

COMPARISON OF SEED GERMINATION AND RECOVERY RESPONSES OF A SALT MARSH HALOPHYTE *HALOPEPLIS PERFOLIATA* TO OSMOTIC AND IONIC TREATMENTS

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Abstract

Salinity affects seed germination of halophytes by inducing ionic toxicity, osmotic constraint or both. Information about the effects of salinity on seed germination of a large number of halophytes exists, but generally little is known about the basis of salinity-induced germination inhibition. In order to partition salinity effects, we studied seed germination and recovery responses of a coastal salt marsh halophyte *Halopeplis perfoliata* to different isotonic treatments (Ψ_s : -0.5, -1.0, -1.5, -2.0 and -2.5, MPa) of various salts and polyethylene glycol (PEG) under two light regimes (12-h light photoperiod and 24-h complete darkness). Highest seed germination was observed in distilled water under 12-h light photoperiod and reduction in osmotic potential of the solution decreased seed germination. However, some seeds of *H. perfoliata* could germinate in as low as -2.5 MPa (~600 mM NaCl), which is equivalent to seawater salinity. Sea-salt treatment was more inhibitory than isotonic NaCl at the lowest osmotic potential (Ψ_s -2.5 MPa). Generally, chloride salts with lowest Ψ_s inhibited germination more than the isotonic sulfate salts. Comparable germination responses of the seeds in NaCl and isotonic PEG treatments as well as high recovery of germination in un-germinated seeds after alleviation of NaCl salinity indicated prevalence of osmotic constraint. These results thus indicate that the seeds of *H. perfoliata* could tolerate high levels of a wide variety of salts found in soil.

Key words: Dormancy, Halophyte, Salinity, Seed germination, Ionic toxicity, Osmotic potential.

Introduction

Coastal salt marshes are transition between marine and terrestrial ecosystems, characterized by highly salt tolerant halophyte vegetation and offer a number of ecological and economic services to mankind (Böer, 1996; Pennings & Bertness 2001; Lee *et al.*, 2006; Gedan *et al.*, 2009; Teixeira *et al.*, 2014). These habitats are however under threat due to various natural and anthropogenic reasons (Yasseen & Al-Thani, 2007; Gedan *et al.*, 2011; Ramadan *et al.*, 2013). Therefore, salt marsh ecosystems warrant special attention in research, which would eventually help in their protection and conservation. Establishment of plants in salt marshes is reportedly dependant on the seed germination responses which are influenced by a number of factors especially salt concentrations in the marsh sediments (Pujol *et al.*, 2000; Khan *et al.*, 2001; Hameed *et al.*, 2006; Gul *et al.*, 2013). However, data on seed germination responses of succulent halophytes of subtropical salt marshes is scanty (Saeed *et al.*, 2011; Gul *et al.*, 2013).

Seeds of salt marsh halophytes are directly influenced by seawater owing to diurnal and seasonal inundations (Gul & Khan, 1998; Gul *et al.*, 2013; Teixeira *et al.*, 2014). NaCl is although dominant but other chloride and sulfate salts and their interactions may also play a significant role in germination, radical emergence and seedling growth of coastal halophytes (Gul & Khan, 1998; Khan, 2003; Zia & Khan, 2008). Most research on the seed germination of halophytes has focused on responses to NaCl (reviewed by Gul *et al.*, 2013), with few studies on comparison of the effects of NaCl and sea-

salt (Zia & Khan, 2002; Atia *et al.*, 2006; Hameed *et al.*, 2006; Liu *et al.*, 2006; Saeed *et al.*, 2011; Shaikh *et al.*, 2013) and even fewer studies on effects of different salts (Ungar, 1991; Egan *et al.*, 1997; Dashtkeyan, 2000; Panuccio *et al.*, 2014). Likewise, investigations to partition osmotic and ionic constraints of various salts (Munns *et al.*, 1995) by comparing their effects on seed germination with germination responses in non-ionic solutes such as polyethylene glycol (PEG) are also limited and inconclusive (Tobe *et al.*, 2000; Sosa *et al.*, 2005; Hameed *et al.*, 2013).

Halopeplis perfoliata Forssk. (Amaranthaceae) is a succulent halophyte of coastal salt marshes along Arabian Peninsula (Al-Oudat & Qadir, 2011), where it acts as an important primary producer and provides shelter to marine life (Pilcher *et al.*, 2003). An earlier report showed that the seeds of *H. perfoliata* can germinate in up to 250 mM NaCl treatment (Mahmoud *et al.*, 1983). Besides, this important perennial plant appears largely unstudied. This study was therefore designed to comparatively investigate the effects of 1) sea-salt 2) various chloride and sulfate salts and 3) polyethylene glycol 6000 (PEG-6000) on germination and recovery of the seeds of *H. perfoliata*.

Materials and Methods

Study site and seed collection: Seeds of *Halopeplis perfoliata* were collected from the coast of Jizan, Saudia Arabia in 2012. Seeds were separated from inflorescence husk manually and the surface was sterilized using 1% bleach solution for 1 minute, followed by rinsing with distilled water and air-drying in laboratory.

Treatments and experimental conditions: Germination experiments were carried out in clear-lid plastic Petri plates (50mm diameter x 15 mm depth) with 5 ml of test solution. Seeds were immersed in distilled water (0 MPa) and isotonic solutions of various salts (NaCl, Na₂SO₄, KCl, K₂SO₄, MgCl₂, MgSO₄, CaCl₂ and sea-salt) and polyethylene glycol 6000 (PEG). Five isotonic levels (Ψ_s : -0.5, -1.0, -1.5, -2.0 and -2.5, MPa) were used. The osmotic potential of the above solutions was measured with Vapor Pressure Osmo-meter (5520 Wescor, Inc.). There were four replicates of 25 seeds each per treatment. The Petri plates were placed in programmed incubators maintained at 20/30°C (optimum temperature for the seed germination of sub-tropical halophytes, Gul *et al.*, 2013), where low temperature coincided with 12-h dark and high temperature with 12-h light ($\sim 25 \mu \text{mol m}^{-2} \text{s}^{-1}$, 400-750 nm, Philips cool-white fluorescent lamps). Seed germination percentage (embryo protrusion, Bewley & Black, 1994) was recorded at 2d intervals for 20d. Rate of germination was estimated by using a modified Timson index of germination velocity given below:

$$\text{Germination velocity} = \frac{\Sigma G}{t}$$

where, G is the percentage of seed germination at 2d intervals and t is the total germination period (Khan & Ungar, 1985). The greater the value, the more rapid is germination. After 20d un-germinated seeds were transferred to distilled water for another 20d and recovery of germination (R_s) from various osmotic treatments of solutes (salts and PEG) was recorded. The recovery percentage was determined by counting the recovered seeds from total number of seeds. The recovery percentage was calculated by using given formula:

$$\text{Recovery (\%)} = \frac{(A - B)}{C} \times 100$$

where, A is total number of seeds germinated after being transferred to distilled water, B is the number of seeds germinated in saline solution and C is total number of

seeds. A parallel set of experiment was conducted by placing Petri plates in dark-envelops under aforementioned temperature and osmotic treatments for 20d. Germination of this experiment was noted once after 20d. After 20d un-germinated seeds were exposed to light in order to study the recovery of germination from dark (R_D).

Statistical analyses: Data were statistically analyzed by using SPSS version 11.0 (SPSS, 2011). Analysis of variance (ANOVA) was performed to determine if various treatments affected the seed germination parameters significantly. A Bonferroni post-hoc was conducted to indicate significant ($p < 0.05$) differences among mean values.

Results

Comparison of the effects of NaCl and sea-salt: A four-way ANOVA indicated significant effects of anions, photoperiod and osmotic potential (Ψ_s) but not of cations on mean final germination (MFG) of *H. perfoliata* seeds (Table 1). Seeds were non-dormant and germinated maximally ($\sim 90\%$) in distilled water under 12-h photoperiod (Fig. 1). Effects of NaCl and sea-salt were comparable in up to -1.0 MPa, wherein there was maximal ($\sim 90\%$) MFG as in distilled water under 12-h photoperiod (Fig. 1). While, in lowest (-2.5 MPa) Ψ_s treatment, sea-salt (MFG = $\sim 10\%$) was found more inhibitory than NaCl (MFG = $\sim 25\%$). Rate of germination in -2.5 MPa was also lowest in sea-salt compared to NaCl (Fig. 2). Un-germinated seeds from low Ψ_s treatments of both NaCl and sea-salt, showed recovery (R_s) when transferred to distilled water and almost all un-germinated seeds recovered (Fig. 1). Dark inhibited seed germination of test species in both NaCl and sea-salt treatments (Fig. 3). When un-germinated seeds from dark were transferred to 12-h photoperiod for another 20d, a significant recovery (R_D) was seen in either salt type. Still un-germinated seeds from low Ψ_s treatments of both NaCl and sea-salt showed complete recovery (R_s) when transferred to distilled water (Fig. 3).

Table 1. Analysis of Variance (ANOVA) indicating effects of cation, anion, photoperiod (Photo) and osmotic potential (Ψ_s) on mean final germination (MFG), germination rate (GR) and recovery of germination (REC) of *Halopeplis perfoliata* seeds.

| Factors | MFG | REC | GR |
|-----------------------------------|--------------------|--------------------|-----------|
| Cation | 2.16 ^{ns} | 1.96 ^{ns} | 5.713** |
| Anion | 13.63*** | 0.53 ^{ns} | 28.65*** |
| Photo | 4341.52*** | 372.55*** | - |
| Ψ_s | 98.5*** | 4.02** | 500.63*** |
| Cation x Anion | 2.46 ^{ns} | 9.20*** | 10.58*** |
| Cation x Photo | 2.35 ^{ns} | 9.08*** | - |
| Anion x Photo | 14.39*** | 45.74*** | - |
| Cation x Anion x Photo | 2.26 ^{ns} | 3.51* | - |
| Cation x Ψ_s | 0.78 ^{ns} | 1.58 ^{ns} | 4.29*** |
| Anion x Ψ_s | 4.65*** | 5.45*** | 9.31*** |
| Cation x Anion x Ψ_s | 2.91** | 2.91** | 16.72*** |
| Photo x Ψ_s | 97.76*** | 189.41*** | - |
| Cation x Photo x Ψ_s | 0.74 ^{ns} | 1.45 ^{ns} | - |
| Anion x Photo x Ψ_s | 4.50** | 3.13** | - |
| Cation x Anion x Photo x Ψ_s | 2.95** | 1.99* | - |

Numbers are F -values. Where, ns = Non-significant, * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$

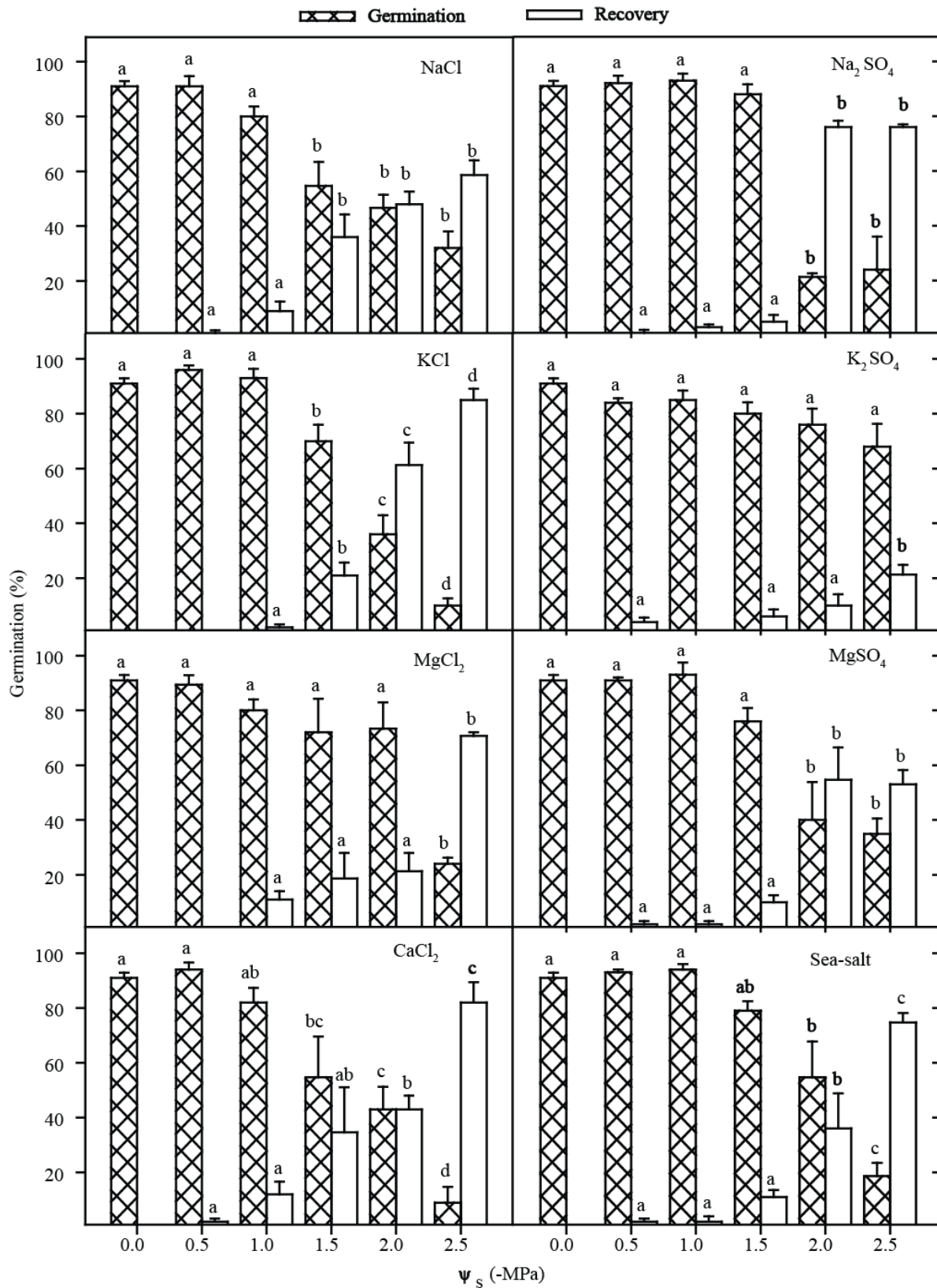


Fig. 1. Effects of NaCl, Na_2SO_4 , KCl, K_2SO_4 , $MgCl_2$, $MgSO_4$, $CaCl_2$ and sea-salt on mean final germination (MFG) and germination recovery in distilled water (R_S) under 12-h photoperiod at 20/30°C. Bars are means \pm standard error. Similar bars with different alphabets are significantly different from each other (Bonferroni test; $p < 0.05$).

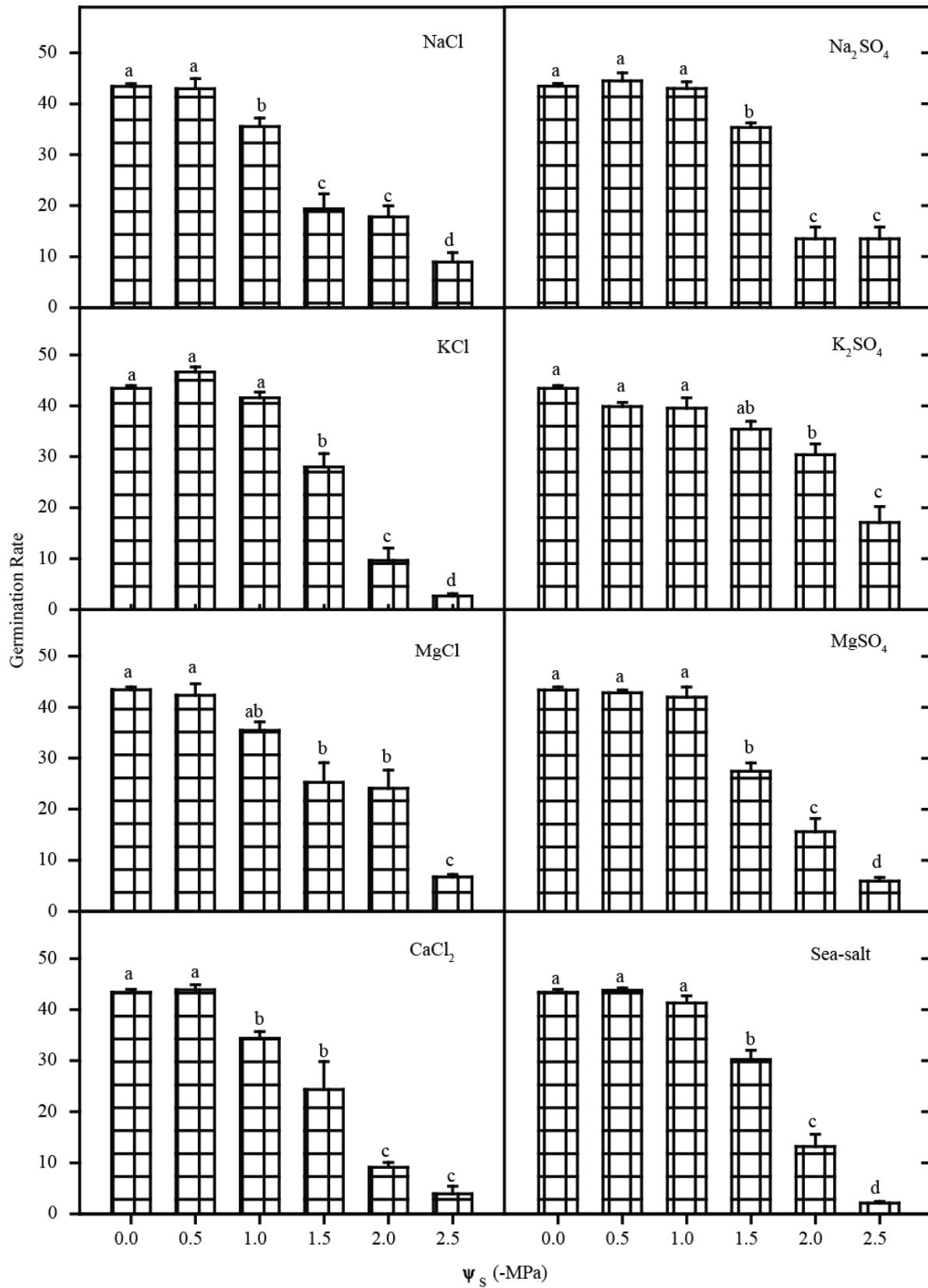


Fig. 2. Effects of NaCl, Na₂SO₄, KCl, K₂SO₄, MgCl₂, MgSO₄, CaCl₂ and sea-salt on rate of germination under 12-h photoperiod at 20/30°C. Bars are means ± standard error. Bars with different alphabets are significantly different from each other (Bonferroni test; $p < 0.05$).

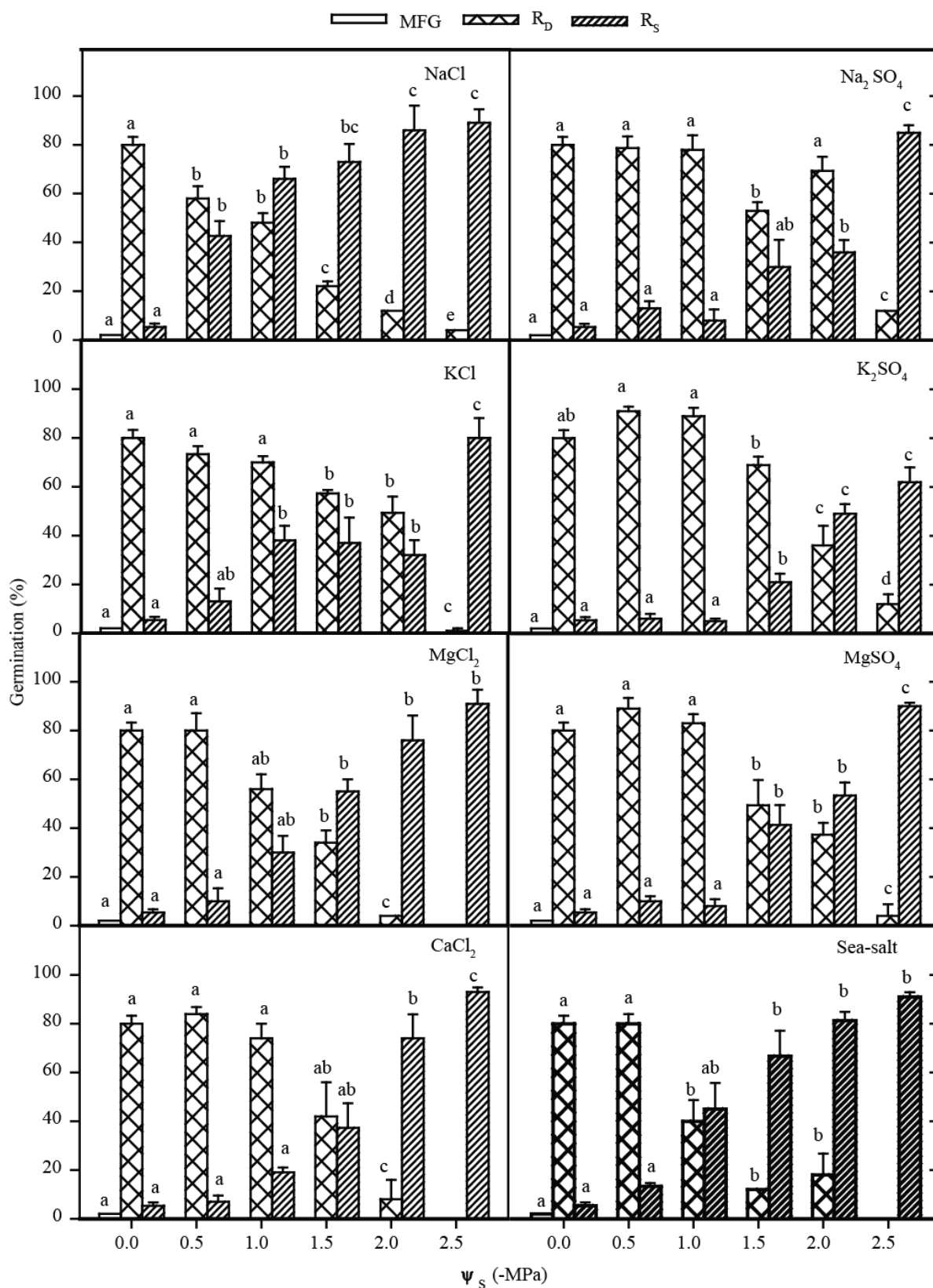


Fig. 3. Effects of isotonic treatments of NaCl, Na_2SO_4 , KCl, K_2SO_4 , $MgCl_2$, $MgSO_4$, $CaCl_2$ and sea-salt on mean final germination (MFG), recovery from Dark (R_D) and recovery from Salinity (R_S) under 24-h dark at 20/30°C. Bars are means \pm standard error. Similar bars with different alphabets are significantly different from each other (Bonferroni test; $p < 0.05$).

Comparison of the effects of different salts: A decrease of up to -1.0 MPa (equivalent to 215 mM NaCl) for chloride salts and -1.5 MPa (equivalent to 400 mM NaCl) for sulfate salts had no inhibitory effect on seed germination of test species (Fig. 1). K_2SO_4 was less inhibitory, in which over 70% seeds germinated in lowest (-2.5 MPa) Ψ_s treatment. On the other hand, $CaCl_2$ and NaCl reduced MFG to ~50% in -1.5 MPa treatments (Fig. 1). Inhibitory effects of chloride salts were in following order: $CaCl_2 > NaCl > KCl > MgCl_2$. While, MFG inhibition among sulfate salts was as follows: $Na_2SO_4 > MgSO_4 > K_2SO_4$. Rate of germination also decreased with decreases in Ψ_s of salts (Fig. 2). However, there was a significant decrease in rate of germination in -1.0 MPa for chloride salts and in -1.5 MPa for sulfate salts. While similar to MFG, NaCl and $CaCl_2$ had higher inhibition and K_2SO_4 caused less inhibition to the rate of germination (Fig. 2). Almost all un-germinated seeds showed recovery of germination (R_s) when transferred to distilled water and generally highest R_s was observed from the lowest (-2.5 MPa) Ψ_s treatments of all salts (Fig. 1). Dark caused substantial inhibition to the MFG of *H. perfoliata*, irrespective of the salt type and Ψ_s treatments (Fig. 3). When un-germinated seeds from dark were exposed to 12-h photoperiod after 20d, a significant recovery of germination (R_D) was observed. The R_D was highest in distilled water and there was decrease in R_D in solution of low Ψ_s (Fig. 3). When still un-germinated seeds from low Ψ_s treatments were transferred to distilled water for another 20d, most of them showed recovery of germination (R_s), irrespective of salt used (Fig. 3).

Comparison of the effects of NaCl and PEG: Effects of NaCl and PEG on MFG and germination rate were generally comparable and these germination parameters decreased with decreases in Ψ_s under 12-h photoperiod (Fig. 4A and 4C). Un-germinated seeds from low Ψ_s treatments of both NaCl and PEG showed high recovery (R_s ; Fig. 4B). Dark caused substantial inhibition to MFG (Fig. 4D). Un-germinated seeds from the dark showed high recovery (R_D) upon transfer to 12-h photoperiod condition (Fig. 4E). However, relatively higher R_D was observed in moderately low (-1.0 to -1.5 MPa) PEG compared to isotonic NaCl treatments. Remaining un-germinated seeds from low Ψ_s treatments of both NaCl and PEG germinated (R_s) when transferred to distilled water (Fig. 4F).

Discussion

Seeds of *H. perfoliata* were non-dormant and showed maximum germination (~90%) in distilled water under 12-h photoperiod, as reported for many other marsh halophytes such as *Arthrocnemum indicum* (Saeed *et al.*, 2011), *Limonium stocksii* (Zia & Khan, 2004) and *Aeluropus lagopoides* (Khan & Gulzar, 2003). Gul *et al.* (2013) reviewed that lack of innate dormancy in most subtropical perennial halophytes is probably a common adaptation to take advantage of brief water availability after rains. In addition, seeds of *H. perfoliata* displayed a high salt tolerance, as some seeds could germinate in as high as seawater (-2.5 MPa NaCl) salinity. Seeds of many other Salicornioideae halophytes such as *Arthrocnemum indicum* (Khan & Gul, 1998) and *Sarcocornia ambigua* (Freitas &

Costa, 2014) also showed tolerance to seawater or higher salinity during their seed germination. Furthermore, un-germinated seeds of *H. perfoliata* showed a high recovery of germination when transferred to distilled water from saline solutions like many other perennial halophytes, indicating that salinity treatments resulted in enforced/conditional dormancy and were no detrimental to seed viability (Khan and Gul, 2006; Cao *et al.*, 2014). Hence, it appears that seeds of *H. perfoliata* are well-adapted for saline environment. However, whether these seed responses to NaCl based salinity are comparable to seawater salinity, have seldom been studied.

Most studies on effects of salinity on seed germination of halophytes are based on NaCl treatments and generally little is known about effects of seawater on seed germination of halophytes (Zia & Khan, 2002; Atia *et al.*, 2006; Hameed *et al.*, 2006; Liu *et al.*, 2006; Saeed *et al.*, 2011; Shaikh *et al.*, 2013). In this study, effects of NaCl and sea-salt were comparable in up to -1.0 MPa but at lowest (-2.5 MPa) Ψ_s treatment sea-salt was more inhibitory than isotonic NaCl. Many studies showed that the sea-salt inhibits seed germination more in comparison to NaCl. For instance, higher concentrations (or lower Ψ_s treatments) of sea-salt were more inhibitory for the seed germination of *Limonium stocksii* (Zia & Khan, 2002), *Aeluropus lagopoides*, *Desmostachya bipinnata* and *Suaeda fruticosa* in comparison to NaCl (Hameed *et al.*, 2006). However, NaCl inhibited seed germination of *Hipophae rhamnoides* (Tirmizi *et al.*, 1993) and *Criethum maritimum* (Atia *et al.*, 2006) more as compared to sea-salt. While, effects of NaCl and sea-salt on seed germination of *Haloxylon stocksii* were comparable (Hameed *et al.*, 2006). These results thus indicate that the comparative effects of NaCl and seawater on seed germination of halophytes are species-specific.

Seawater consists of several salts, of which NaCl is the major (>85%) fraction (Murray, 2004; Khan & Gul, 2006). Other notable cations of seawater in order of magnitude are $Mg^{++} > Ca^{++} > K^+$ and SO_4^- is second major anion after Cl^- (Murray, 2004). Typically, these six ions constitute >99% of the seawater (<http://oceanplasma.org/documents/chemistry.html>). Therefore, we examined the effects of these ions on seed germination of coastal marsh halophyte *H. perfoliata* and found significant effect of anions but not of cations on seed germination of test species. A decrease of up to -1.0 MPa (~ 0.2 mol L⁻¹ NaCl) for chloride salts and -1.5 MPa (~ 0.4 mol L⁻¹ NaCl) for sulfate salts had no inhibitory effect on seed germination of test species but a further decrease in Ψ_s of solutions was inhibitory. Likewise, seed germination of three perennial salt marsh halophytes *Arthrocnemum macrostachyum*, *Juncus acutus* and *Schoenus nigricans* was inhibited more in chloride than sulfate salts of sodium and magnesium (Vicente *et al.*, 2007). Seed germination characteristics of *Halostachys caspica* (Assareh *et al.*, 2010), *Haloxylon ammodendron* (Tobe *et al.*, 2004) and *Kalidium capsicum* (Tobe *et al.*, 2002) were also more sensitive to chloride than sulfate salts. These data including ours thus indicate that sulfate salts are comparatively less detrimental to seed germination of many halophytes than isotonic chloride salts. However eco-physiological significance of this differential effect is yet to be determined by further research.

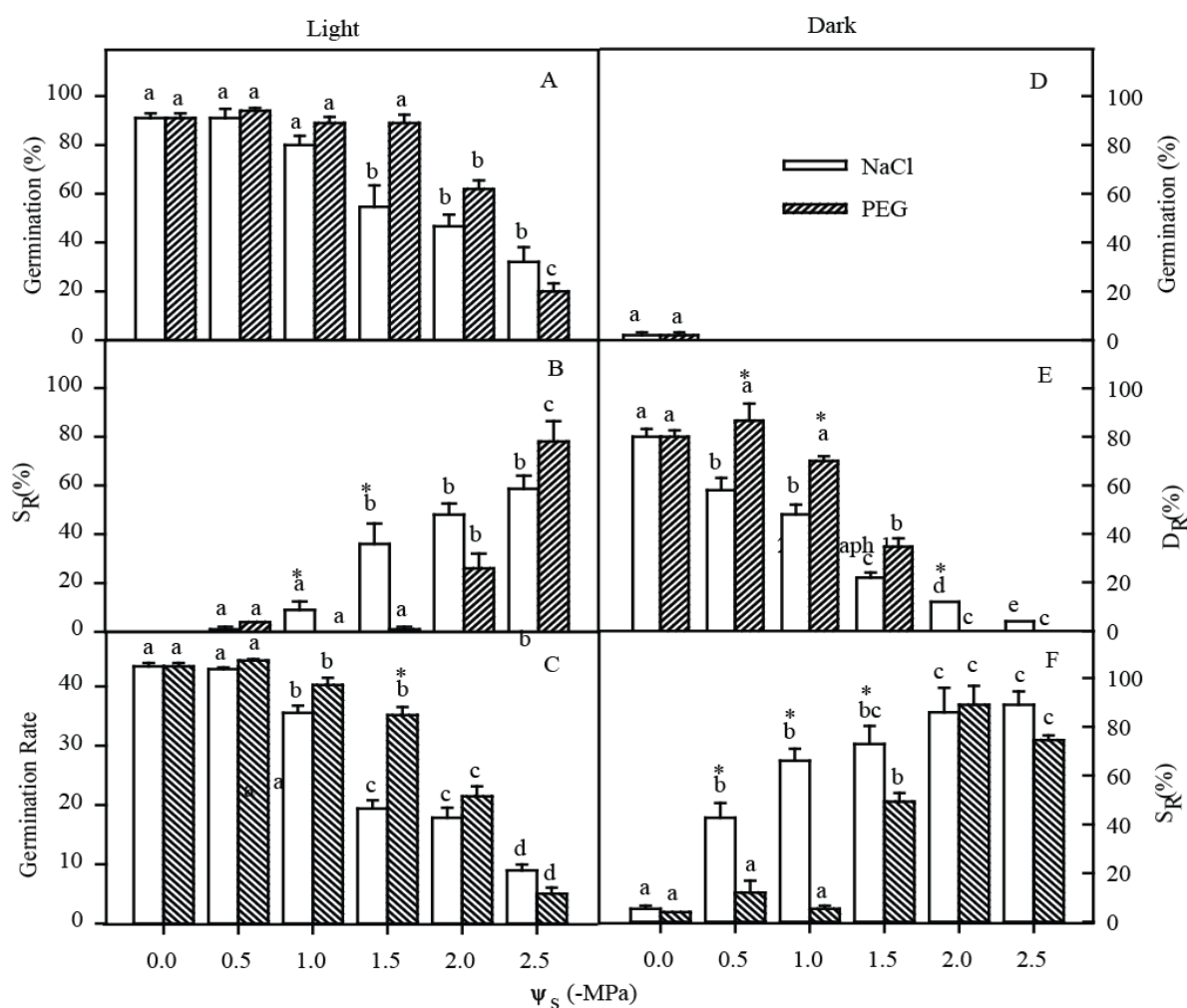


Fig. 4. Comparative effects of NaCl and PEG on mean final germination (MFG), recovery from salinity (R_S) and recovery from dark (R_D) under 12-h photoperiod and 24-h dark at 20/30°C. Bars are means \pm standard error. Similar bars with different alphabets are significantly different from each other (Bonferroni test; $p < 0.05$). Asterisks (*) indicate significant differences in germination within an isotonic treatment of NaCl and PEG (student's t-test; $p < 0.05$).

Salinity affects seed germination by reducing soil water potential so low that seed imbibition for germination is compromised (osmotic effect) and/or by excessive entry of Na^+ which is toxic to metabolism (ionic toxicity) (Khan & Gul, 2006; Kramer & Seal, 2013; Hameed *et al.*, 2014). Uptake of salts could lower seed's water potential thereby facilitate imbibition, however ionic toxicity may overshadow such beneficial osmotic effects (Collis-George & Sands, 1962; Khan *et al.*, 1987; Song *et al.*, 2005; Gul *et al.*, 2013). In order to partition osmotic and ionic components of the salinity, often seed germination response in a salt solution is compared with that in an isotonic solution of a non-ionic solute such as polyethylene glycol (Hardegree & Emmerich, 1990; Bajji *et al.*, 2002; Song *et al.*, 2005; Hameed *et al.*, 2013). In this study, effects of NaCl and PEG on seed germination of *H. perfoliata* were generally comparable. Likewise, similar effects of NaCl and non-ionic solutes (PEG or mannitol) were observed on seed germination of *Atriplex halimus* (Bajji *et al.*, 2002) and *Chrysothamnus nauseosus* (Dodd & Donovan, 1999). These findings including ours thus indicate greater incidence of osmotic constraint of

salinity on seed germination than ionic toxicity. High recovery of un-germinated seeds in this study after alleviation of salinity also supports this assumption. On the other hand, salinity caused ionic toxicity in some species like *Aristida adscensionis*, *Prosopis strombulifera* (Sosa *et al.*, 2005) and *Suaeda heterophylla* (Hameed *et al.*, 2013).

Based on the results discussed above, *H. perfoliata* seeds appear highly tolerant to salinity, as some seeds could germinate in NaCl treatments as low as -2.5 MPa (~ 600 mM), which is equivalent to seawater salinity. However, a sea-salt treatment of -2.5 MPa inhibited seed germination more than isotonic NaCl treatment. Furthermore, chloride salts were generally more inhibitory to seed germination than isotonic sulfate salts (Fig. 5). Un-germinated seeds from low osmotic potential treatments of all salts showed high recovery of germination when transferred to distilled water, indicating that these treatments were not too toxic for the seed viability. Generally, comparable seed germination response of *H. perfoliata* in isotonic NaCl and PEG treatments also indicate greater incidence of osmotic effect rather than ionic effect of NaCl salinity.

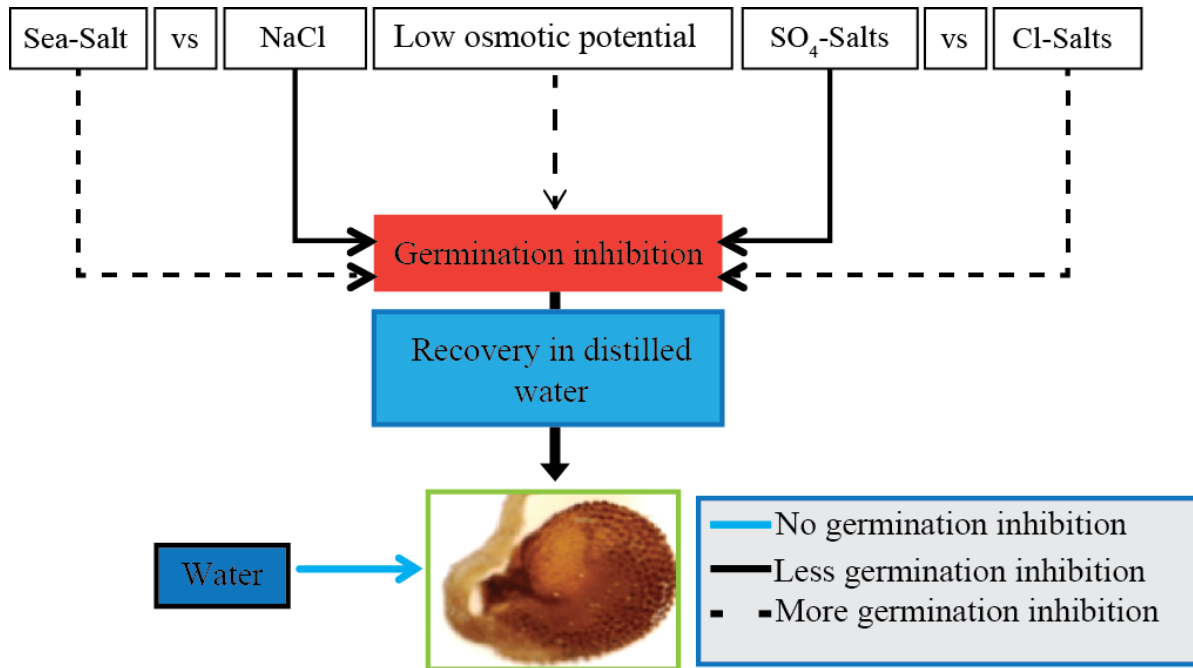


Fig. 5. Differential inhibitory effects of iso-osmotic treatments with NaCl, seasalt, and various chloride (Cl⁻) and sulphate (SO₄²⁻) salts on seed germination of *Halopeplis perfoliata*.

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(Received for publication 13 May 2015)