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Effects of different salts and mannitol on seed imbibition, germination and ion content of *Crithmum maritimum* L. (Apiaceae)

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Saline habitats contain various salt types that differently affect seed germination and subsequent seedling establishment. Most studies on the germination process have been carried out using NaCl, which may limit the accuracy of the conclusions drawn, especially regarding the plant behaviour under field conditions. We compare here the impact of iso-osmotic solutions of four salts (NaCl, Na_2SO_4, $MgCl_2$ and $MgSO_4$) and mannitol on seed imbibition, germination, germination recovery, viability and seedling ion relations of the halophyte *Crithmum maritimum* L. Seed imbibition percentage declined as osmotic potentials decreased. $MgCl_2$ and NaCl were the most and less adverse salt on the germination, respectively. As for seed germination and viability, K^+, Ca^{2+}, NO_3^- and PO_4^{3-} contents within seedlings appeared to be salt-diminished. This was associated with higher ion (K^+ and Ca^{2+}) leakage. In conclusion, both osmotic and toxic salt components impaired seed germination. This may be related to the effects of different salts on ion content, seed imbibition, and nutrient leakage through membranes.

Key words: *Crithmum maritimum* L., halophytes, ion relations, salinity, seed germination.

INTRODUCTION

Seed germination starts with water uptake by the dry seed, i.e. imbibition, and ends with radicle elongation (Bewley & Black, 1994). Water uptake under favourable conditions, after the breaking down of seed dormancy if present, leads to the activation of metabolic processes, so that germination can successfully take place. In halophytes, which undergo substantial fluctuation in soil salinity levels over time and space, imbibition is the most affected procedure by salt exposure process (Ungar, 1996). This may partly explain why these species (native of saline habitats) may behave as salt-sensitive species at the germinative stage.

Salt presence in the medium frequently impairs seed germination (Ungar, 1996), either by restricting water supply (osmotic effect), or by causing a specific injury related to ion toxicity (ionic effect) (Duan *et al*., 2004). Seed germination in salt-affected soils may be influenced not only by the total concentration of dissolved salts, but also by the salt type (Ryan *et al*., 1975). Indeed, it is well known that saline soils contain multiple salt constituents that have different physiological effects on plant development (Tobe *et al*., 2002, 2004). The most common salt components in saline soils are Na^+, Mg^{2+}, and Ca^{2+} cations, and Cl^- and SO_4^{2-} anions (Shainberg, 1975). However, most of the studies dealing with the salinity effects on seed germination have been focusing on the effect of a single salt, namely NaCl, and explained the germination inhibition by the osmotic component of salts, *i.e.* the restriction of water uptake (Egan *et al*., 1997; Keiffer & Ungar, 1997; Gul & Weber, 1998; Pujol *et al*., 2000; Debez *et al*., 2004). Therefore, little is known about the impact of other salts on germination (Sosa *et al*., 2005). Further, data regarding seed imbibition under salt conditions for halophytes are scarce.

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Crithmum maritimum L. is a typical halophyte of rocky coastal ecosystems, which is subjected to regular variation in their climatic conditions (Abdelly *et al*., 2006). This species shows substantial economical and medicinal importance: its leaves display high antioxidant and antimicrobial activities (Meot-Duros *et al*., 2008; Meot-Duros & Magné, 2009), whereas seeds are rich in essential oils and other bioactive substances (Atia *et al*., 2009). In addition, seeds contain significant amounts of oil, potentially edible due to its fatty acid composition close to olive oil (Zarrouk *et al*., 2003). In a preliminary work, we observed that salinities exceeding 50 mM NaCl, severely inhibited the germination of Tunisian population of *C. maritimum* L. (Atia *et al*., 2006). Hence, one may hypothesize that the combination of both osmotic and ionic components of salt may inhibit seed germination of *C. maritimum* L. As for halophytes, seed germination of *C. maritimum* L. may be strongly influenced by the nature of ions, such as Na^+, Mg^{2+}, Ca^{2+}, Cl^-, and SO_4^{2-}. We address in this study the impact of iso-osmotic solutions of different salts (NaCl, Na_2SO_4, $MgCl_2$, $MgSO_4$) and mannitol on: i) seed germination capacity and imbibition over time, ii) seedling ion accumulation, and iii) seedling cell membrane stability (assessed by Ca^{2+} and K^+ leakage).

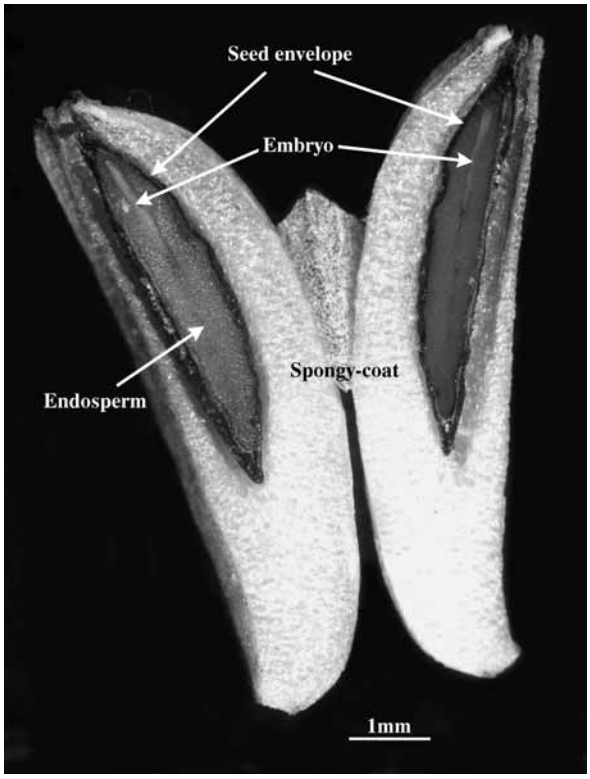

FIG. 1. Stereomicroscope photograph of *C. maritimum* L. fruit, showing the seed within the spongy coat.

MATERIALS AND METHODS

Fruit harvesting and seed germination experiments

Mature fruits were collected in December 2005 from Tabarka (NW of Tunisia) and were stored dry under laboratory conditions at 18-23°C. The fruit of *C. maritimum* L. is a schizocarp divided into two mericarps. The mericarp is composed of a spongy outer coat, a secretory envelope delimiting the large endosperm, and a rudimentary embryo (Fig. 1). At fruit maturation, the mesocarp is a spongy coat that is easy to remove. However, the endocarp and the secretory envelope remain firmly attached to the seed. Therefore, in this study the term seed refers to the seed and the endocarp and the secretory envelope. In May 2006, after the spongy coat was removed, seeds were disinfected in calcium hypochlorite solution for 5 min before starting the germination tests. Twenty five seeds were sown in 9-cm diameter Petri dishes and covered with a double layer of filter paper (type *Filtrak*), moistened with 5 ml distilled water or a suitable solution containing either NaCl, Na_2SO_4, $MgCl_2$, $MgSO_4$, or mannitol (Sigma Chemicals) in concentrations calculated to obtain the following osmotic potentials: –0.4, –0.8, and –1.2 MPa (Tobe *et al*., 2002; Sosa *et al*., 2005). The Petri dishes were sealed with transparent plastic film to prevent solution evaporation. Every week, the solution and the filter paper were changed. No changes in the solution volume in the Petri dishes were observed during the treatment. Seed germination was carried out in growth chambers under the following conditions: 16/8 hrs and 23°/18°C temperature and light/dark regime. White light was produced by five fluorescent lamps (Type OSRAM 40 W, fluorescence rate of 25 μmol m^{-2} s^{-1}, 400-700 nm).

Germination and imbibition parameters

Seed imbibition percentage was determined after 8 days as the relative water content (RWC) using the following formula: RWC (%) = [(FW – DW)/DW] × 100, where DW and FW stand for seed initial dry weight and seed fresh weight, respectively (Li *et al*., 2005).

Germinated seeds were counted at two days interval, a seed being considered as germinated at the radicle appearance. Besides the final germination percentage, the index of germination velocity was determined according to a modified Timson's index

(Khan & Ungar, 1984) as: S = G/T, with G representing the germination percentage, calculated at two days interval and T the total germination time. The index of germination recovery was calculated using the relation [(a-b)/(c-b)] × 100, where a is the total number of seeds germinated after being transferred to distilled water, b is the total number of seeds germinated in saline solution, and c is the total number of seeds. Seed viability was evaluated by the percentage of seeds germinated in saline or mannitol solution plus those transferred on distilled water (previously non germinated in presence of salts or mannitol).

Ion relations

Ions were extracted by boiling grinded seeds previously germinated at –0.4 MPa at 100°C for 10 min. K^+ and Na^+ were assayed by flame photometry, Ca^{2+} and Mg^{2+} by atomic absorption spectrophotometry, and Cl^-, NO_3^-, SO_4^{2-}, and PO_4^{3-} by ion chromatography. In order to assess the salt treatment effect on membrane stability, 25 seeds were sown in 9-cm diameter Petri dishes without using filter paper, and moistened with 5 ml of the suitable solution (i.e. distilled water, saline or mannitol) at -0.4 MPa. Cation (K^+ and Ca^{2+}) leakage was assessed at 10 days after imbibition.

Statistical analysis

Data presented are the mean values of 4 replicates (± SE). A two-way ANOVA was used, using the SPSS 10.0 for Windows software, in order to assess the significance of the osmotic agent (OA), i.e. salt or mannitol, the osmotic potential (OP) and their interaction (OA*OP) on the seed imbibition and germination. Before the statistical analysis, germination data were arcsine transformed.

RESULTS

Salt effect on seed imbibition

The two-way ANOVA revealed a significant effect of osmotic agent (OA) and osmotic potential (OP) on the seed imbibition percentage after 8 days of treatment, but no significant effect of their interaction (OA × OP) was found (Table 1). The lower was the external osmotic potential, the lower seed imbibition (Fig. 2). The mannitol-treated seeds showed a higher imbibition percentage as compared to those treated with salt. For instance, the imbibition capacity was not significantly affected by mannitol at –0.4 MPa and remained higher than in the salt-treated seeds at –0.8 MPa and –1.2 MPa, respectively (Fig. 2). Na_2SO_4 was the most adverse salt on seed imbibition, NaCl was the less one, whereas $MgSO_4$ and $MgCl_2$ impacts were intermediate (Fig. 2).

Salt effect on seed germination and seed viability

The two-way ANOVA showed that OA, OP and their interaction had a significant impact on the final germination percentage and germination velocity ($p < 0.001$)

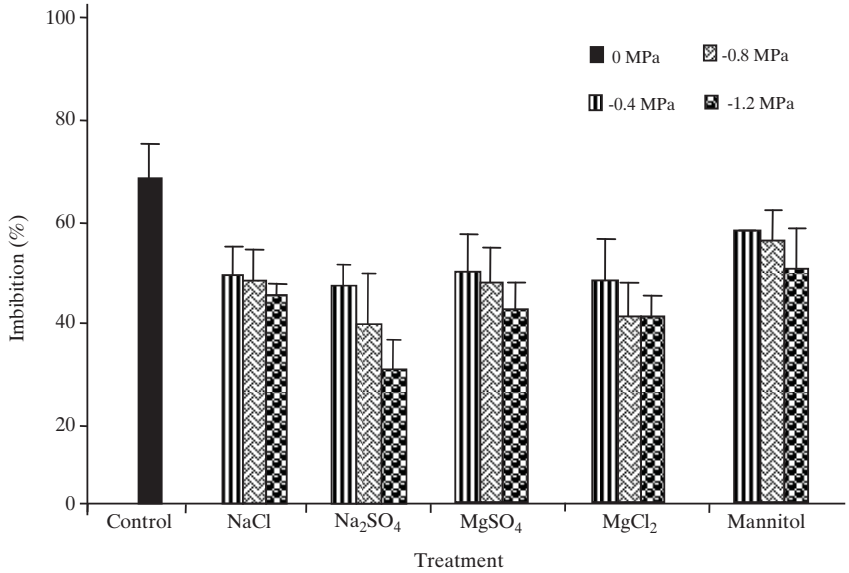

FIG. 2. Effect of 8 day-long exposure with monosaline solutions (osmotic potential: –0.4, –0.8, and –1.2 MPa) of NaCl, Na_2SO_4, $MgCl_2$, $MgSO_4$ and mannitol on imbibition percentage (mean ± SE).

TABLE 1. F-values of two-way ANOVA analysis for characteristics of seed germination and imbibition for seeds moistened with distilled water, different salts (NaCl, Na_2SO_4, $MgCl_2$, and $MgSO_4$) and mannitol at –0.4, –0.8 and –1.2 MPa

Independent variable	Osmotic potential (OP)	Osmotic agent (OA)	OA × OP
Imbibition percentage	51.639****	5.268***	0.479^{NS}
Final germination percentage	398.493****	75.433****	19.622****
Germination velocity	627.076****	71.481****	17.647****
Seed viability	7.806****	4.351**	1.920^{NS}
Recovery	9.584****	2.951*	1.204^{NS}

*significant difference at $p < 0.05$, **significant difference at $p < 0.01$, ***significant difference at $p < 0.001$, ****significant difference at $p < 0.0001$, ^{NS} no significant difference

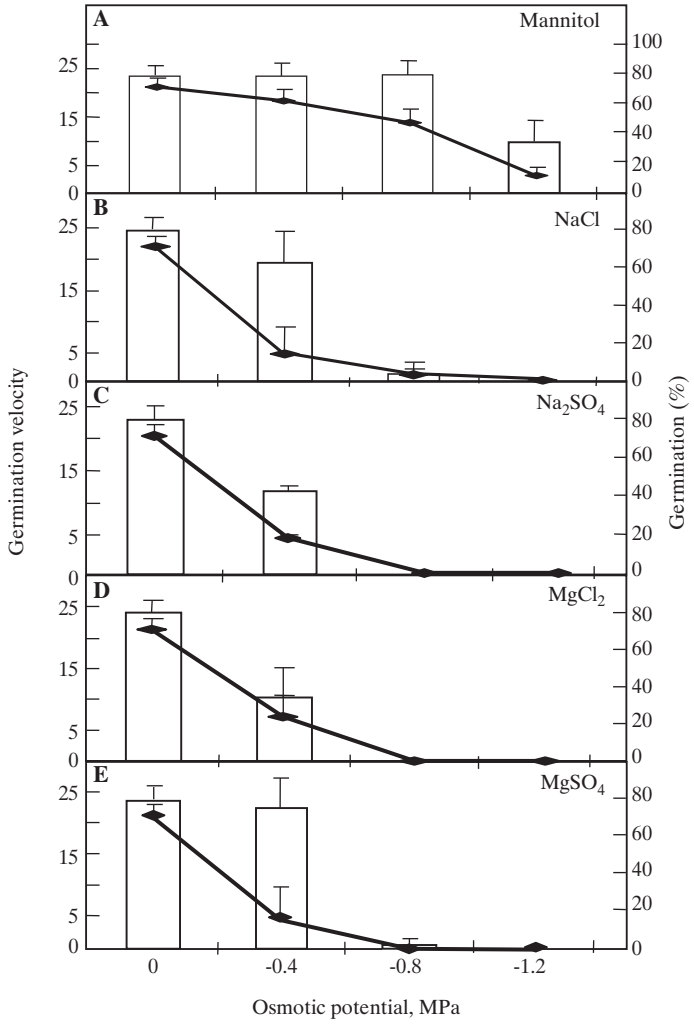

FIG. 3. Final germination percentage (bars) and germination velocity (curve) for seeds germinated in saline and mannitol solutions (mean ± SE).

(Table 1). Mannitol treatment up to –0.8 MPa did not affect final seed germination percentage, but delayed the germination process, since germination velocity was reduced (Fig. 3A). At –0.4 MPa, seed germination was significantly affected and delayed by Na_2SO_4 and $MgCl_2$ (Fig. 3C and D), whereas NaCl and $MgSO_4$ reduced only seed germination velocity (Fig. 3B and E). Lowering of the osmotic potentials, suppressed the germination process, irrespective of salt treatment (Fig. 3B, C, D and E). Both seed germination recovery and seed viability were significantly influenced by OA and OP but not their interaction (Table 1). While mannitol strongly altered seed viability at –1.2 MPa (Fig. 4A), a specific salt effect was observed for both germination recovery and seed viability, especially at –1.2 MPa, in the following decreasing order: $MgCl_2$, $MgSO_4$, NaCl, and Na_2SO_4 (Fig. 4D, E, B and C).

Salt effect on seedling ion content

There was a high significant effect ($p < 0.0001$) of OA and OA × OP on the seedling Na^+ content (Table 2), the highest accumulation being recorded for NaCl and Na_2SO_4 treatments (Table 2). OA, OP and their interaction also significantly affected ($p < 0.0001$) K^+ content (Table 2). The treatment with sodium salts (NaCl and Na_2SO_4) reduced seedling K^+ content as compared to the control. In contrast, the $MgSO_4$-treated seeds showed the highest K^+ content (Table

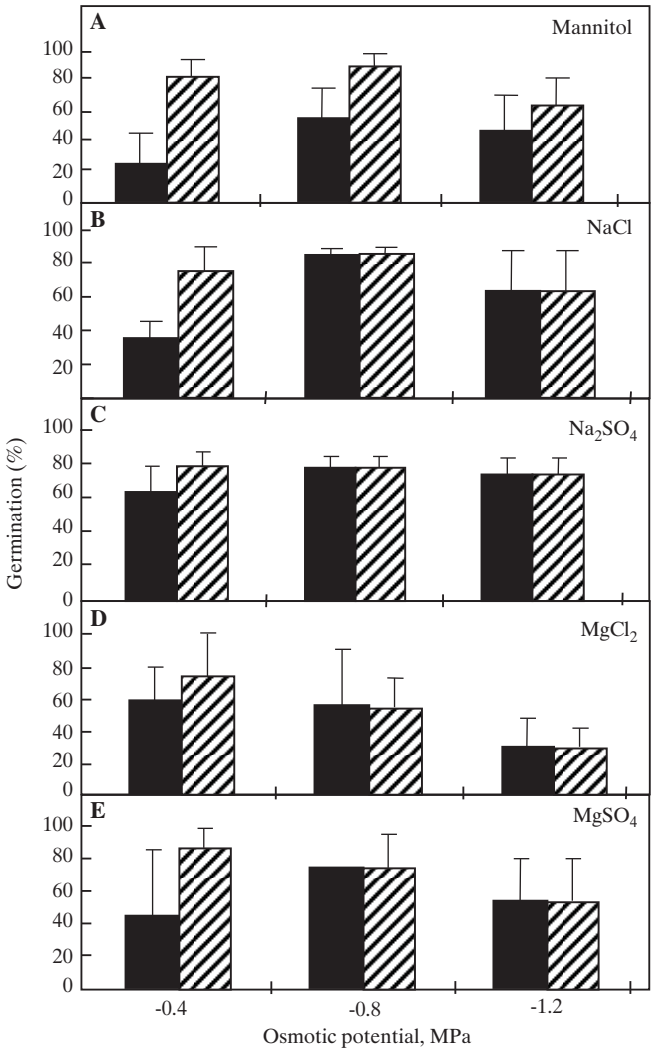

FIG. 4. Germination recovery (full bars) and seed viability (hatched bars) for seeds germinated in saline and mannitol solutions (mean ± SE).

TABLE 2. F-values of two-way ANOVA analysis of seed ion relations. Seeds were moistened with either distilled water or iso-osmotic solutions (–0.4 MPa) of salts (NaCl, Na_2SO_4, $MgCl_2$, and $MgSO_4$) and mannitol

Independent variable	Osmotic potential (OP)	Osmotic agent (OA)	OA × OP
Na^+	3.810^{NS}	102.284****	101.005****
K^+	250.898****	97.045****	86.322****
Ca^{2+}	0.769 ^{NS}	4.514**	5.071**
Mg^{2+}	202.430****	29.933****	29.273****
Cl^-	8.603****	27.164****	22.894****
NO_3^-	24.895****	1.019 ^{NS}	1.260 ^{NS}
PO_4^{3-}	15.262****	31.964****	30.802****
SO_4^{2-}	326.941****	174.905****	174.762****

*significant difference at $p < 0.05$, **significant difference at $p < 0.01$, ***significant difference at $p < 0.001$, ****significant difference at $p < 0.0001$, ^{NS} no significant difference

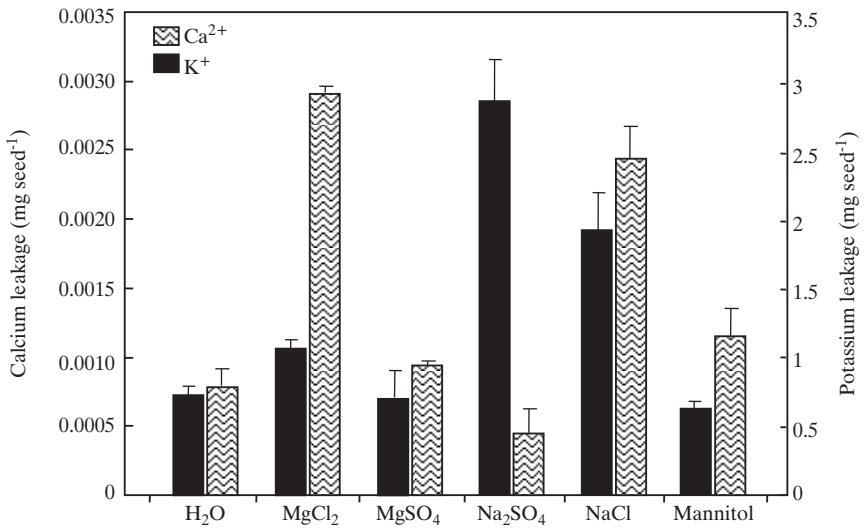

FIG. 5. Effect of monosaline solutions (osmotic potential: –0.4 MPa) of NaCl, Na_2SO_4, $MgCl_2$, $MgSO_4$ and mannitol on calcium and potassium leakage (mg seed^{-1}). Both parameters were calculated after 10 days from the beginning of imbibition (mean ± SE).

TABLE 3. Seedling ion content (mg g^{-1} dry weight) after 10 days of imbibition in either distilled water or in –0.4 MPa osmotic potential solutions (mean ± SE)

	H_2O	Mannitol	NaCl	Na_2SO_4	$MgCl_2$	$MgSO_4$
Na^+	2.50 ± 0.48	2.33 ± 0.16	6.5 ± 0.28	6.50 ± 0.48	2.75 ± 3.20	2.66 ± 0.16
K^+	5.26 ± 0.68	5.66 ± 0.73	2.6 ± 0.11	4.36 ± 0.42	6.53 ± 0.36	7.23 ± 0.72
Ca^{2+}	1.70 ± 0.21	1.99 ± 0.22	1.5 ± 0.36	2.02 ± 0.01	1.09 ± 0.12	1.81 ± 0.08
Mg^{2+}	0.78 ± 0.07	0.87 ± 0.10	1.18 ± 0.12	0.84 ± 0.15	1.59 ± 0.18	1.46 ± 0.08
Cl^-	3.88 ± 0.88	3.05 ± 0.82	6.60 ± 0.42	3.01 ± 1.27	7.01 ± 0.64	2.60 ± 0.75
NO_3^-	0.19 ± 0.05	0.16 ± 0.07	0.14 ± 0.00	0.11 ± 0.00	0.10 ± 0.03	0.15 ± 0.03
PO_4^{3-}	5.49 ± 1.30	6.64 ± 0.73	7.85 ± 0.74	1.69 ± 0.16	1.16 ± 0.51	5.57 ± 0.91
SO_4^{2-}	1.10 ± 0.12	0.45 ± 0.13	1.53 ± 0.44	7.11 ± 1.24	0.36 ± 0.10	6.16 ± 0.70

3). OA and OA × OP affected significantly the Ca^{2+} ($p < 0.01$), Mg^{2+}, Cl^-, PO_4^{3-} and SO_4^{2-} ($p < 0.0001$) contents (Tables 2 and 3), but only OP had a significant impact on the NO_3^- content ($p < 0.0001$) (Table 2). Sulphate salts ($MgSO_4$ and Na_2SO_4) decreased Cl^- contents in seedlings as compared to Cl^- salts (Table 3). Moreover, the seeds exposed to Na_2SO_4 and $MgCl_2$ showed lower NO_3^- and PO_4^{3-} contents (Table 3). OA and OA × OP significantly affected the SO_4^- content ($p < 0.0001$) (Table 2). $MgCl_2$ treatment reduced the SO_4^{2-} content. In contrast, NaCl treatment increased SO_4^{2-} content in comparison to the control (Table 3).

Salt effect on membrane stability

At –0.4 MPa, the chloride salts (NaCl and $MgCl_2$) as well as mannitol led to higher calcium leakage as compared to the control, whereas sulphate salts had no significant effect (Fig. 5). Seed treatment with sodium salts (NaCl and Na_2SO_4) caused higher potassium release in the external medium, while no significant trend was observed for mannitol and the remaining salts (Fig. 5).

DISCUSSION

Whether osmotic (Gul & Weber, 1998), toxic (Al-Karaki, 2001; Tobe *et al*., 2002) or combination of both (Rehman *et al*., 1996; Katembe *et al*., 1998; Sosa *et al*., 2005), the nature of salt effect on seed germination in halophytes is still controversial, despite being intensively investigated. Low water potentials reduce water uptake by seeds, thereby inhibiting germination (Katembe *et al*., 1998). Our results indicate that the different salt solutions as well as mannitol solution decreased water uptake (in terms of imbibition percentage and velocity), final germination percentage, and germination velocity in *C. maritimum* L. Consistent with previous reports on *Prosopis strombulifera* (Sosa *et al*., 2005), *Atriplex patula* and *A. prostrata* (Katembe *et al*., 1998), we found that imbibition, and subsequent germination were less affected by mannitol than by other salts. Both germination recovery and seed viability were particularly altered at the lowest osmotic potential (–1.2 MPa). Thus, salinity may inhibit seed germination of *C. maritimum* L. through the combination of both osmotic and ionic components. *Crithmum maritimum* L. seed germination was not only affected by salt concentration, but also by the nature of the salt applied. This is in agreement with previous studies on halophytic species like *Puccinellia festucaeformis* (Ungar, 1996), *Chenopodium glaucum* (Duan *et al*., 2004), *Prosopis strombulifera* (Sosa *et al*., 2005), *Sporobolus madraspatanus*, and *Aeluropus lagopoides* (Joshi *et al*., 2005).

The strongest inhibition on the final germination percentage, germination recovery, and seed viability was observed with $MgCl_2$, while $MgSO_4$ altered seed viability only at the lowest potential (–1.2 MPa). Na_2SO_4 and NaCl had not effect on seed viability, despite the strong inhibition of germination observed at –0.8 and –1.2 MPa. The intensity at which salts impair seed germination greatly varies among halophytes. For instance, the order was $MgCl_2$ > NaCl > KCl > $MgSO_4$ in *Puccinellia festucaeformis* seeds (Katembe *et al*., 1998), $MgCl_2$ > Na_2SO_4 > $NaCO_3$ > NaCl > $MgSO_4$ in *Chenopodium glaucum* (Duan *et al*., 2004), and KCl > NaCl > $MgSO_4$ > $MgCl_2$ > Na_2SO_4 (Joshi *et al*., 2005) in *Sporobolus madraspatanus* and *Aeluropus lagopoides*.

The analysis of ion relations indicated that Na^+-treated seeds showed similar contents of Ca^{2+} and Mg^{2+} to those of the control. However, they were characterised by lower K^+ content in concomitance with higher K^+ leakage, which may suggest that the Na^+-salt specific effect was related to potassium loss. Such a pattern was also reported in *Haloxylon ammodendron* (Tobe *et al*., 2004) and in several species thriving in Mediterranean salt marshes (Álvarez-Rogel *et al*., 2006). These authors observed decreasing contents of Ca^{2+} and K^+ as salinity increased, leading to an imbalance in favor of the most toxic cations, such as Na^+ and Mg^{2+}. K^+ is an important osmoticum and high K^+/Na^+ ratio is often considered as indicative of salt tolerance (Muhammed *et al*., 1987; Hosseini *et al*., 2002). The regulation of Na^+ and K^+ uptake and their distribution in plant tissues is notably ensured by highly K^+-selective inward- and outward-rectifying K^+ channels (Maathuis & Amtmann, 1999) and Na^+/H^+ antiporters, that extrude out Na^+ against a concentration gradient (Blumwald *et al*., 2000). As stated by Akram *et al.* (2009), lower mineral uptake under saline conditions may be ascribed to Na^+-induced blockage or reduced activity of these transporters.

NaCl and Na_2SO_4 treated seeds displayed a high germination recovery percentage, which indicates that the salt specific effects are rather osmotic. In pepper, Na_2SO_4 as well as $MgCl_2$ treated seeds, showed a strong decline of P content, in concomitance with the

loss of membrane integrity (Xu & Kafkafi, 2003). The two above-cited salts decreased the phosphate and nitrate contents in our experiment, which could also explain the seed lower germination capacity. Sulphate content was also highly affected in $MgCl_2$ treated seeds. In plants, sulphate is a major component of proteins, especially of the amino acids cysteine and methionine and the vitamin thiamin and the coenzyme A (Epstein, 1972). Sulphate loss from seeds is considered as an indication of amino acid and vitamin degradation (Ouyang *et al*., 2002), hence highlighting the toxic effect of $MgCl_2$. It is noteworthy that in our conditions, $MgCl_2$-exposed seeds showed the lowest germination capacity and seed viability. This was associated with the lowest Ca^{2+} content and the highest Ca^{2+} leakage. Calcium is essential to preserve the structural and functional integrity of plant membranes, stabilize cell wall structures, regulate ion transport and selectivity, and control ion-exchange behavior as well as cell wall enzyme activities (Rengel, 1992; Marschner, 1995). These functions may be seriously impaired under low Ca^{2+} availability, due to calcium displacement from its membrane binding sites by other cations. For instance, calcium deficiency symptoms are common when Na^+/Ca^{2+} ratio is high in soil water (Shannon & Grieve, 1999; Tobe *et al*., 2004).

In conclusion, both osmotic and toxic salt components impaired seed germination of *C. maritimum* L. by reducing seed imbibition and ion content, and increasing nutrient leakage. The salt-induced inhibition of germination was salt-specific and in following order: $MgCl_2 > MgSO_4 > Na_2SO_4 > NaCl$. $MgCl_2$ exerted a strong toxic effect that may be explained by the highest loss of nutrients, especially phosphorus, nitrate, sulphate, and calcium. $MgSO_4$ decreased germination by a toxic effect only at the lowest osmotic potential (–1.2 MPa), whereas Na_2SO_4 and NaCl inhibited germination mainly via an osmotic effect, since high germination recovery was registered after seed transfer in distilled water. Both Na^+-containing salts caused a high leakage of K^+. *Crithmum maritimum* L. usually grows on rocky coasts in the vicinity of seawater, which contains multiple ions among which Na^+, Mg^{2+}, Ca^{2+}, Cl^-, and SO_4^{2-}. The seasonal exposure to high salinity levels may reduce the availability of seed reserves, thereby impairing germination. Yet, seeds may remain viable and germinate after the winter rains, so that the plant can successfully establish.

REFERENCES

Abdelly C, Barhoumi Z, Ghnaya T, Debez A, Ben Hamed K, Ksouri R, Talbi O, Zribi F, Ouerghi Z, Smaoui A, Huchzermeyer B, Grignon C, 2006. Potential utilisation of halophytes for the rehabilitation and valorisation of salt-affected areas in Tunisia. In: Özturk M, Waisel Y, Khan MA, Görk G, eds. *Biosaline agriculture and salinity tolerance in plants*. Birkhauser Verlag Publisher, Switzerland: 161-172.

Akram MS, Ashraf M, Akram NA, 2009. Effectiveness of potassium sulfate in mitigating salt-induced adverse effects on different physio-biochemical attributes in sunflower (*Helianthus annuus* L.). *Flora*, 204: 471-483.

Al-Karaki G, 2001. Germination, sodium, and potassium concentrations of barley seeds as influenced by salinity. *Journal of Plant Nutrition*, 24: 511-522.

Álvarez-Rogel J, Martínez-Sánchez JJ, Carrasco L, Marín CM, 2006. Vegetal bioindicators for monitoring hydrological and saline gradients in a coastal dune salt marsh of southeast Spain: a conceptual model. *Wetlands*, 26: 703-717.

Atia A, Ben Hamed K, Debez A, Abdelly C, 2006. Salt and seawater effects on the germination of *Crithmum maritimum*. In: Özturk M, Waisel Y, Khan MA, Görk G, eds. *Biosaline agriculture and salinity tolerance in plants*. Birkhauser Verlag Publisher, Switzerland: 29-33.

Atia A, Debez A, Barhoumi Z, Abdelly C, Smaoui A, 2009. Histochemical localization of essential oils and bioactive substances in the seed coat of the halophyte *Crithmum maritimum* L. (Apiaceae). *Journal of Plant Biology*, 52: 448-452.

Bewley JD, Black M, 1994. *Seeds: Physiology of development and germination*. Plenum, New York.

Blumwald E, Aharon GS, Apse MP, 2000. Sodium transport in plant cells. *Biochimica et Biophysica Acta*, 1465: 140-151.

Debez A, Ben Hamed K, Grignon C, Abdelly C, 2004. Salinity effects on germination, growth, and seed production of the halophyte *Cakile maritima*. *Plant and Soil*, 262: 179-189.

Duan D, Liu X, Khan MA, Gul B, 2004. Effects of salt and water stress on the seed germination of *Chenopodium glaucum* L. *Pakistan Journal of Botany*, 36: 793-800.

Egan TP, Ungar IA, Meekins JF, 1997. The effect of different salts of sodium and potassium on the germination of *Atriplex prostrata* (Chenopodiceae). *Journal of Plant Nutrition*, 20: 1723-1730.

Epstein E, 1972. *Mineral nutrition in plants*. Wiley, New York.

Gul B, Weber DJ, 1998. Effect of dormancy relieving compounds on the seed germination of non-dormant *Allenrolfea occidentalis* under salinity stress. *Annals of Botany*, 82: 555-560.

Hosseini MK, Powell AA, Bingham IJ, 2002. Comparison

of the seed germination and early seedling growth of soybean in saline conditions. *Seed Science Research*, 12: 165-172.

Joshi AJ, Mali BS, Hinglajia H, 2005. Salt tolerance at germination and early growth of two forage grasses growing in marshy habitats. *Environmental and Experimental Botany*, 54: 267-274.

Katembe WJ, Ungar IA, Mitchell JP, 1998. Effect of salinity on germination and seedlings growth of two *Atriplex* species (Chenopodiaceae). *Annals of Botany*, 82: 167-175.

Keiffer CH, Ungar IA, 1997. The effect of extended exposure to hypersaline conditions on the germination of five inland halophyte species. *American Journal of Botany*, 84: 104-111.

Khan MA, Ungar IA, 1984. Effects of salinity and temperature on the germination and growth *Atriplex triangalus* Willd. *American Journal of Botany*, 71: 481-489.

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 seeds of *Suaeda salsa* under saline conditions. *Journal of Plant Research*, 118: 207-214.

Maathuis FJM, Amtmann A, 1999. K^+ nutrition and Na^+ toxicity: the basis of cellular K^+/Na^+ ratios. *Annals of Botany*, 84: 123-133.

Marschner H, 1995. *Mineral nutrition of higher plants*. Academic Press, London.

Meot-Duros L, Le Floch G, Magné C, 2008. Radical scavenging, antioxidant and antimicrobial activities of halophytic species. *Journal of Ethnopharmacology*, 116: 258-262.

Meot-Duros L, Magné C, 2009. Antioxidant activity and phenol content of *Crithmum maritimum* L. leaves. *Plant Physiology and Biochemistry*, 47: 37-41.

Muhammed S, Akbar M, Neue HU, 1987. Effect of Na/Ca and Na/K ratios in saline culture solution on the growth and mineral nutrition in rice (*Oryza sativa* L.). *Plant and Soil*, 104: 57-62.

Ouyang X, Voorthuysen T, Toorop PE, Hilhorst HWM, 2002. Seed vigor, aging, and osmopriming affect anion and sugar leakage during imbibition of maize (*Zea mays* L.) caryopses. *International Journal of Plant Sciences*, 163: 107-112.

Pujol JA, José FC, Luis R, 2000. Recovery germination from different osmotic conditions by four halophytes from south-eastern Spain. *Annals of Botany*, 85: 279-286.

Rehman S, Harris PJC, Bourne WF, Wilkin J, 1996. The effect of sodium chloride on germination and the potassium and calcium contents of *Acacia* seeds. *Seed Science and Technology*, 25: 45-57.

Rengel Z, 1992. The role of calcium in salt toxicity. *Plant, Cell and Environment*, 15: 625-632.

Ryan J, Miyamoto S, Stroehlen JL, 1975. Salt and specific ion effects on germination of four grasses. *Journal of Range Management*, 28: 61-64.

Shainberg I, 1975. Salinity of soils-effects of salinity on the physics and chemistry of soils. In: Gale J, ed. *Plants in saline environment*. Springer-Verlag Publisher, Berlin: 39-55.

Shannon MC, Grieve CM, 1999. Tolerance of vegetable crops to salinity. *Scientia Horticulturae*, 78: 5-38.

Sosa L, Llanes A, Reinoso H, Reginato M, Luna V, 2005. Osmotic and specific ions effect on the germination of *Prospis strombulifera*. *Annals of Botany*, 96: 261-267.

Tobe K, Li X, Omasa K, 2002. Effect of sodium, magnesium and calcium salts on seed germination and radicle survival of a halophyte, *Kalidium caspicum* (Chenopodiaceae). *Australian Journal of Botany*, 50: 163-169.

Tobe K, Li X, Omasa K, 2004. Effects of five different salts on seed germination and seedling growth of *Haloxylon ammodendron* (Chenopodiaceae). *Seed Science Research*, 4: 345-353.

Ungar IA, 1996. Effect of salinity on seed germination, growth, and ion accumulation of *Atriplex patula* (Chenopodiaceae). *American Journal of Botany*, 83: 604-607.

Xu BG, Kafkafi U, 2003. Seasonal differences in mineral content, distribution and leakage of sweet pepper seeds. *Annals of Applied Biology*, 143: 45-52.

Zarrouk M, El Almi H, Ben Youssef N, Sleimi N, Ben Miled D, Smaoui A, Abdelly C, 2003. Lipid composition of seeds of local halophyte species: *Cakile maritima*, *Zygophyllum album* and *Crithmum maritimum*. In: Lieth H, ed. *Cash crop halophytes: Recent studies*. Kluwer Academic Publisher, Dordrecht: 121-126.