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Changes of nutritional status of coastal plants *Hydrocotyle vulgaris* and *Aster tripolium* at elevated soil salinity

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Abstract

The aim of the present paper was to examine the effect of increased substrate NaCl on concentration of nutrients in tissues of two coastal marsh plants *Hydrocotyle vulgaris* and *Aster tripolium*. Increased substrate salinity due to watering with NaCl solution led to accumulation of both Na and Cl ions in tissues of both species studied. In *H. vulgaris* leaf blade and leaf petiole tissues both Na and Cl concentrations were saturated. In contrast there was an increase of Na and Cl concentration in both leaf and root tissues of *A. tripolium* with increasing substrate concentration. N and P concentrations were differentially affected by increasing substrate NaCl. While both minerals increased in tissues of *H. vulgaris*, for *A. tripolium* concentration of N decreased and that of P increased in roots. The effect of NaCl on S concentration was species-specific – it increased in leaf petioles and stolons of *H. vulgaris* and decreased in both leaves and roots of *A. tripolium*. The most pronounced stimulation of mineral concentration by NaCl was found for Mn. Increase in Cu concentration was characteristic for all tissues of both species while Fe concentration increased in *A. tripolium* and leaf tissues of *H. vulgaris*. In conclusion, possible adaptive responses leading to maintenance of an optimal supply of mineral nutrients in conditions of high Na and Cl concentrations in cells can be seen.

Key words: coastal plants, *Aster tripolium*, halophytes, *Hydrocotyle vulgaris*, mineral nutrition, salinity, wild plants.

Introduction

Elevated soil salinity, which is a major concern in many regions (Pitman, Läuchli 2002) changes physico-chemical properties of the soil in turn affecting availability of minerals and their uptake (Grattan, Grieve 1993). Thus, soil salinity decreases solubility of micronutrients. In addition, ion toxicity and osmotic stress may affect transport rates and cellular concentrations of certain nutrients. These processes could lead to nutrient imbalance and changes in ion homeostasis as a result of soil salinity. Together with disturbance of cellular functions due to NaCl toxicity and osmotic stress, raised salinity may lead to suppression of vital physiological functions (Flowers et al. 1977; Hasegawa et al. 2000). Consequently plants native to habitats with fluctuating soil salinity should

possess adaptive mechanisms to compensate for consequences of nutrient imbalance.

While general aspects of mineral nutrition of wild plants have been considered (Chapin 1980; Aerts, Chapin 2000) most recent studies concentrate on several main macronutrients. However, for optimal plant growth all the essential mineral nutrients must be present in adequate levels and correct proportions, which may differ for various species and different habitats. In addition, edaphic factors have been considered as limiting, explaining species zonation in a salt marsh (Levine et al. 1998; Pennings et al. 2005). Studies on the effect of salinity on mineral nutrition of wild plants, particularly halophytes, are rare. Very few data can be found on the effect of salinity on micronutrient concentration. Therefore, the aim of the present paper was to examine the effect of increased substrate NaCl level on concentration of macronutrients and micronutrients in tissues of different organs of two coastal marsh plants *Hydrocotyle vulgaris* and *Aster tripolium*.

Materials and methods

Aster tripolium plants were propagated by tissue culture from shoot apical explants (Klavina et al. 2006). Plants representing genetically identical material with four to five leaves were transferred to plastic pots (12 × 12 cm, 15 cm deep) filled with a commercial neutralized (pH 5.5 - 6.3) peat with mineral nutrients (NPK 14-16-18).

Stock plant material of *Hydrocotyle vulgaris* was introduced in laboratory culture from one genet of naturally growing plants during summer 2005. For experiments, plants were propagated during early spring in 2007 and 2008 and represented genetically identical clonal material. As starting material, five small plants with three ramets each was planted in 30 × 40 cm plastic trays filled with a commercial neutralized peat with mineral nutrients (NPK 14-16-18).

Plants were cultivated in a growth chamber with 120 μmol m^{-2} s^{-1} of photosynthetically active radiation at the plant level provided by three fluorescent lamps, photoperiod of 16 h, temperature 20 ± 2 °C.

Plants were watered three times a week with tap water or tap water with different concentrations of NaCl. Salt was added in steps of 25 mM per day in order to avoid osmotic shock. Final NaCl concentrations in a watering solution were 0, 25, 50, 100 mM for *H. vulgaris* and 0, 25, 50, 100, 200, 400 mM for *A. tripolium*. Preliminary experiments showed that substrate Na and Cl concentration was affected not only by the concentration of the ions in the respective watering solution but also on frequency and amount of watering solution applied. Indirectly, the concentration was affected also by cultivation temperature because of increased transpiration and consequently need for more water with increasing temperature.

Plants were harvested at four weeks after the start of the treatment. *H. vulgaris* plants were separated into leaf blades, leaf petioles and stolons, *A. tripolium* plants into leaves and roots. Three separate samples per treatment were harvested for each time point. The tissues were dried in oven (60 °C), weighed and ground into a fine powder using a ball mill. The samples were dry-ashed in concentrated HNO_3 vapor and redissolved in HCl solution (HCl : deionized water 3 : 100, v/v) and analyzed for nutrient concentrations (Rinkis et al. 1987).

The levels of Ca, Mg, Fe, Cu, Zn, and Mn were measured by atomic absorption spectrophotometer AAnalyst 700 (Perkin Elmer) with an acetylene-air flame (Haswell

1991). The amount of N, P, Mo and B was assayed by colorimetry, concentration of S by turbidimetry. K and Na were measured by a flame photometer PFP7 (Jenwey) with an air-propane/butane flame. Chloride was determined by $AgNO_3$ titration (Patnaik 1997). All results were expressed on a dry mass basis.

Substrate samples for Na and Cl analysis were air-dried and sieved through a metal sieve (2-mm mesh size). Samples were extracted with 1M HCl in a 1 : 5 soil to extractant volume ratio and measured by a flame photometer (for Na) or by $AgNO_3$ titration (for Cl). Experiments were repeated two times. Only data from a representative experiment are shown.

Results

Nutrient concentration in different organs of H. vulgaris *and* A. tripolium

When cultivated in control conditions *H. vulgaris* accumulated significantly higher concentrations of N, Ca, Mg, Fe, Mn and Zn in the leaf blade tissues in comparison to leaf tissues of *A. tripolium* (Table 1). Concentrations of nutrients in tissues of *H. vulgaris* decreased in the order leaf blades > leaf petioles > stolons for N, Ca, Mg, S, Fe, Mn and Zn. In contrast, higher concentration of K was evident in leaf petioles and stolons in comparison to leaf blades of *H. vulgaris*. For *A. tripolium* leaf tissues had higher concentrations than root tissues for all the nutrients measured except Mg, Fe, Zn and Cu.

Substrate NaCl level, corresponding NaCl concentrations in tissues and plant growth

Increased substrate salinity due to watering with NaCl solution led to accumulation of both Na (Fig. 1) and Cl (Fig. 2) ions in tissues of both species studied. However contrasting trends of concentration-dependence characteristics were found for *H. vulgaris* and *A.*

Table 1. Concentration of mineral nutrients in tissues of different organs of *Hydrocotyle vulgaris* and *Aster tripolium*. Data are means from 3 measurements ± SE

	Hydrocotyle vulgaris			*Aster tripolium*	
	Leaf blades	**Leaf petioles**	**Stolons**	**Leaves**	**Roots**
Macronutrients (% DM)					
N	2.00 ± 0.06	1.35 ± 0.08	1.00 ± 0.09	1.25 ± 0.03	0.90 ± 0.02
P	0.32 ± 0.03	0.40 ± 0.02	0.36 ± 0.02	0.39 ± 0.04	0.29 ± 0.03
K	2.14 ± 0.15	6.40 ± 0.16	3.98 ± 0.10	3.24 ± 0.10	0.90 ± 0.03
Ca	4.10 ± 0.11	1.90 ± 0.14	0.39 ± 0.02	0.96 ± 0.04	0.37 ± 0.02
Mg	0.65 ± 0.03	0.28 ± 0.01	0.11 ± 0.01	0.35 ± 0.01	0.29 ± 0.02
S	0.34 ± 0.02	0.07 ± 0.01	0.10 ± 0.01	0.43 ± 0.02	0.21 ± 0.01
Micronutrients (mg kg^{-1})					
Fe	142 ± 3	56 ± 6	44 ± 4	60 ± 2	225 ± 3
Mn	90 ± 3	19 ± 1	8 ± 1	32 ± 2	11 ± 1
Zn	150 ± 4	48 ± 4	24 ± 3	26 ± 1	30 ± 2
Cu	6.2 ± 0.4	3.4 ± 0.2	4.8 ± 0.2	6.8 ± 0.2	9.0 ± 0.3
Mo	2.2 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	2.7 ± 0.2	1.3 ± 0.2
B	30 ± 2	10 ± 1	14 ± 1	28 ± 2	7 ± 1

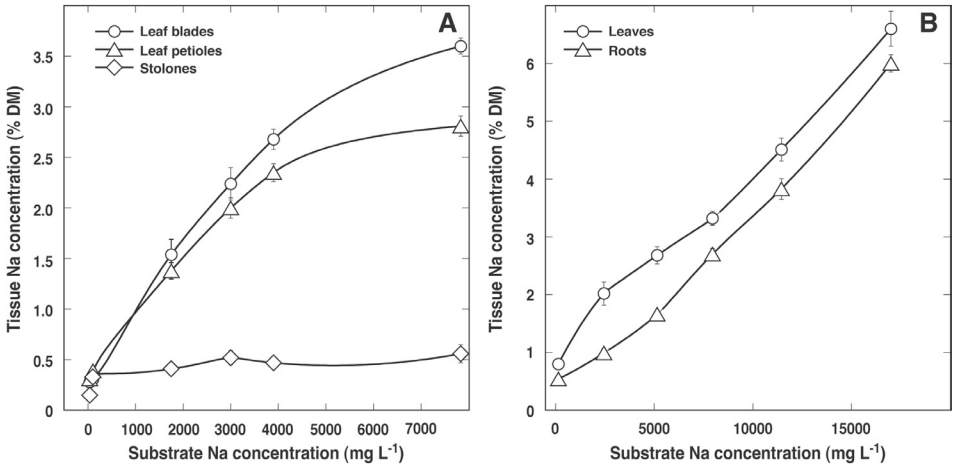

Fig. 1. Relationship between substrate Na concentration and tissue Na concentration of different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B).

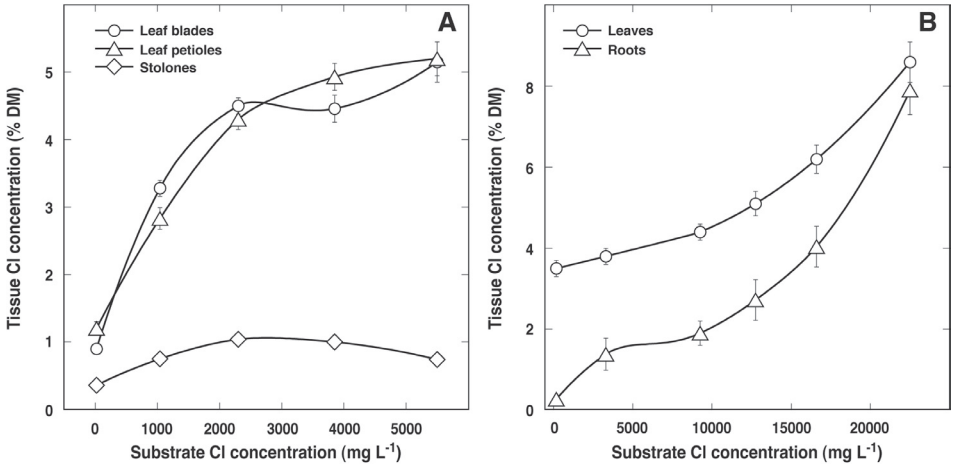

Fig. 2. Relationship between substrate Cl concentration and tissue Cl concentration of different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B).

tripolium. In *H. vulgaris* leaf blade and leaf petiole tissues both Na and Cl concentrations were saturated at soil ion concentration of about 4000 mg L^{-1} (Fig. 1A, 2A). In stolon tissues of *H. vulgaris* increase of Na and Cl concentration with increasing substrate NaCl concentration was significantly lower. In contrast to *H. vulgaris* there was a linear increase of Na concentration in both leaf and root tissues of *A. tripolium* with increasing substrate concentration up to 17 000 mg L^{-1} (Fig. 1B). However tissue Cl concentration increased in a polynomial manner (Fig. 2B).

Increased salinity resulted in a near-linear decrease of dry mass of leaf blades, leaf petioles and stolons of *H. vulgaris* (Fig. 3A). In *A. tripolium* low NaCl concentration (up to 50 mM) had no effect on growth of leaves although a progressive decrease in leaf mass

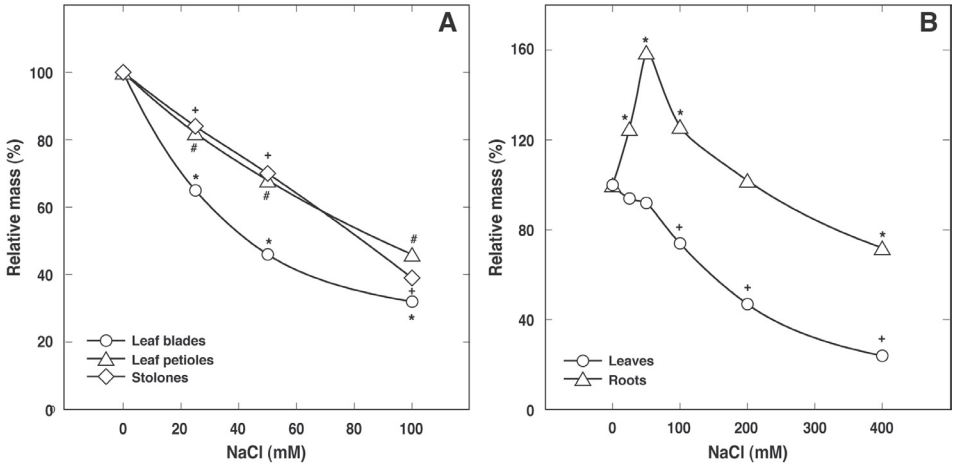

Fig. 3. Effect of different NaCl concentrations on a relative final mass of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B) organs. ⋆, #, +, statistically significant differences from control ($P < 0.01$) for a particular species and tissues.

was evident at higher concentrations (Fig. 3B). In contrast low NaCl (up to 100 mM) stimulated root growth while inhibition was visible only at 400 mM NaCl.

Effect of NaCl on nutrient concentration

Concentration of N increased in all tissues of *H. vulgaris* treated with 25 to 100 mM NaCl (Fig. 4A). However only 100 mM NaCl treatment resulted in increase of N concentration in leaves of *A. tripolium* (Fig. 4B). In contrast significant decrease of N concentration was found in roots of *A. tripolium* treated with 25 to 200 mM NaCl. Tissue P concentration of NaCl-treated *H. vulgaris* plants showed a concentration-dependent increase (Fig. 5A). In *A. tripolium* treated with NaCl P decreased in leaves (25 to 200 mM) while increased in roots (200 to 400 mM; Fig. 5B).

Response of K concentration in NaCl-treated *H. vulgaris* plants depended on the tissues analyzed. While a decrease of K was found in leaf blades, there was a stimulation of increase in the concentration in leaf petioles by NaCl and no significant changes in stolons (Fig. 6A). In tissues of both leaves and roots of *A. tripolium* 50 to 100 mM NaCl caused a small but statistically significant decrease of K concentration with a following increase at higher NaCl (Fig. 6B).

Increased substrate NaCl resulted in a small but statistically significant decrease of Ca concentration in leaf blade tissues of *H. vulgaris* and increase in leaf petiole tissues (data not shown). Only nonsignificant changes were found for both leaf and root tissues of *A. tripolium* in respect to Ca concentration. No changes in Mg concentration were observed in leaf petioles and stolons of *H. vulgaris* and both leaves and roots of *A. tripolium* (data not shown). NaCl caused significant decrease in Mg concentration only in leaf blade tissues of *H. vulgaris*.

One of most contrasting species-dependent effects of NaCl was found for changes in S concentration. There was a decrease in S concentration in leaf blades of *H. vulgaris* treated with 50 to 100 mM NaCl (Fig. 7A). However the same concentration resulted in increase

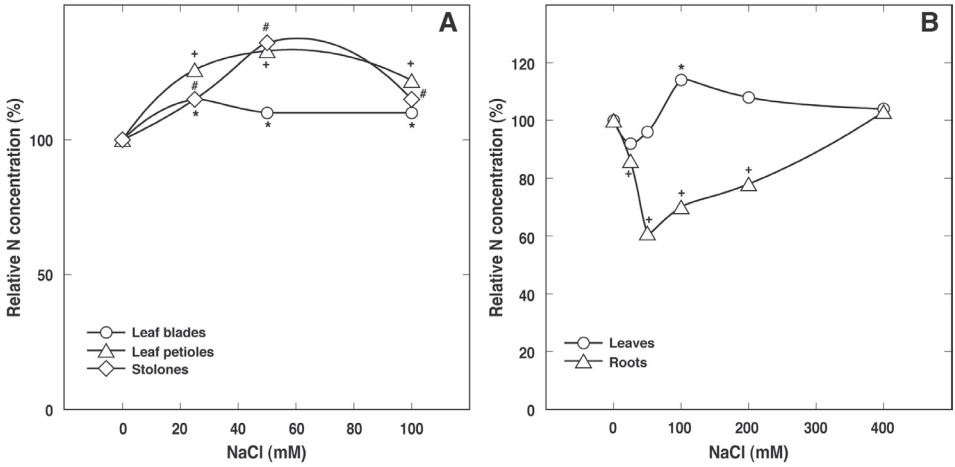

Fig. 4. Effect of different NaCl concentrations on relative tissue N concentration in different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B). ⋆, #, +, statistically significant differences from control (P < 0.01) for a particular species and tissues.

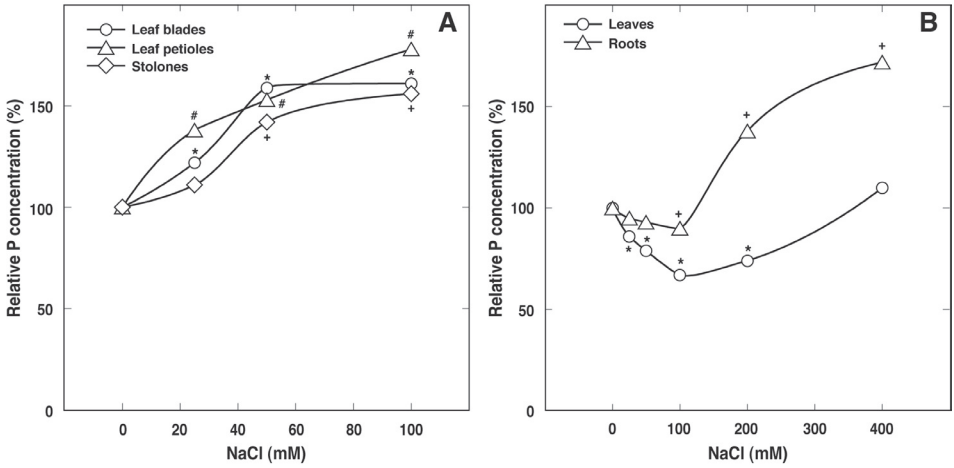

Fig. 5. Effect of different NaCl concentrations on relative tissue P concentration in different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B). ⋆, #, +, statistically significant differences from control (P < 0.01) for a particular species and tissues.

of S level in stolons while in leaf petioles NaCl treatment resulted in more than a two-fold increase in tissue S concentration. In contrast, S concentration decreased in both leaf and root tissues of *A. tripolium* (Fig. 7B).

Similar to macronutrients NaCl treatment resulted in different effect in respect to concentration of various micronutrients in tissues of *H. vulgaris* and *A. tripolium*. Only minor changes due to NaCl treatment were found in Fe concentration in leaf blades and stolons of *H. vulgaris*, where 100 mM NaCl slightly stimulated it in the blades while inhibiting in stolons (Fig. 8A). However, there was linear increase of Fe concentration in leaf petiole tissues with increasing NaCl concentration. Similarly NaCl treatment resulted

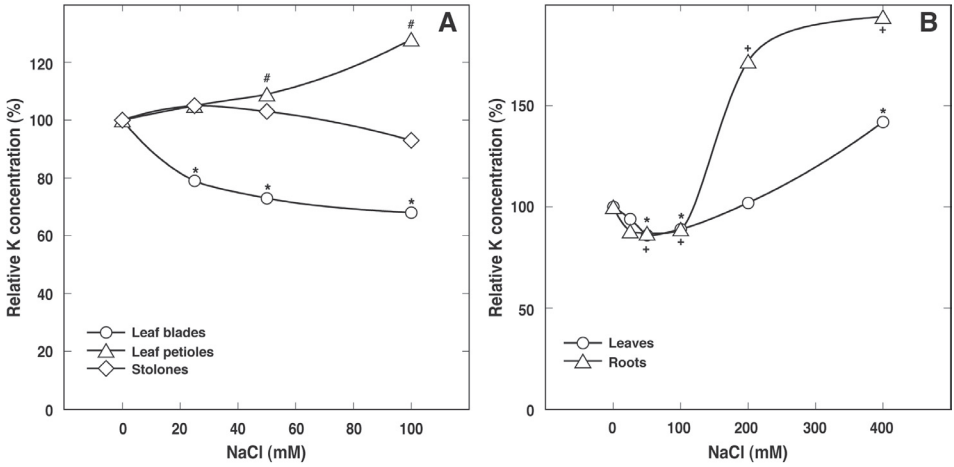

Fig. 6. Effect of different NaCl concentrations on relative tissue K concentration in different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B). ⋆, #, +, statistically significant differences from control ($P < 0.01$) for a particular species and tissues.

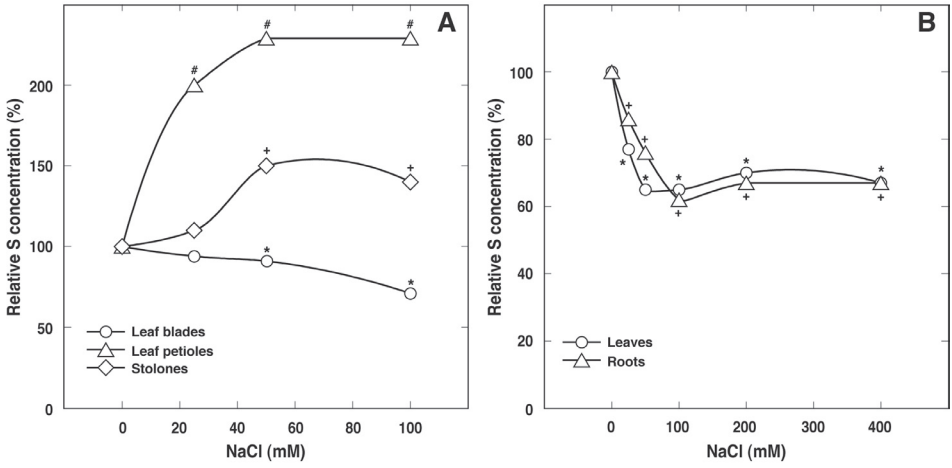

Fig. 7. Effect of different NaCl concentrations on relative tissue S concentration in different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B). ⋆, #, +, statistically significant differences from control ($P < 0.01$) for a particular species and tissues.

in increase of Fe concentration in both leaves and roots of *A. tripolium* (Fig. 8B).

The most pronounced stimulation of mineral concentration by NaCl was found for Mn. Concentration of Mn increased in all tissues analyzed from both species (Fig. 9A, B). A maximum increase in *H. vulgaris* was more than five-fold in leaf petiole tissues treated by 100 mM NaCl. In roots of *A. tripolium* the highest increase (by four times) was observed for 200 mM NaCl treatment.

No changes in Zn concentration were caused by NaCl in tissues of both *H. vulgaris* and *A. tripolium* (data not shown).

In all tissues of both *H. vulgaris* and *A. tripolium* plants treated with NaCl there was an

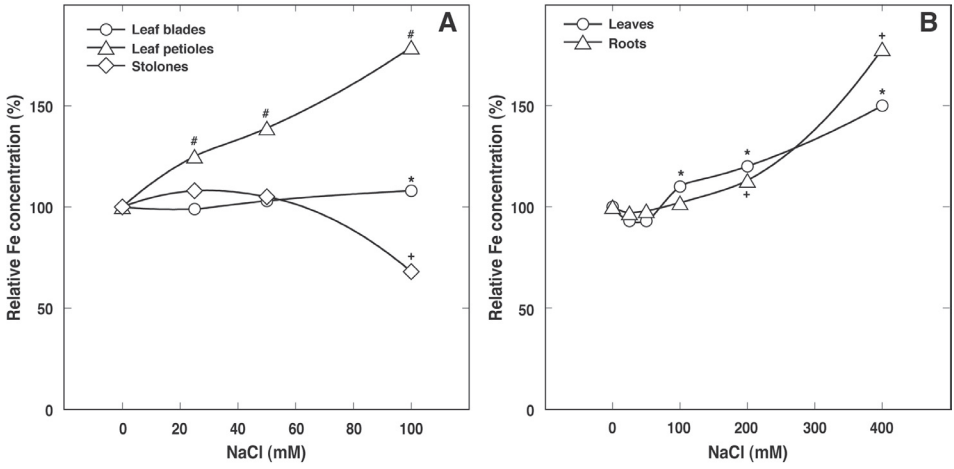

Fig. 8. Effect of different NaCl concentrations on relative tissue Fe concentration in different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B). ⋆, #, +, statistically significant differences from control ($P < 0.01$) for a particular species and tissues.

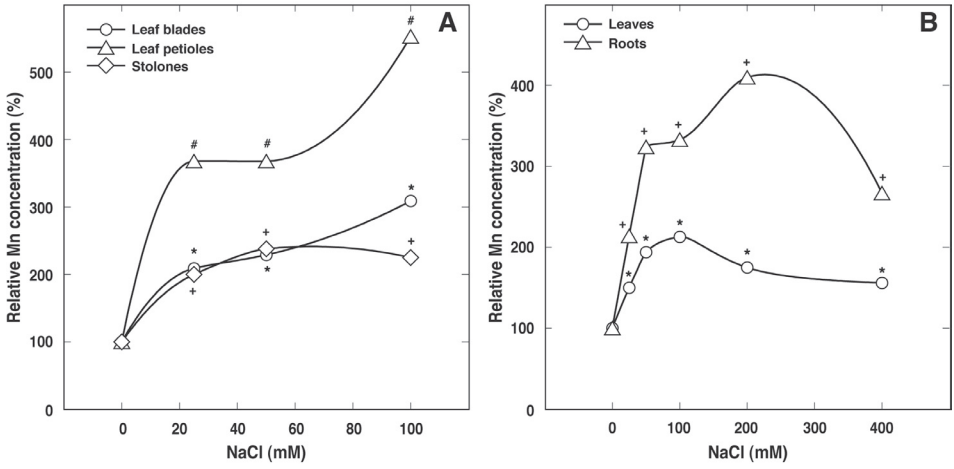

Fig. 9. Effect of different NaCl concentrations on relative tissue Mn concentration in different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B). ⋆, #, +, statistically significant differences from control ($P < 0.01$) for a particular species and tissues.

increase in Cu concentration (Fig. 10A, B). However there were no statistically significant changes at 25 to 50 mM NaCl for leaf blades and stolons of *H. vulgaris* (Fig. 10A) and at 25 to 100 mM and 25 to 50 mM for leaves and roots of *A. tripolium*, respectively (Fig. 10B).

A slight increase in B concentration was found in *A. tripolium* leaves at 200 to 400 mM NaCl (data not shown). Tissue Mo concentration showed an increase in leaf petioles and stolons of *H. vulgaris* under the effect of NaCl while no changes were visible in *A. tripolium* (data not shown).

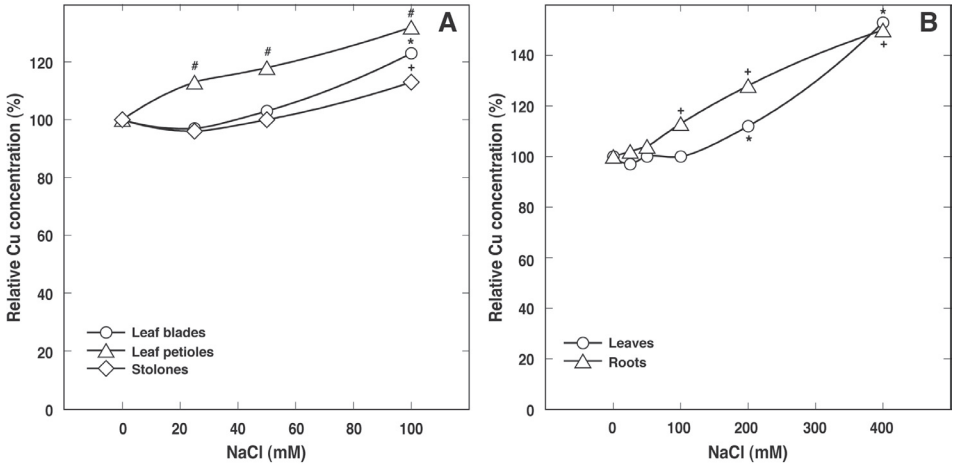

Fig. 10. Effect of different NaCl concentrations on relative tissue Cu concentration in different organs of *Hydrocotyle vulgaris* (A) and *Aster tripolium* (B). ⋆, #, +, statistically significant differences from control ($P < 0.01$) for a particular species and tissues.

Discussion

It is generally recognized that increased soil salinity differently affects concentration of different mineral elements in plant tissues (Romero, Marañón 1996). The presented data clearly show that the two species studied possess both similar and different responses of nutrient uptake in conditions of elevated salinity, thus reflecting a presence/absence of particular biochemical mechanisms of potential adaptive character. The differences in part could be due to different levels of salt tolerance in these species. *H. vulgaris* can be characterized as relatively salt-tolerant glycophyte with no increase in growth under elevated salinity (Fig. 3). *A. tripolium* is a moderately tolerant halophyte where only growth of underground parts are stimulated at moderate salinity (25 to 100 mM NaCl, Fig. 3). Consequently, some effects of elevated mineral concentrations under high salinity might be attributed to maintaining a constant uptake in a situation when growth of the organ is inhibited, resulting in increase of concentration of a particular mineral (Rinkis et al. 1989), which could be the case for *H. vulgaris* in all treatments and *A. tripolium* at NaCl higher than 200 mM. In addition, increased concentration of a particular mineral could be related to maintaining a nutrient balance at elevated Na and Cl concentrations in plant tissues (Grattan, Grieve 1993).

In respect to NaCl itself it is generally believed that more than 90 % of the Na in halophytes is located in the shoot (Flowers et al. 1977). In the present study this was the case for *H. vulgaris* but not for *A. tripolium*. At highest substrate NaCl concentration both leaves and roots of *A. tripolium* accumulated similar concentrations of both Na and Cl (Fig. 1, 2). Another difference between the species in terms of Na and Cl accumulation was related to saturability of the response in *H. vulgaris* in contrast to *A. tripolium* where no saturation was evident. However it can not be ruled out that concentration of Na and Cl in tissues of *A. tripolium* is saturable at higher substrate NaCl concentration.

In terrestrial ecosystems both N as well as P can be growth-limiting macronutrients

(Aerts, Chapin 2000). Under salt stress conditions, the uptake of N by plants is generally affected. Reports show both inhibitory (Bernstein 1974; Messedi et al, 2004) and stimulatory (Sági, Erdei 2005) effects on the plant N uptake under high salinity for different species. In contrast, only minor changes in N uptake were found in NaCl-treated plants in the present experiments (Fig. 4). While most of the studies demonstrating stimulative effect of salinity on tissue P concentration were performed in sand or solution cultures (Grattan, Grieve 1993) our results supported the idea that salinity enhances uptake of P by roots (Fig. 5). This effect was most pronounced for *H. vulgaris*. These observations were contradictory to the earlier study by Ullrich-Eberius and Yingchol (1974).

The maintenance of a high cytosolic K/Na concentration ratio is a key requirement for plant growth in salt (Glenn et al. 1999). Higher K/Na ratio can improve plant resistance to salinity (Asch et al. 2000). It is widely recognized that a high Na concentration inhibits K uptake by plants (Grattan, Grieve 1993; Dorsaf et al 2004; Fuchs et al. 2005). On the other hand, Na appeared to stimulate the K content in several species (Mahmooad 1996; Basra, Basra 1997). No difference in K uptake was evident in previous experiments with *A. tripolium* leading to significant increase in the ratio Na to K (Ramani et al. 2006). In the vacuole the amount of Na clearly increased with increasing NaCl concentration while the amount of K was relatively unaffected. In contrast, Cooper (1982) found about a three-fold decrease in K concentration in *A. tripolium* leaves together with a decline in Ca content. In the present experiments K concentration increased both in leaves and roots of *A. tripolium* and decreased in leaf blades of *H. vulgaris* under the effect of increasing NaCl concentration (Fig. 6) thus supporting the idea that a higher K/Na ratio is indeed associated with higher salinity tolerance and can be regarded as an adaptive response (Ben Hamed 2008).

Calcium is known to play a special role in tolerance under salinity. Increased concentration of Ca in cells has a certain protective effect against high NaCl concentration including minimization of leakage of cytosolic K as well as protection of membrane integrity against Na replacement of Ca and Mg (Cramer et al. 1988). In the present experiments no significant changes in Ca level were observed indicating that this was not the case. Reduced accumulation of Ca in leaves and increased in roots is a common response of halophytic species to increased salinity (Romero, Marañón 1996). In addition it was suspected that the sensitivity of *Arabidopsis* plants to 50 mM NaCl was due to inhibition of K or Ca root transport (Attia et al. 2008). A high K and Ca level could contribute to osmoprotection (Bohnert et al. 1999). However, it was shown that salinity caused a decrease in concentrations of K and Ca in wheat plants only at deficient nutrient solution macronutrient concentrations (Hu, Schmidhalten 1997)

The most striking effect of elevated substrate NaCl was found in respect to Mn concentration, which increased in all the organs of both species (Fig. 8). Increase of Mn concentration with salinity has been noted for the annual legume *Melilotus segetalis*, which is well adapted to elevated salinity (Romero, Marañón 1996) and for other halophytic plant species (Williams 1994). It could be assumed that increased uptake of Mn, Fe and Cu with increasing substrate salinity in the present study is related to equalization of ion uptake. In contrast to our results, in another study with *A. tripolium* increased substrate salinity resulted in a three-fold decrease in shoot K and Mn concentration as well as a statistically significant decrease of Ca and Fe (Cooper 1982). Surprisingly, NaCl treatment in drained conditions did not result in elevated shoot Na concentration in these experiments.

Sulfur is a key element in plant stress responses because of a well known role of glutathione in antioxidative defense (Rausch, Wachter 2005; Baker, Pilbeam 2007). A striking difference was found in the present experiments between the studied species in respect to the effect of increased substrate NaCl on tissue S concentration (Fig. 6). While a decrease in S content was found in leaves of both species and in root tissues of *A. tripolium*, a significant increase was evident both in leaf petioles and stolons of *H. vulgaris* indicating that the observed changes in the latter case of could be attributed to an indirect effect of NaCl.

While no general trend was found in the present experiments for the effect of high NaCl on mineral concentrations in tissues of *H. vulgaris* and *A. tripolium*, adaptive responses leading to maintenance of an optimal supply of mineral nutrients in conditions of high Na and Cl concentrations in cells can be seen. When the same changes of a particular nutrient were evident under the effect of elevated substrate NaCl, both in leaves and roots or in leaf blades and leaf petioles of *A. tripolium* and *H. vulgaris*, respectively, where comparable concentrations of NaCl accumulated, the direct effect of high tissue concentration of Na and Cl could be expected. In particular, this was the case with significantly decreased concentration of a particular mineral. When considering increased concentration of particular minerals in tissues at elevated substrate salinity both active equalization of ion uptake and an effect of growth inhibition-related ion accumulation should be taken in to the account.

Acknowledgements

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Minerālā statusa izmaiņas piekrastes augiem *Hydrocotyle vulgaris* un *Aster tripolium* paaugstināta augsnes sāļuma ietekmē

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Kopsavilkums

Darba mērķis bija izpētīt paaugstināta NaCl satura substrātā ietekmi uz minerālvielu koncentrāciju divu jūras piekrastes augu *Hydrocotyle vulgaris* un *Aster tripolium* audos. Paaugstinātais substrāta sāļums, ko panāca, laistot augus ar NaCl šķīdumu, izsauca Na un Cl jonu uzkrāšanos abu pētīto augu sugu audos. *H. vulgaris* lapu plātnēs un kātos gan Na, gan Cl koncentrācija bija piesātināma. Pretēji tam, Na un Cl koncentrācija *A. tripolium* lapu un sakņu audos pieauga, palielinoties to koncentrācijai substrātā. N un P koncentrāciju atšķirīgi ietekmēja pieaugošs substrāta NaCl daudzums: N un P līmenis palielinājās *H. vulgaris* audos, N koncentrācija samazinājās , bet P koncentrācija – pieauga *A. tripolium* saknēs. NaCl ietekme uz S saturu bija pretēja abām pētītajām sugām – tas pieauga *H. vulgaris* lapu kātos un stolonos, bet samazinājās gan *A. tripolium* lapās, gan saknēs. Visizteiktākais pieaugums NaCl ietekmē bija novērojams attiecībā uz Mn. Cu koncentrācijas pieaugums bija raksturīgs abu sugu visiem audiem, bet Fe koncentrācija pieauga *A. tripolium*, kā arī *H. vulgaris* lapās. Var secināt, ka pētāmajiem augiem piemīt iespējami adaptīvas reakcijas, kas vērstas uz optimāla minerālvielu satura nodrošināšanu augstas šūnu Na un Cl koncentrācijas apstākļos.