, and North America	Salt marsh near Faust, Utah, USA
<i>Halogeton glomeratus</i> (Bieb.) C.A. Mey	Saltlover, Aral barilla	Annual	Herb	Saline -alkaline soils in Russia, China, Pakistan and western United States	Salt flats 2.5 miles northwest of Faust, Utah, USA
<i>Krascheninnikovia ceratoides</i> (L.) Gueldenst. (Syn. <i>Ceratoides lanata</i> (Pursh) J.T. Howell)	Winterfat, White-sage	Annual	Shrub	Central and southern Europe, northern Africa, and parts of Asia and western North America	Salt marsh near Faust, Utah, USA
<i>Salicornia rubra</i> A. Nelson	Red Glasswort, red swampfire	Annual	Herb	Central North America specially Manitoba to British Columbia and southwards.	Salt playas near Goshen, Utah, USA
<i>Sarcobatus vermiculatus</i> (Hook.) Torr.	Greasewood, seepwood, and saltbush	Perennial	Leaf Succulent Shrub	Medium to heavy textured soils in the Western USA (Richards, 1982; Welsh et al. 1987)	Salt flats in Utah, USA
<i>Sarcocornia utahensis</i> (Tidestrom) A.J. Scott (Syn. <i>Salicornia utahensis</i> )	Utah glasswort, Utah swampfire	Perennial	Stem succulent herbaceous	Southwestern United States	Salt playas 1–2 km east of Goshen, Utah, USA
<i>Suaeda nigra</i> (Raf.) J.F.Macbr. (Previously <i>Suaeda moquinii</i> (Torr.) Greene)	Mojave seablite	Perennial	Leaf Succulent Shrub	Western North America (from central Canada through the Western United States and Great Basin to the Mojave Desert in California) and northern Mexico	Salt marsh near Faust, Utah, USA

was once part of Lake Bonneville, a prehistoric pluvial ice-age lake that covered much of western Utah in past (Fisher 1974). Soil salinity of the area may range from 27 to 145 dS m<sup>-1</sup> and water table varies from 1 to 3 m below the surface (Gul et al. 2001). It was a temperate area, where precipitation mainly occurs in the winter months. Seeds of test species were collected randomly from large number (>100) of plants, to ensure adequate representation of population's genetic diversity. Seeds were separated from inflorescence husk manually and dry-stored at 4 °C after

surface sterilization with fungicide Phygon (2, 3 dichloro-1, 4-naphthoquinone) prior to use.

## 2.2 Experiment 01: Determining Salt Tolerance of Halophyte Seeds During Germination

Salt tolerance limits of halophyte seeds during germination were determined in growth chamber set at alternating temperature regimes (See Table 6.2), where the higher temperature coin-

**Table 6.2** Salinity and temperature treatments used in germination experiments, based on preliminary trials

Species	NaCl (mM)				Temperature (°C)
	CK	Low	Medium	High	
<i>Atriplex rosea</i> L. – Black Seeds	0	200	400	600	20/30
<i>Atriplex rosea</i> L. – Brown Seeds	0	300	600	900	20/30
<i>Bassia scoparia</i> (L.) A.J.Scott	0	300	600	900	25/35
<i>Halogeton glomeratus</i> (Bieb.) C.A. Mey	0	300	600	900	25/35
<i>Krascheninnikovia ceratoides</i> (L.) Gueldenst.	0	300	600	900	25/35
<i>Salicornia rubra</i> A. Nelson	0	300	600	900	25/35
<i>Sarcobatus vermiculatus</i> (Hook.) Torr.	0	300	600	900	20/30
<i>Sarcocornia utahensis</i> (Tidestrom) A.J. Scott	0	300	600	900	25/35
<i>Suaeda nigra</i> (Raf.) J.F.Macbr.	0	400	800	1200	5/15

cided with the 12-h light period (Sylvania cool white fluorescent lamps, 25  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , PAR 400–750 nm) and the lower temperature coincided with the 12-h dark period. Germination was carried out in clear-lid plastic Petri-plates (50×9 mm; Gelman No. 7232) with 5 mL of test solution (0–1200 mM NaCl; Table 6.2). Each Petri-plate was placed in another 10-cm diameter plastic Petri-plate as an added precaution against loss of water by evaporation. There were four replicates of 25 seeds each per treatment. Seeds were considered to be germinated with emergence of the radicle (Bewley and Black 1994). Percent germination was recorded on alternate day for 20 days. The rate of seed germination was calculated with the help of a modified Timson's index of germination velocity, which is given below:

$$\text{Germination rate (Timson Index)} = \frac{\Sigma G}{t}$$

Where, G is the percentage of seed germination at 2-day intervals and t is the total germination

period (Timson 1965; Khan and Ungar 1984). Maximum value possible for this index with our data was 50 (i.e., 1000/20). The higher the value, the more rapid was the germination.

### 2.3 Experiment 02: Examining Efficacy of Different DRC Treatments in Improving Salt Tolerance of Halophyte Seeds

Seeds were germinated in different salinity treatments (Table 6.2) under optimal thermoperiod (Table 6.2) and 12-h light/12-h dark photoperiod in presence and absence of different dormancy regulating chemicals (DRCs). Ethephon (10 mM), fusicoccin (5  $\mu\text{M}$ ), gibberellic acid ( $\text{GA}_3$ ; 3 mM), glycine-betain (1 mM), kinetin (0.05 Mm), nitrate ( $\text{KNO}_3$ ; 20 mM), Proline (0.1 mM) and thiourea (10 mM) were used. Germination data were noted, as described above. Effects of these DRCs were expressed as change (in folds) in seed germination as compared to no-DRC treatment, as shown below:

$$\text{Change (folds)} = \frac{(\text{Germination with DRC} - \text{Germination without DRC})}{\text{Germination without DRC}}$$

A positive value indicated promotion in seed germination, while negative value was indicator of germination inhibition by a DRC.

## 2.4 Statistical Analyses

Germination data were arcsine transformed before statistical analysis. Analyses of variance (ANOVAs) were used to determine if treatments (salinity and DRCs) had significant effect on seed germination. While, a Bonferroni test was carried out to compare mean values for significant ( $P < 0.05$ ) differences. Software SPSS Version 11.0 (SPSS 2011) was used for data analysis.

## 3 Results

### 3.1 Salt Tolerance of Halophyte Seeds During Germination

Seed germination of all test species, irrespective of their habit and life cycle traits, decreased ( $P < 0.05$ ) with increases in salinity (Fig. 6.1). However, some (<20%) seeds of *Suaeda nigra* could germinate in up to 1200 mM NaCl treatment (Fig. 6.1i), those of *Atriplex rosea* (brown seeds; Fig. 6.1a), *Bassia scoparia* (Fig. 6.1c), *Halogeton glomeratus* (Fig. 6.1d), *Krascheninnikovia ceratoides* (Fig. 6.1e), *Salicornia rubra* (Fig. 6.1f), *Sarcobatus vermiculatus* (Fig. 6.1g) and *Sarcocornia utahensis* (Fig. 6.1h) in up to 600 mM NaCl, while of *Atriplex rosea* (black seeds Fig. 6.1b) in up to 400 mM NaCl. Seed germination rate (Timson's index) of all test species also decreased with increases in salinity, with highest value ( $\geq 40$ ) in absence of salinity and lowest ( $\leq 10$ ) under high NaCl treatments (Fig. 6.1a–e).

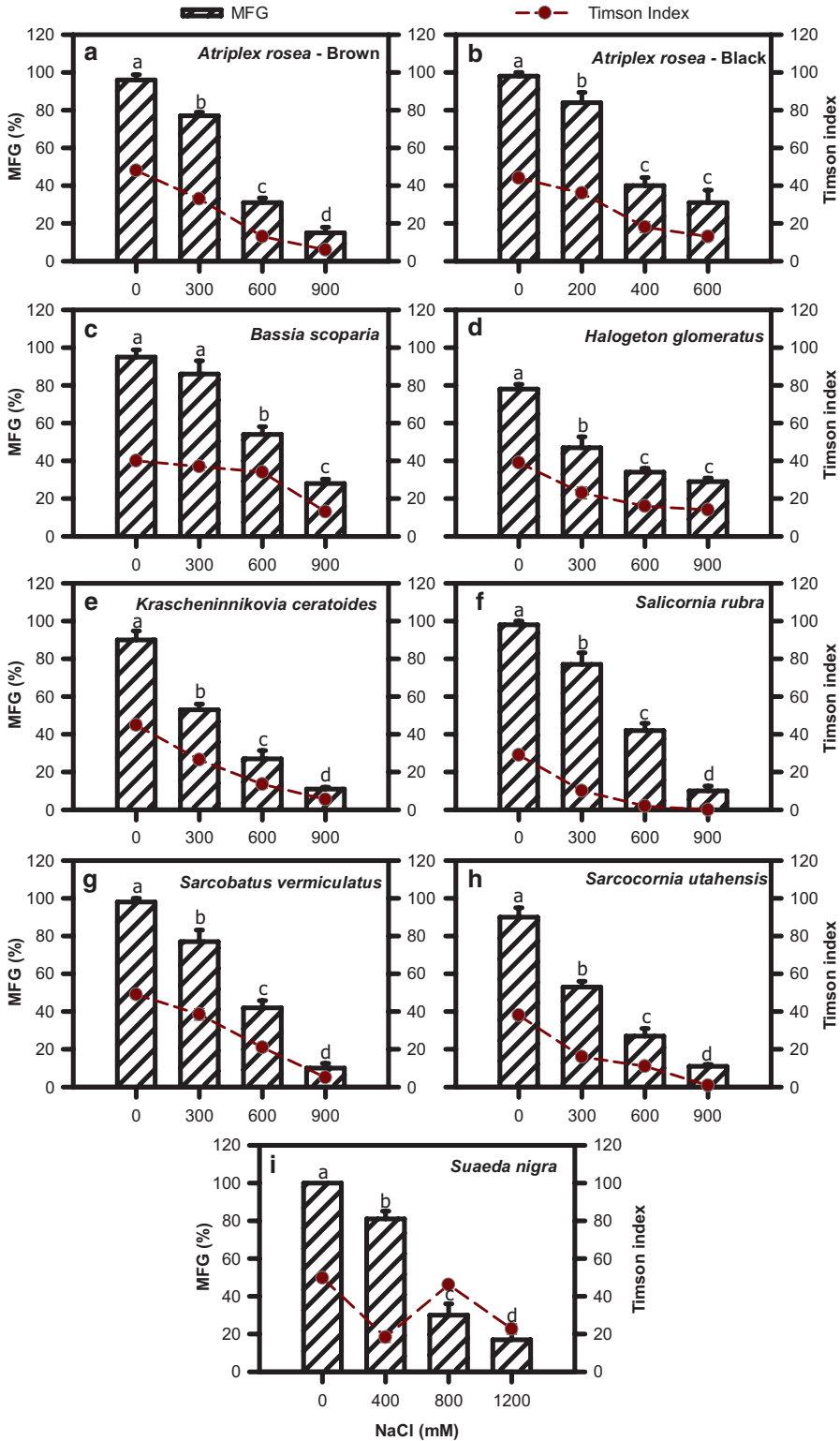
### 3.2 Efficacy of DRC Treatments in Improving Salt Tolerance of Halophyte Seeds

All DRC treatments improved seeds germination of halophytes but response varied among seeds

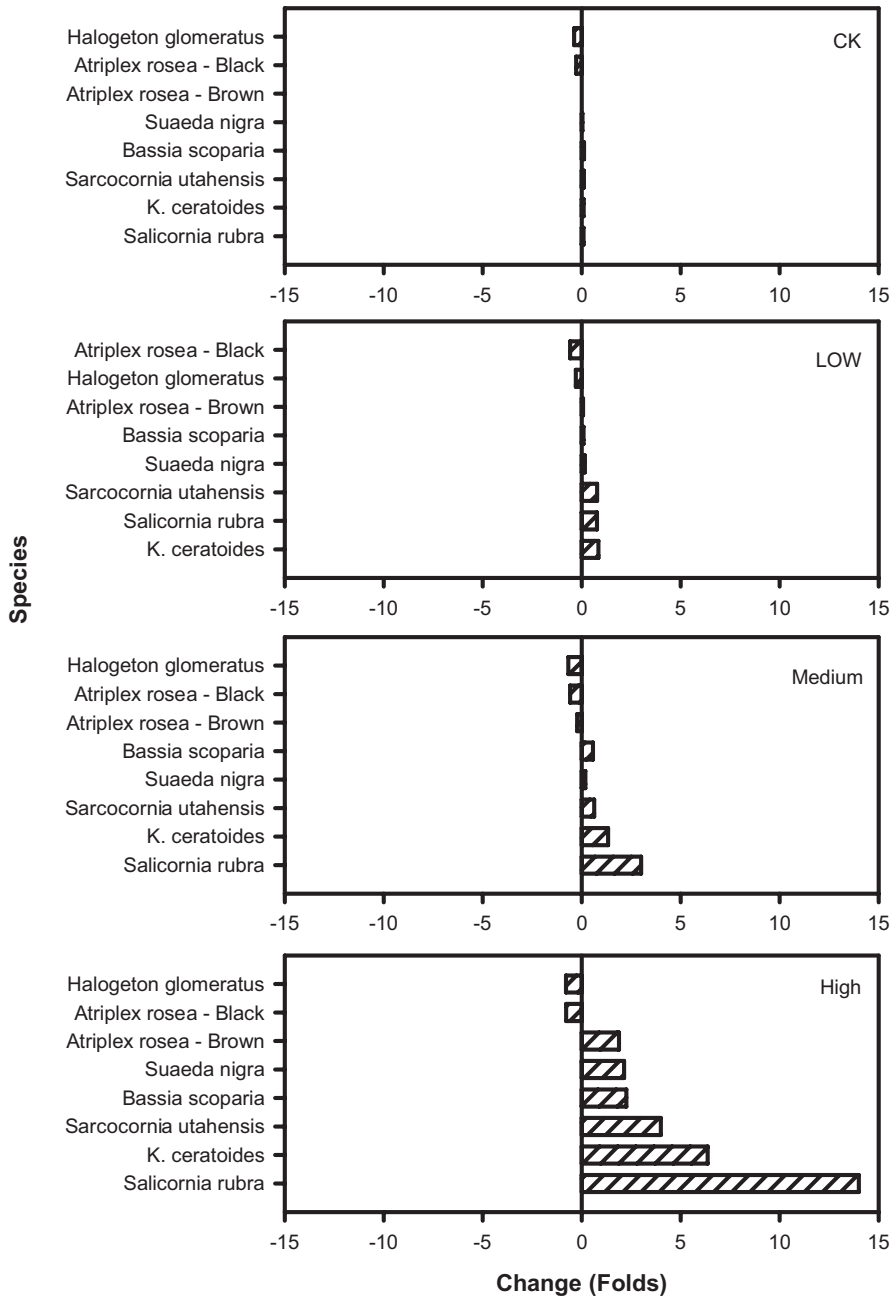
from different species and with the differential effect of NaCl concentrations. Higher seed germination was recorded by the DRC applications at NaCl concentrations where it was inhibited substantially. Exogenous application of ethephon could improve seed germination of *Salicornia rubra*, *Krascheninnikovia ceratoides* and *Sarcocornia utahensis* more than other species under high salinity (Fig. 6.2). Fusicoccin ameliorated seed germination of *Sarcocornia utahensis*, *Krascheninnikovia ceratoides* and *Bassia scoparia* more than other species under high salinity (Fig. 6.3). Gibberellic acid ( $GA_3$ ) alleviated inhibitory effects of high salinity in *Salicornia rubra*, *Sarcocornia utahensis* and *Bassia scoparia* more in comparison to other species (Fig. 6.4). Glycinebetaine (GB) enhanced seed germination of *Sarcocornia utahensis*, *Salicornia rubra* and *Bassia scoparia* under high salinity stress more than other species tested (Fig. 6.5). Kinetin showed more pronounced ameliorative effects on seed germination of *Sarcocornia utahensis*, *Salicornia rubra* and *Sarcobatus vermiculatus* under high salinity as compared to other species (Fig. 6.6). Nitrate treatment could improve seed germination in *Sarcocornia utahensis* and *Salicornia rubra* under high salinity in comparison to other species (Fig. 6.7). Proline had more pronounced ameliorative effects on seed germination of in *Sarcocornia utahensis*, *Salicornia rubra* and *Halogeton glomeratus* than other species (Fig. 6.8). While, thiourea alleviated high salinity effects in *Sarcocornia utahensis* and *Salicornia rubra* more as compared to other species (Fig. 6.9).

## 4 Discussion

Seeds of Great Basin halophytes used in this study were non-dormant and germinated maximally in distilled water; however increases in salinity decreased their germination which is in agreement with the general trend of halophyte seeds reviewed by Ungar (1978) and Gul et al. (2013). Similar results have been reported for the seeds of *Halocnemum strobilaceum* (Pujol et al. 2001), *Arthrocnemum macrostachyum* (Vicente



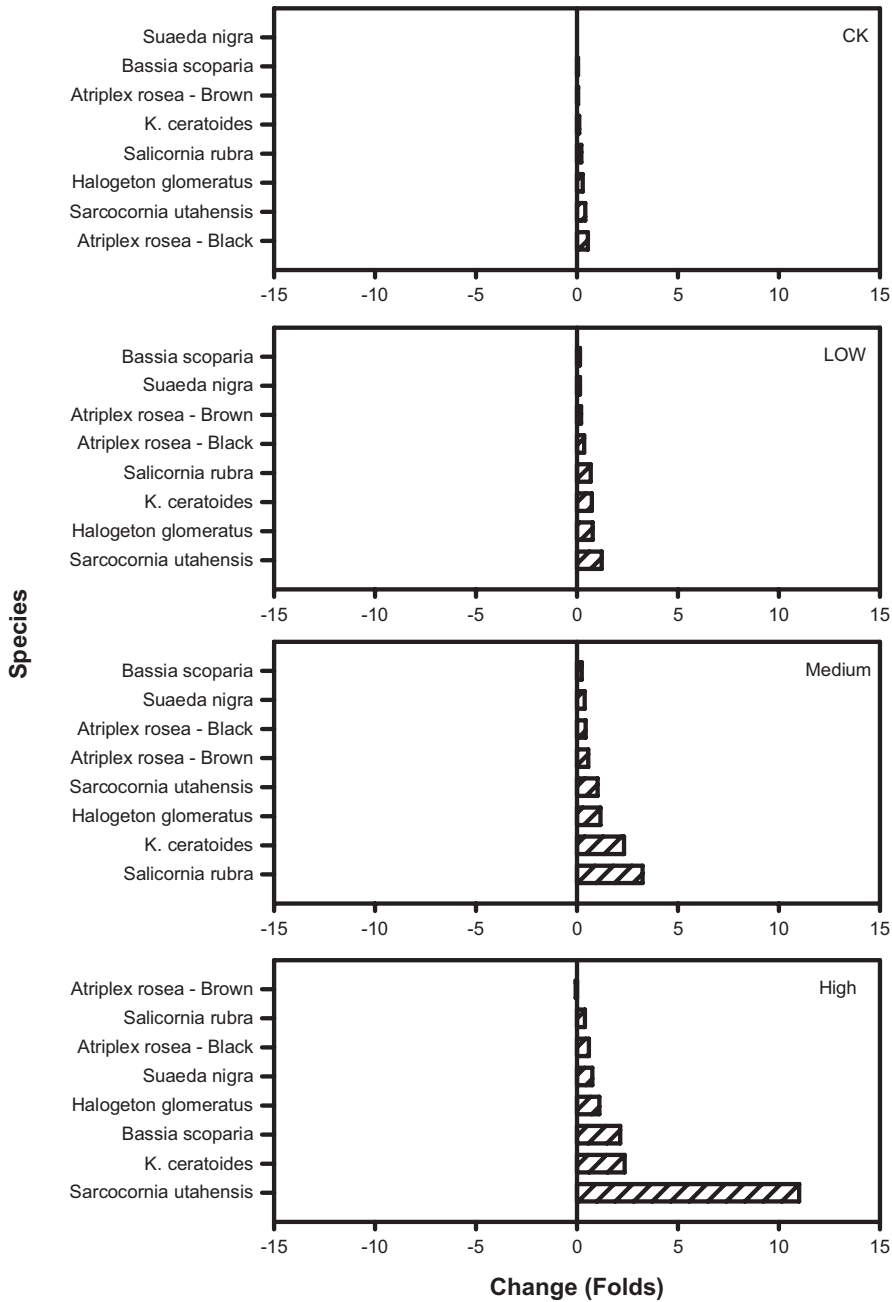
**Fig. 6.1** Effect of salinity on mean final (MFG) and rate of seed germination (Timson's index) of Great Basin halophytes. Data is given as mean ± standard error. Bars with different alphabets are significantly different from each other (Bonferroni test,  $P < 0.05$ )



**Fig. 6.2** Effects of Ethephon on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Ethephon

et al. 2007) and *Sarcocornia* spp (Redondo et al. 2004). This reduction in seed germination could be a result of decreasing osmotic potential of the solution caused by salinity that impedes adequate seed hydration essential for radicle protrusion

(Ramoliya and Pandey 2002; Hameed et al. 2014). Furthermore, a substantial inhibition of seed germination was observed, when seeds of all test species were exposed to hyper-salinity (>600 mM NaCl). Such high germination inhibi-

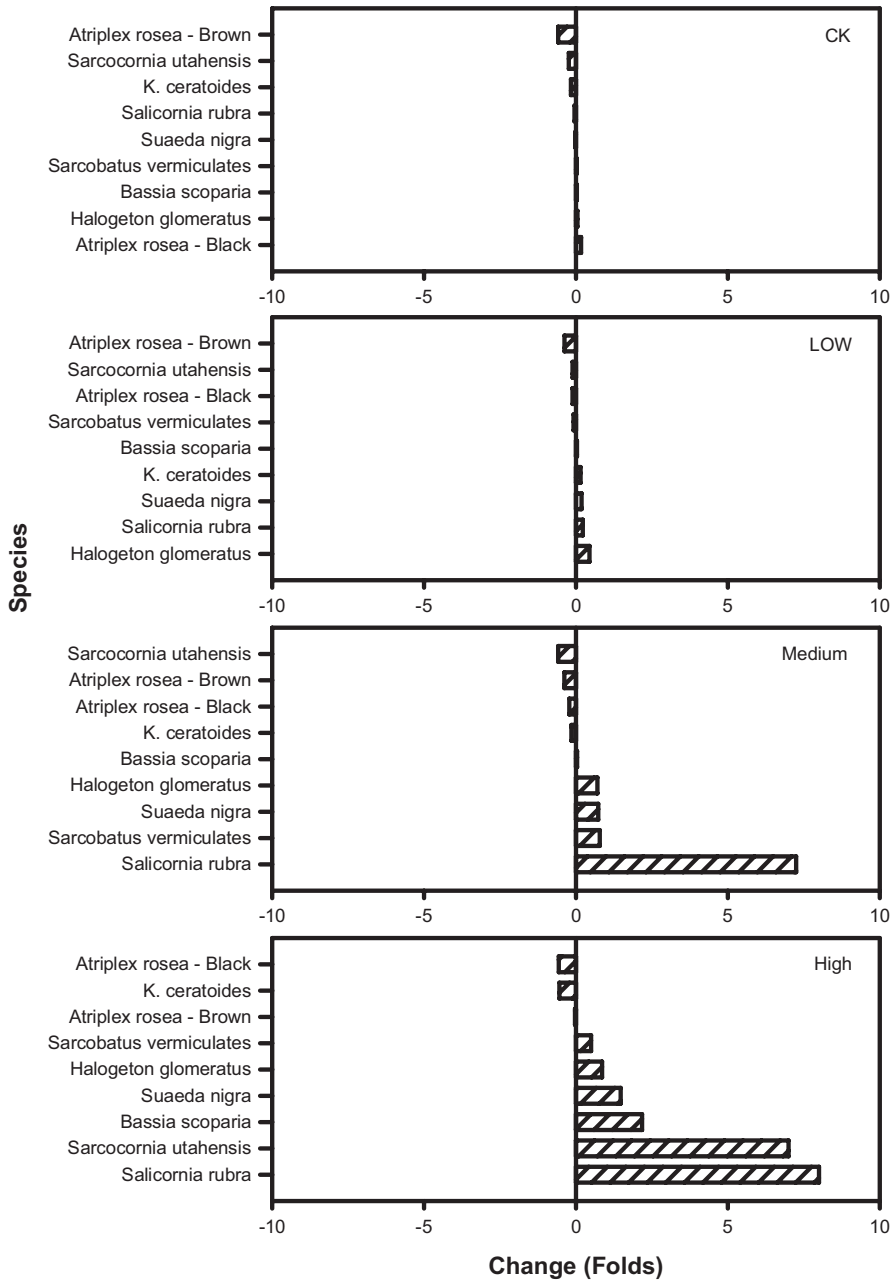


**Fig. 6.3** Effects of Fusicoccin on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Fusicoccin

tion under hyper-salinity could be a general strategy of Great Basin halophytes to circumvent summer drought accompanying high soil salinity, which is not conducive for seedling survival. While, high seed germination of Great Basin

halophytes in distilled water and low (300 mM NaCl) salinity indicates that they would germinate only after winter rains, which create “window of germination” (Noe and Zedler 2001) or “window of opportunity” (Eriksson and Fröberg



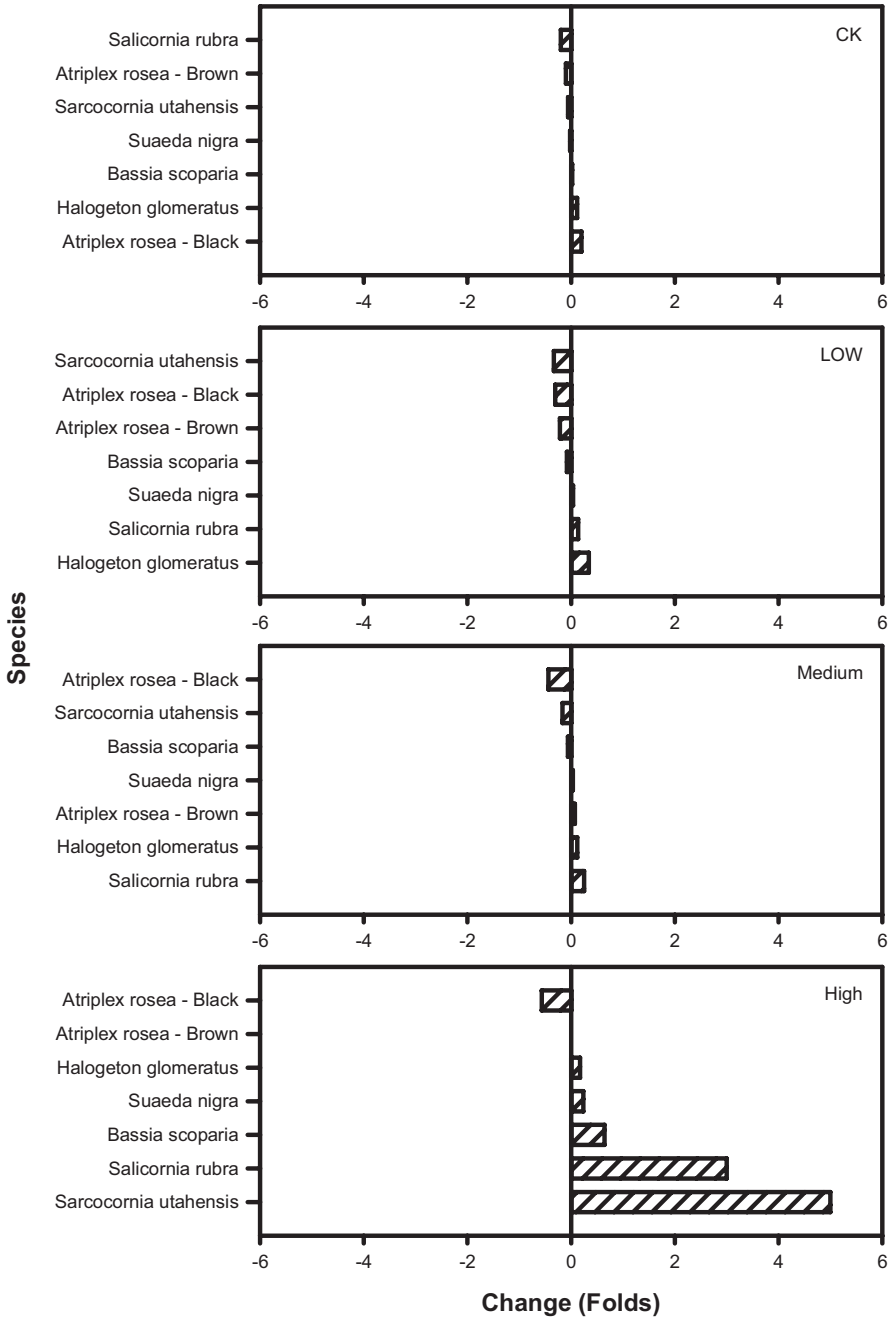


**Fig. 6.4** Effects of GA<sub>3</sub> on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without GA<sub>3</sub>

1996) by diluting soil salinity and providing moisture.

Salt tolerance of Great Basin halophytes during their seed germination varied considerably among species. Seeds of *Suaeda nigra* could germinate in up to 1200 mM NaCl solution, those of

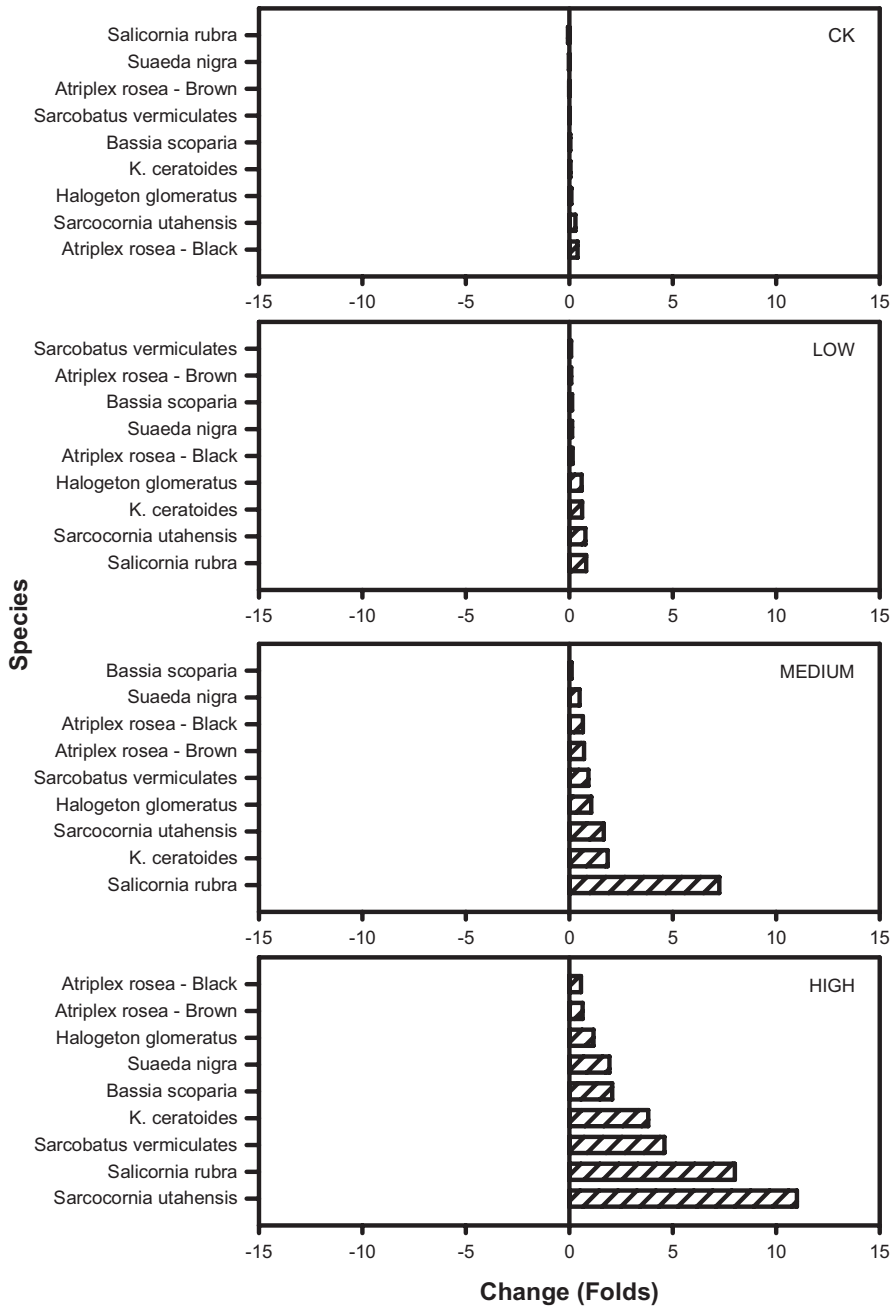
*Atriplex rosea* (brown seeds), *Bassia scoparia*, *Halogeton glomeratus*, *Krascheninnikovia ceratoides*, *Salicornia rubra*, *Sarcobatus vermiculatus* and *Sarcocornia utahensis* in up to 600 mM NaCl, while black seeds of *Atriplex rosea* germinated in up to 400 mM NaCl treatment. Gul



**Fig. 6.5** Effects of GB on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without GB

et al. (2013) recently reviewed that the salt tolerance of halophyte seeds ranges from 1700 mM NaCl (*Salicornia herbacea*, Chapman 1960) to  $\leq 300$  mM NaCl (*Chenopodium album*, Yao

et al. 2010; *Tanacetum cinerariifolium*, Li et al. 2011). This variability in salt tolerance is often related to the habitat conditions of the species (Khan and Gul 2006; Easton and Kleindorfer

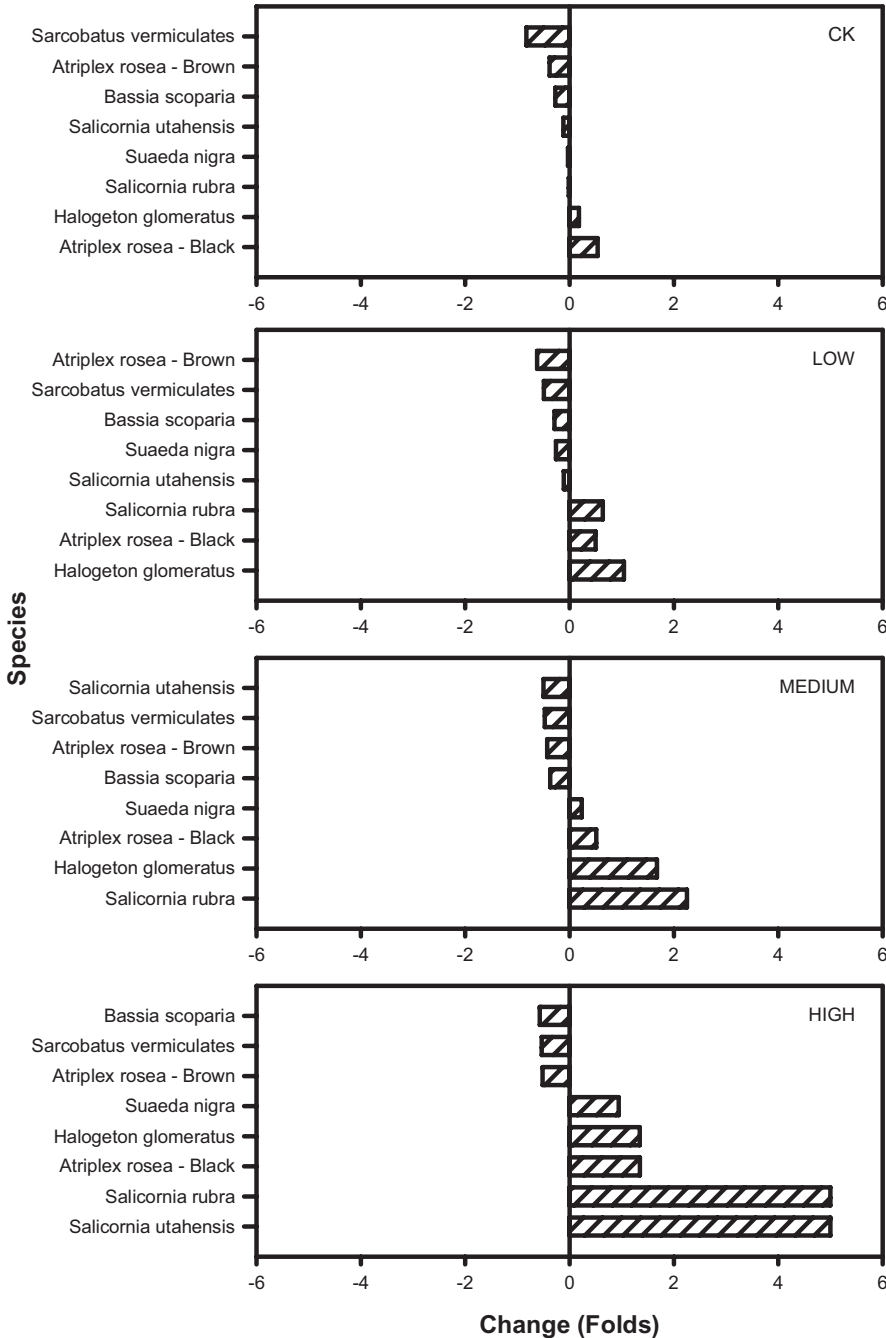


**Fig. 6.6** Effects of Kinetin on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Kinetin

2008). Populations found in habitats with high soil salinity generally have higher salt tolerance than those found in less saline habitats (Debez et al. 2001; Ghars et al. 2009; Gul et al. 2013). However, salt tolerance of plants during their seed

germination is generally 10–100 times lesser than during mature vegetative phase (Mayer and Poljakoff-Mayber 1975; Hameed and Khan 2011).

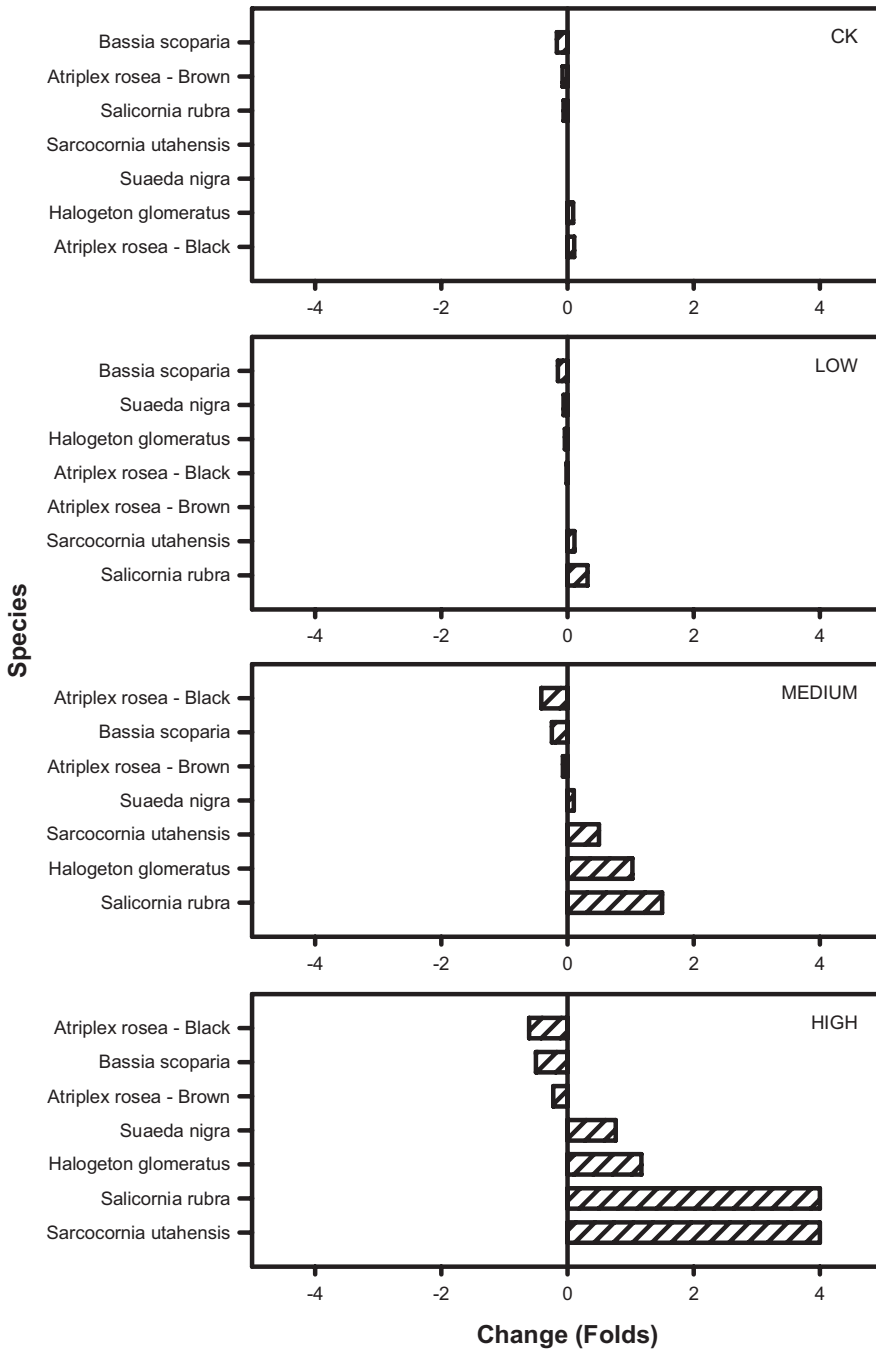
Salinity exposure disturbs the endogenous levels of various dormancy regulating chemicals



**Fig. 6.7** Effects of  $KNO_3$  on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without  $KNO_3$

(DRCs) in seeds, which leads to germination inhibition or even loss of seed viability (Atia et al. 2009; Gul et al. 2013; Ahmed et al. 2014; Li et al. 2015). Therefore, exogenous application of

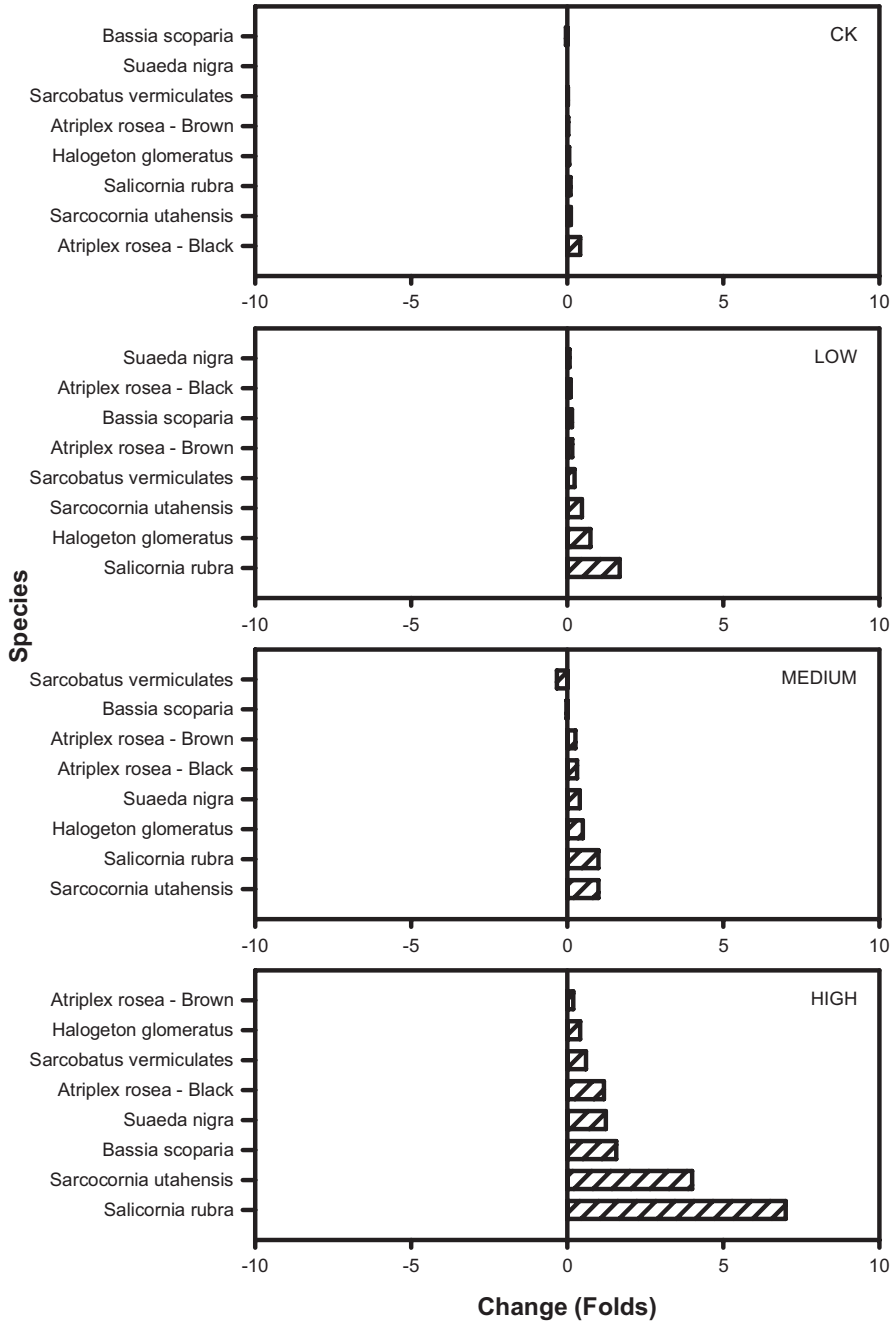
different DRCs such as phyto-hormones and protective compounds is often reported to enhance seed germination under salinity stress (Khan and Gul 2006; El-Keblawy 2013; Li et al. 2005; Khan



**Fig. 6.8** Effects of Proline on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Proline

and Ungar 2001a, b). However, success of chemical treatments applied to seeds depends on multiple factors (Khan and Gul 2006; Cohn 2002). In this study, we observed improvement in

seed germination of Great Basin halophytes by different DRCs, but ameliorative effects were chemical, salinity and species specific. Ahmed et al. (2014) also reported that the ameliorative



**Fig. 6.9** Effects of Thiourea on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Thiourea

effects of DRC treatments for the seeds of salt-playa halophytes of Pakistan *Halogeton glomeratus*, *Lepidium latifolium* and *Peganum harmala* were both species and environment-dependant.

Plant hormone gibberellic acid ( $GA_3$ ) is a key positive regulator of seed germination owing to its signaling in endosperm cap weakening, expansion of embryo cells, expression of  $\alpha$ -amylase

genes, antagonizing effects of ABA and opposing the activities of DELLA proteins (Peng and Harberd 2002; Miransari and Smith 2014). A decline in endogenous GA<sub>3</sub> levels is often reportedly linked to the seed germination inhibition under saline conditions (Kabar and Baltepe 1989; Bewley and Black 1994; Khan and Gul 2006). Exogenous application of GA<sub>3</sub> is thus often used to enhance seed germination of plants under saline conditions (Khan and Gul 2006). In this study, exogenous application of GA<sub>3</sub> could alleviate inhibitory effects of high salinity in nearly all species, but its ameliorative effects were more pronounced in *Salicornia rubra*, *Sarcocornia utahensis* and *Bassia scoparia* as compared to other species. GA<sub>3</sub> application could also mitigate salinity effects on seed germination of *Allenrolfea occidentalis* (Gul and Khan 2008), *Crithmum maritimum* (Atia et al. 2009), *Lepidium latifolium* (Ahmed et al. 2014), *Phragmites karka* (Zehra et al. 2013), *Zygophyllum simplex* (Syn. *Tetraena simplex*) (Khan and Gul 2006) and *Halopyrum mucorantum* (Khan and Ungar 2001a, b) and *Panicum turgidum* (El-Keblawy et al. 2011).

Cytokinins are also plant hormones, which are implicated in a number of plant activities including seed germination (Chiwocha et al. 2005; Riefler et al. 2006; Nikolić et al. 2007). They are also involved in mitigating stresses such as salinity and drought (Khan and Ungar 1997; Atici et al. 2005; Khan and Gul 2006). Kinetin mitigated salinity effects on seed germination of *Sarcocornia utahensis*, *Salicornia rubra* and *Sarcobatus vermiculatus* to higher extent than other test species in this study. A similar effect of kinetin was reported for *Allenrolfea occidentalis* (Gul and Khan 2008), *Atriplex halimus* (Debez et al. 2001) and *Zygophyllum simplex* (Khan and Ungar 1997), but not in *Zygophyllum qatarense* (Ismail 1990), *Sporobolus arabicus* (Khan and Ungar 2001b). These findings thus indicate that responses to kinetin are highly variable. However, Debez et al. (2001) indicated that salinity decreased levels of many endogenous chemical regulators in *Atriplex halimus* during seed germination and exogenous kinetin could improve seed germination probably by overcoming its dwindling endogenous contents.

Ethylene, which is a gaseous plant hormone, is also involved in promoting seed germination particularly under stress conditions (Khan and Gul 2006; Khan et al. 2009). For instance, it alleviated salinity effects on seed germination of many halophytes such as *Triglochin maritima* (Khan et al. 2009) and *Zygophyllum simplex* (Khan et al. 2009). Similarly, in this study, ethephon (a common source of ethylene) treatment also improved germination of salinity-stressed seeds of many halophytes particularly of *Salicornia rubra*, *Krascheninnikovia ceratoides* and *Sarcocornia utahensis*. Ethylene production in salinity-stressed seeds of *Cucumis sativus* decreased with concomitant reduction in their germination (Chang et al. 2010). Similarly, seed germination inhibition in *Stylosanthes* spp. under saline condition was linked to salinity-induced reduction in ethylene production (Silva et al. 2014). However, mechanisms underlying ethylene action in improving seed germination and salt tolerance are yet inconclusive (Khan et al. 2009; Petruzzelli et al. 2000; Rinaldi 2000). A literature search indicates that ethylene might control germination of salt-stressed seeds by interacting with other hormones such as abscisic acid (Linkies et al. 2009; Linkies and Leubner-Metzger 2012), brassinosteroids (Wang et al. 2011) and polyamines (Zapata et al. 2004). While, ethylene alleviated salinity effects on seed germination of model plant *Arabidopsis thaliana* by decreasing reactive oxygen species (Lin et al. 2013).

Fusicoccin, which is a diterpene glycoside initially isolated as a toxin from fungus *Fusicoccum amygdali* (Ballio et al. 1976), is also widely reported to promote seed germination of halophytes (Gul and Weber 1998; Gul et al. 2000; Khan and Gul 2006; El-Keblawy and Al-Shamsi 2008). For example, fusicoccin mitigated salinity effects on seed germination of *Zygophyllum simplex* (Khan and Ungar 2002), *Salsola drummondii* (Rasheed et al. 2015), *Panicum turgidum* and *Lasiurus scindicus* (El-Keblawy et al. 2011). It also improved seed germination of Great Basin halophytes particularly of *Sarcocornia utahensis*, *Krascheninnikovia ceratoides* and *Bassia scoparia* under salinity. It may promote seed germination probably by enhancing cell elongation

growth through ATPase mediated proton extrusion (Galli et al. 1979; Marre 1979). According to Cocucci et al. (1990) fusicocin reversed the inhibitory effects of salinity in *Raphanus sativus* seeds by enhancing H<sup>+</sup> extrusion and malic acid synthesis. While, Lutsenko et al. (2005) suggested that fusicocin affects the ionic balance particularly the K<sup>+</sup>/Na<sup>+</sup> ratio.

Seeds use nitrate (NO<sub>3</sub><sup>-</sup>) as “spatial signal” for the dormancy loss and germination promotion (Alboresi et al. 2005; Huang et al. 2015). Nitrate levels could be a good indicator for seeds to detect gaps, as competing plants deplete soil nitrates (Pons 1989). It can also mitigate effects of various stresses such as of salinity on seed germination of plants. For instance, exogenous NO<sub>3</sub><sup>-</sup> could mitigate salinity-induced germination inhibition in *Crithmum maritimum* (Atia et al. 2009) and *Sporobolus arabicus* (Khan and Ungar 2001b). Similarly, seed germination of our test species especially of *Sarcocornia utahensis* and *Salicornia rubra* was also improved under saline conditions. Action of NO<sub>3</sub><sup>-</sup> in modulating seed germination and dormancy could be ascribed to its role in decreasing seeds’ ABA level probably by inducing expression of *CYP707A2* gene (Ali-Rachedi et al. 2004; Matakadiadis et al. 2009).

Thiourea is another nitrogenous compounds that also contains a redox active thiol (–SH) group and is known to improve germination and salinity tolerance of halophytes seeds (Khan and Gul 2006; El-Keblawy 2013). For example, it could alleviate salinity induced germination inhibition in *Triglochin maritima* (Khan and Ungar 2001a) and *Distichlis spicata* var. *stricta* (Shahba et al. 2008). In this study, thiourea application alleviated salinity-induced germination inhibition of *Salicornia rubra* and *Sarcocornia utahensis* seeds to greater extent than in other species. Action of thiourea in mitigating salinity effects on seed germination could be ascribed to its roles in enhancing the antioxidant defense system (Srivastava et al. 2010), altering the cell’s redox status (Srivastava et al. 2010), controlling membrane kinetics for ion uptake (Aldasoro et al. 1981) and/or regulating activity and turnover of many enzymes (Srivastava et al. 2010).

Exogenous application of glycine betaine (GB) and proline is often reported to enhance salt

tolerance of halophyte seeds. For example, exogenously applied GB and proline improved seed germination of a Great Basin halophyte *Allenrolfea occidentalis* (Gul and Khan 2008) and two subtropical halophytes *Zygophyllum simplex* and in *Arthrocnemum macrostachyum* (Khan and Gul 2006). Similarly, these chemicals could also improve germination of salt-stressed seeds of Great Basin halophytes especially of *Sarcocornia utahensis* and *Salicornia rubra*. Ameliorative effects of these chemical could be linked to their multiple roles in plant stress tolerance. For example, GB and proline are two important osmoprotectants/compatible solutes, which are involved in osmotic adjustment in halophytes in response to salinity (Flowers and Colmer 2008; Hameed and Khan 2011). They might also act as antioxidants to eliminate toxic reactive oxygen species, which are known to accumulate under stress conditions (Chen and Murata 2008, 2011; Szabados and Savouré 2010). Poljakoff-Mayber et al. (1994) reported that *Kosteletzkya virginica* seeds contain significant amounts of GB and proline. GB contents increased during seed germination of *Suaeda japonica* under saline conditions (Yokoishi and Tanimoto 1994).

Efficacy of DRC treatments in this study was generally dependent on magnitude of salinity imposed. Under non-saline conditions nearly all DRCs were ineffective in improve seed germination of halophytes, however their ameliorative effects increased with increases in salinity. Likewise, most DRC treatments were ineffective in enhancing seed germination of *Panicum turgidum*, *Lasiurus scindicus* (El-Keblawy et al. 2011), *Coelachyrum brevifolium*, *Pennisetum divisum* (El-Keblawy 2013) and *Limonium stocksi* (Khan and Gul 2006) under non-saline conditions. Furthermore, in some species such as in *Salsola imbricata* (Mehrun-Nisa and Weber 2007) DRC treatments inhibited the seed germination under non-saline condition. These findings could be explained by the fact that the unstressed seeds contain adequate levels of various DRCs (Miransari and Smith 2014; Khan and Gul 2006; Li et al. 2015), thereby exogenous supply is ineffective or may cause feedback inhibition (Khan and Gul 2006). Extent of amelioration



in seed germination under saline conditions was also dependent on nature of chemicals used. Ethephon, fusicoccin and kinetin were generally more effective than other DRCs used. Aforementioned DRCs were also most effective in alleviating salinity effects on seed germination of most sub-tropical halophytes (Khan and Gul 2006). Likewise, DRC treatments had varying effects on the seed germination of *Crithmum maritimum* (Meot-Duros and Magné 2008), and three salt playa halophytes (Ahmed et al. 2014).

## 5 Conclusions

Great Basin halophytes used in this study lacked innate dormancy and germinated maximally in distilled water. Increases in salinity generally decreased their seed germination; however some ( $\geq 20\%$ ) seeds of nearly all species could germinate in/above 600 mM NaCl (equivalent to seawater salinity). Exogenous application of all DRCs improved seed germination of test species, especially under high salinity. Ethephon, fusicoccin and kinetin treatments were generally most effective. While, *Salicornia rubra* and *Sarcocornia utahensis* responded to nearly all DRCs than other species (Table 6.3). These find-

ings indicate that the efficacy of DRC treatments could be salinity, species and chemical specific. However, detailed biochemical and/or molecular studies are recommended to understand the basis of variability in ameliorative effects of various DRC treatments on seed germination.

## References

- Ahmed MZ, Khan MA (2010) Tolerance and recovery responses of playa halophytes to light, salinity and temperature stresses during seed germination. *Flora* 205:764–771
- Ahmed MZ, Gulzar S, Khan MA (2014) Role of dormancy regulating chemicals in alleviating the seed germination of three playa halophytes. *Ekoloji* 23:1–8
- Alboresi A, Gestin C, Leydecker MT, Bedu M, Meyer C, Truong HN (2005) Nitrate, a signal relieving seed dormancy in *Arabidopsis*. *Plant Cell Environ* 28:500–512
- Aldasoro JJ, Matilla A, Nicolás G (1981) Effect of ABA, fusicoccin and thiourea on germination and  $K^+$  and glucose uptake in chick-pea seeds at different temperatures. *Physiol Plant* 53:139–145
- Ali-Rachedi S, Bouinot D, Wagner MH, Bonnet M, Sotta B, Grappin P, Jullien M (2004) Changes in endogenous abscisic acid levels during dormancy release and maintenance of mature seeds: studies with the Cape Verde Islands ecotype, the dormant model of *Arabidopsis thaliana*. *Planta* 219:479–488
- Atia A, Debez A, Barhoumi Z, Smaoui A, Abdelly C (2009) ABA, GA 3, and nitrate may control seed germination of *Crithmum maritimum* (Apiaceae) under saline conditions. *C R Biol* 332(8):704–710
- Atici Ö, Açar G, Battal P (2005) Changes in phytohormone contents in chickpea seeds germinating under lead or zinc stress. *Biol Plant* 49:215–222
- Ballio A, d'Alessio V, Randazzo G, Botalico A, Graniti A, Sparapano L, Gribanovski-Sassu O (1976) Occurrence of fusicoccin in plant tissues infected by *Fusicoccum amygdali* Del. *Physiol Plant Pathol* 8:163–169
- Bewley JD, Black M (1994) *Seeds: physiology of development and germination*. Plenum Press, New York
- Billings WD (1945) *The plant associations of the Carson Desert region, Western Nevada*. Butler University. *Bot Stud* 7:89–123
- Chang C, Wang B, Shi L, Li Y, Duo L, Zhang W (2010) Alleviation of salt stress-induced inhibition of seed germination in cucumber (*Cucumis sativus* L.) by ethylene and glutamate. *J Plant Physiol* 167:1152–1156
- Chapman VJ (1960) *Salt marshes and salt deserts of the world*. Interscience, New York
- Chen TH, Murata N (2008) Glycinebetaine: an effective protectant against abiotic stress in plants. *Trends Plant Sci* 13:499–505

**Table 6.3** Top species, in order of magnitude, showing positive effects of DRCs on seed germination

DRC	Species
Ethephon	<i>Salicornia rubra</i> , <i>Krascheninnikovia ceratoides</i> , <i>Sarcocornia utahensis</i>
Fusicoccin	<i>Sarcocornia utahensis</i> , <i>Krascheninnikovia ceratoides</i> , <i>Bassia scoparia</i>
Gibberellic acid	<i>Salicornia rubra</i> , <i>Sarcocornia utahensis</i> , <i>Bassia scoparia</i>
Glycine betaine	<i>Sarcocornia utahensis</i> , <i>Salicornia rubra</i> , <i>Bassia scoparia</i>
Kinetin	<i>Sarcocornia utahensis</i> , <i>Salicornia rubra</i> , <i>Sarcobatus vermiculatus</i>
Nitrate	<i>Sarcocornia utahensis</i> , <i>Salicornia rubra</i>
Proline	<i>Sarcocornia utahensis</i> , <i>Salicornia rubra</i> , <i>Halogeton glomeratus</i>
Thiourea	<i>Salicornia rubra</i> , <i>Sarcocornia utahensis</i>

- Chen TH, Murata N (2011) Glycinebetaine protects plants against abiotic stress: mechanisms and biotechnological applications. *Plant Cell Environ* 34:1–20
- Chiwocha SD, Cutler AJ, Abrams SR, Ambrose SJ, Yang J, Ross AR, Kermode AR (2005) The *etr1-2* mutation in *Arabidopsis thaliana* affects the abscisic acid, auxin, cytokinin and gibberellin metabolic pathways during maintenance of seed dormancy, moist-chilling and germination. *Plant J* 42:35–48
- Cocucci SM, Morgutti S, Abruzzese A, Alisi C (1990) Response to osmotic medium and fusicoccin by seeds of radish (*Raphanus sativus*) in the early phase of germination. *Physiol Plant* 80:294–300
- Cohn MA (2002) Reflections on investigating dormancy-breaking chemicals—a balance of logic and luck. *Weed Sci* 50:261–266
- Debez A, Chaibi W, Bouzid S (2001) Effect of NaCl and growth regulators on germination of *Atriplex halimus* L. *Cah Agric* 10:135–138
- Easton LC, Kleindorfer S (2008) Interaction effects of seed mass and temperature on germination in Australian species of *Frankenia* (Frankeniaceae). *Fol Geobotanica* 43:383–396
- El-Keblawy A (2004) Salinity effects on seed germination of the common desert range grass, *Panicum turgidum*. *Seed Sci Technol* 32:873–878
- El-Keblawy A (2013) Effects of seed storage on germination of two succulent desert halophytes with little dormancy and transient seed bank. *Acta Ecol Sin* 33:338–343
- El-Keblawy A, Al-Shamsi N (2008) Effects of salinity, temperature and light on seed germination of *Haloxylon salicornicum*, a common perennial shrub of the Arabian deserts. *Seed Sci Technol* 36:679–688
- El-Keblawy A, Al-Ansari F, Al-Shamsi N (2011) Effects of temperature and light on salinity tolerance during germination in two desert glycophytic grasses, *Lasiurus scindicus* and *Panicum turgidum*. *Grass Forage Sci* 66:173–182
- Eriksson O, Fröborg H (1996) “Windows of opportunity” for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. *Can J Bot* 74:1369–1374
- Fisher KD (1974) Cartographic study of Lake Bonneville. Master’s thesis, Brigham Young University
- Flowers TJ, Colmer TD (2008) Salinity tolerance in halophytes. *New Phytol* 179:945–963
- Galli MG, Miracca P, Sparvoli E (1979) Interaction between abscisic acid and fusicoccin during germination and post-germinative growth in *Haplopappus gracilis*. *Plant Sci Lett* 14:105–111
- Ghars MA, Debez A, Abdelly C (2009) Interaction between salinity and original habitat during germination of the annual seashore halophyte *Cakile maritima*. *Commun Soil Sci Plant Anal* 40:3170–3180
- Gul B, Khan MA (2008) Effect of compatible osmotic and plant growth regulators in alleviating salinity stress on the seed germination of *Allenrolfea occidentalis*. *Pak J Bot* 40:1957–1964
- Gul B, Weber DJ (1998) Role of dormancy relieving compounds and salinity on the seed germination of *Allenrolfea occidentalis*. *Ann Bot* 82:555–562
- Gul B, Khan MA, Weber DJ (2000) Alleviation of salinity and dark-enforced dormancy in *Allenrolfea occidentalis* seeds under various thermoperiods. *Aust J Bot* 48:745–752
- Gul B, Khan MA, Weber DJ (2001) Seed germination of *Sarcobatus vermiculatus*: a halophytic shrub from Great Basin Desert. *Pak J Bot* 33:28–37
- Gul B, Ansari R, Flowers TJ, Khan MA (2013) Germination strategies of halophyte seeds under salinity. *Environ Exp Bot* 92:4–18
- Gulzar S, Khan MA (2002) Alleviation of salinity-induced dormancy in perennial grasses. *Biol Plant* 45:617–619
- Hameed A, Khan MA (2011) Halophytes: biology and economic potentials. *Karachi University J Sci* 39:40–44
- Hameed A, Ahmed MZ, Gulzar S, Gul B, Alam J, Hegazy AK, Alatar ARA, Khan MA (2013) Seed germination and recovery responses of *Suaeda heterophylla* to abiotic stresses. *Pak J Bot* 45:1649–1656
- Hameed A, Rasheed A, Gul B, Khan MA (2014) Salinity inhibits seed germination of perennial halophytes *Limonium stocksii* and *Suaeda fruticosa* by reducing water uptake and ascorbate dependent antioxidant system. *Environ Exp Bot* 107:32–38
- Huang Z, Zhang X, Zheng G, Gutterman Y (2003) Influence of light, temperature, salinity and storage on seed germination of *Haloxylon ammodendron*. *J Arid Environ* 55:453–464
- Huang Z, Ölçer-Footitt H, Footitt S, Finch-Savage WE (2015) Seed dormancy is a dynamic state: variable responses to pre- and post-shedding environmental signals in seeds of contrasting *Arabidopsis* ecotypes. *Seed Sci Res* 25:159–169
- 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
- Kabar K, Baltepe S (1989) Effect of kinetin and gibberellic acid in overcoming high temperature and salinity (NaCl) stresses on the germination of barely and lettuce seeds. *Phyton* 30:65–74
- Khan MA, Gul B (2006) Halophyte seed germination. In: *Ecophysiology of high salinity tolerant plants*. Springer, Netherlands, pp 11–30
- Khan MA, Ungar IA (1984) The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. *Am J Bot* 71:481–489
- 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 (2001a) Effect of dormancy regulating chemicals on the germination of *Triglochin maritima*. *Biol Plant* 44:301–303

- Khan MA, Ungar IA (2001b) 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 (2002) Influence of dormancy regulating compounds and salinity on the germination of *Zygophyllum simplex* L. seeds. *Seed Sci Technol* 30:507–514
- Khan MA, Ahmed MZ, Hameed A (2006) Effect of sea salt and L-ascorbic acid on the seed germination of halophytes. *J Arid Environ* 67:535–540
- Khan MA, Ansari R, Gul B, Li W (2009) Dormancy and germination responses of halophyte seeds to the application of ethylene. *C R Biol* 332:806–815
- Li W, Liu X, Khan MA, Yamaguchi S (2005) The effect of plant growth regulators, nitric oxide, nitrate, nitrite and light on the germination of dimorphic seed of *Suaeda salsa* under saline conditions. *J Plant Res* 118:207–214
- Li J, Yin LY, Jongsma MA, Wang CY (2011) Effect of light, hydro-priming and abiotic stress on seed germination, and shoot and root growth pyrethrum (*Tanacetum cinerariifolium*). *Ind Crop Prod* 34:1543–1549
- Li W, Khan MA, Yamaguchi S, Liu X (2015) Hormonal and environmental regulation of seed germination in salt cress (*Theellungiella halophila*). *Plant Growth Regul* 76:41–49
- Linkies A, Leubner-Metzger G (2012) Beyond gibberellins and abscisic acid: how ethylene and jasmonates control seed germination. *Plant Cell Rep* 31:253–270
- Linkies A, Müller K, Morris K, Turečková V, Wenk M, Cadman CS, Leubner-Metzger G (2009) Ethylene interacts with abscisic acid to regulate endosperm rupture during germination: a comparative approach using *Lepidium sativum* and *Arabidopsis thaliana*. *Plant Cell* 21:3803–3822
- Liu X, Qiao H, Li W, Tadano T, Khan MA, Yamaguchi S, Kamiya Y (2006) Comparative effect of NaCl and seawater on seed germination of *Suaeda salsa* and *Atriplex centralasiatica*. In: Ozturk M, Waisel Y, Khan MA, Gork G (eds) *Biosaline agriculture and salinity tolerance in plants*. Birkhauser, Berlin, pp 45–54
- Lutsenko EK, Marushko EA, Kononenko NV, Leonova TG (2005) Effects of fusicoccin on the early stages of sorghum growth at high NaCl concentrations. *Russ J Plant Physiol* 52:332–337
- Marre E (1979) Fusicoccin: a tool in plant physiology. *Annu Rev Plant Physiol* 30:273–288
- Matakiadis T, Alboresi A, Jikumaru Y, Tatematsu K, Pichon O, Renou JP, Truong HN (2009) The *Arabidopsis* abscisic acid catabolic gene CYP707A2 plays a key role in nitrate control of seed dormancy. *Plant Physiol* 149:949–960
- Mayer AM, Poljakoff-Mayber A (1975) *The germination of seeds*. Pergamon Press/The Macmillan Co, New York
- Mehr-un-Nisa, Khan MA, Weber DJ (2007) Dormancy, germination and viability of *Salsola imbricata* seeds in relation to light, temperature and salinity. *Seed Sci Technol* 35:595–606
- Meot-Duros L, Magné C (2008) Effect of salinity and chemical factors on seed germination in the halophyte *Crithmum maritimum* L. *Plant Soil* 313:83–87
- Miransari M, Smith DL (2014) Plant hormones and seed germination. *Environ Exp Bot* 99:110–121
- Nikolić R, Mitić N, Živković S, Grubišić D, Nešković M (2007) Cytokinins and urea derivatives stimulate seed germination in *Lotus corniculatus* L. *Arch Biol Sci* 59:125–128
- Noe GB, Zedler JB (2001) Variable rainfall limits the germination of upper intertidal marsh plants in southern California. *Estuaries* 24:30–40
- Peng J, Harberd NP (2002) The role of GA-mediated signalling in the control of seed germination. *Curr Opin Plant Biol* 5:376–381
- Petrzell L, Coraggio I, Leubner-Metzger G (2000) Ethylene promotes ethylene biosynthesis during pea seed germination by positive feedback regulation of 1-aminocyclo-propane-1-carboxylic acid oxidase. *Planta* 211:144–149
- Poljakoff-Mayber A, Somers GF, Werker E, Gallagher JL (1994) Seeds of *Kosteletzkya virginica* (Malvaceae): their structure, germination, and salt tolerance. II. Germination and salt tolerance. *Am J Bot* 81:54–59
- Pons TL (1989) Breaking of seed dormancy by nitrate as a gap detection mechanism. *Ann Bot* 63:139–143
- Pujol JA, Calvo JF, Ramírez-Díaz L (2001) Seed germination, growth, and osmotic adjustment in response to NaCl in a rare succulent halophyte from southeastern Spain. *Wetlands* 21:256–264
- Ramoliya PJ, Pandey AN (2002) Effect of increasing salt concentration on emergence, growth and survival of seedlings of *Salvadora oleoides* (Salvadoraceae). *J Arid Environ* 51:121–132
- Rasheed A, Hameed A, Khan MA, Gul B (2015) Effects of salinity, temperature, light and dormancy regulating chemicals on seed germination of *Salsola drummondii* Ulbr. *Pak J Bot* 47:11–19
- Redondo S, Rubio-Casal AE, Castillo JM, Luque CJ, Álvarez AA, Luque T, Figueroa ME (2004) Influences of salinity and light on germination of three *Sarcocornia* taxa with contrasted habitats. *Aquat Bot* 78:255–264
- Richards WH (1982) Cation content of leaves of desert shrubs and its relationship to taxonomic and ecological classification. *Am Midl Nat* 108:311–316
- Riefler M, Novak O, Strnad M, Schömlling T (2006) *Arabidopsis* cytokinin receptor mutants reveal functions in shoot growth, leaf senescence, seed size, germination, root development, and cytokinin metabolism. *Plant Cell* 18:40–54
- Rinaldi LMR (2000) Germination of seeds of olive (*Olea europaea* L.) and ethylene production: effects of harvesting time and thidiazuron treatment. *J Hort Sci Biotechnol* 75:727–732

- Shahba MA, Qian YL, Lair KD (2008) Improving seed germination of saltgrass under saline conditions. *Crop Sci* 48:756–762
- Silva PO, Medina EF, Barros RS, Ribeiro DM (2014) Germination of salt-stressed seeds as related to the ethylene biosynthesis ability in three *Stylosanthes* species. *J Plant Physiol* 171:14–22
- SPSS (2011) Software SPSS Version 11.0, SPSS Inc
- Srivastava AK, Ramaswamy NK, Suprasanna P, D'Souza SF (2010) Genome-wide analysis of thiourea-modulated salinity stress-responsive transcripts in seeds of *Brassica juncea*: identification of signalling and effector components of stress tolerance. *Ann Bot* 106:663–674
- Szabados L, Savouré A (2010) Proline: a multifunctional amino acid. *Trends Plant Sci* 15:89–97
- Timson J (1965) New method of recording germination data. *Nature* 207:216–217
- Ungar IA (1978) Halophyte seed germination. *Bot Rev* 44:233–264
- Vicente MJ, Conesa E, Álvarez-Rogel J, Franco JA, Martínez-Sánchez JJ (2007) Effects of various salts on the germination of three perennial salt marsh species. *Aquat Bot* 87:167–170
- Wang L, Huang Z, Baskin CC, Baskin JM, Dong M (2008) Germination of dimorphic seeds of the desert annual halophyte *Suaeda aralocaspica* (Chenopodiaceae), a C4 plant without kranz anatomy. *Ann Bot* 102:757–769
- Wang B, Zhang J, Xia X, Zhang WH (2011) Ameliorative effect of brassinosteroid and ethylene on germination of cucumber seeds in the presence of sodium chloride. *Plant Growth Regul* 65:407–413
- Welsh SL, Atwood ND, Goodrich S, Higgins LC (1987) A Utah flora. *Great Basin Naturalist Mem* 9:1–894
- Yao S, Lan H, Zhang F (2010) Variation of seed heteromorphism in *Chenopodium album* and the effect of salinity stress on the descendants. *Ann Bot* 105:1015–1025
- Yıldız M, Cenkci S, Kargioglu M (2008) Effects of salinity, temperature, and light on seed germination in two Turkish endemic halophytes, *Limonium iconicum* and *L. lilacinum* (Plumbaginaceae). *Seed Sci Technol* 36:646–656
- Yokoishi T, Tanimoto S (1994) Seed germination of the halophyte *Suaeda japonica* under salt stress. *J Plant Res* 107:385–388
- Zapata PJ, Serrano M, Pretel MT, Amorós A, Botella MÁ (2004) Polyamines and ethylene changes during germination of different plant species under salinity. *Plant Sci* 167:781–788
- Zehra A, Gul B, Ansari R, Alatar ARA, Hegazy AK, Khan MA (2013) Action of plant growth regulators in alleviating salinity and temperature effects on the germination of *Phragmites karka*. *Pak J Bot* 45:1919–1924
- Zia S, Khan MA (2004) Effect of light, salinity and temperature on the germination of *Limonium stocksii*. *Can J Bot* 82:151–157