

# Different plant species accumulate various concentration of Na<sup>+</sup> in a sea-affected coastal wetland during a vegetation season

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## Abstract

The aim of the present study was to determine if plant species coexisting in highly heterogeneous conditions of coastal wetland display different strategies in respect to accumulation of Na<sup>+</sup> in their tissues. A 50-m-long transect was established in a sea-affected wetland on the coast of the Riga Bay of the Baltic Sea in the territory of Mērsrags, Latvia. Several plant species both in a wetland part (*Rumex hydrolapathum* Huds., *Bolboschoenus maritimus* (L.) Palla, *Scirpus tabernaemontani* C.C.Gmel., *Juncus compressus* Jacq.) and drier part [*Trifolium pratense* L., *Taraxacum officinale* (L.) Weber ex F.H.Wigg. and *Festuca arundinacea* Schreb.] of the transect were sampled four times during the vegetation season. Soil electrical conductivity as well as Na<sup>+</sup> and K<sup>+</sup> concentration in soil solution were monitored along the transect. Soil electrical conductivity measured in field was highly fluctuating both on temporal and spatial scales, and concentration of Na<sup>+</sup> in soil solution showed high temporal variability. Na<sup>+</sup> concentration in leaf extracts showed a species-specific pattern with pronounced changes along the transect and during a vegetation season. Leaf Na<sup>+</sup> concentration showed only species-specific weak to moderate correlation with Na<sup>+</sup> concentration in soil solution indicating that other factors determined rate of Na<sup>+</sup> accumulation in leaves. Leaf K<sup>+</sup> concentration had only weak positive or even negative correlation with K<sup>+</sup> concentration in soil solution, with exception of *J. compressus* and *T. pratense*, which had a moderately tight relationship. Leaf K<sup>+</sup>/Na<sup>+</sup> concentration ratio was extremely variable. The highest values were evident in plants (*T. pratense*, *T. officinale* and *F. arundinacea*) from the drier part of the transect, especially, at low Na<sup>+</sup> concentration in soil solution. In general, a positive correlation between K<sup>+</sup>/Na<sup>+</sup> ratio and Na<sup>+</sup> concentration in soil solution was characteristic for all plant species and it was moderate to high. For *R. hydrolapathum*, Na<sup>+</sup> was excluded both from roots and flowers, and preferentially accumulated in the oldest leaves and their petioles. *R. hydrolapathum* emerged as a potential Na<sup>+</sup> accumulator species, as leaf Na<sup>+</sup> concentration of plants growing in a sea-affected wetland was constantly higher than that of other adjacent species. These characteristics indicate potential of *R. hydrolapathum* in metal accumulation and as useful model species for phytoremediation studies.

**Key words:** coastal wetland, electrical conductivity, halophytes, K<sup>+</sup>/Na<sup>+</sup> concentration ratio, potassium, salinity, sodium.

**Abbreviations:** EC, electrical conductivity.

## Introduction

Soil chemical heterogeneity is one of the fundamental abiotic features of sea-affected coastal wetlands (Bedford et al. 1999; Ievinsh 2006; Ji et al. 2009). In this type of habitats, changes in both sea level as well as amount of precipitation result in highly dynamic hydrological regimes, in further affecting soil chemical features and fluctuations in water and oxygen availability in soil (Karlsons et al. 2017). Ecophysiological adaptations to abiotic heterogeneity in coastal wetlands are a relatively little studied aspect of ecophysiology of wild plants. Most studies so far have focused on different aspects of salinity tolerance of individual wetland plant species (e.g., Tabot, Adams 2012; Touchette et al. 2012; Benzarti et al. 2014; Lee et al. 2016).

The two main physiological strategies of salinity tolerance are related either to salt exclusion or salt accumulation

(Flowers, Colmer 2008). Typical dicotyledonous halophyte species are salt-tolerant accumulators, with leaf Na<sup>+</sup> concentration significantly increasing at a greater rate than in roots. Given the fact that not all plant species in saline wetlands are typical halophytes, it is reasonable to suggest that plants with clearly distinctive adaptation strategies can coexist in these conditions. It has been already discussed that species-specific variation in salt tolerance mechanisms is important for vegetation zonation in salt marshes at different scales (Shumway, Bertness 1994). As an indicator for the presence of different strategies, tissue concentration of Na<sup>+</sup> could be used.

The aim of the present study was to determine if plant species coexisting in highly heterogeneous conditions of coastal wetland display different strategies in respect to accumulation of Na<sup>+</sup> in their tissues.

## Materials and methods

The selected study site was located on the coast of the Riga Bay of the Baltic Sea in the territory of Mērsrags, Latvia (N 57°20'39", E 23°07'39"). A transect was selected in a north–south direction starting 110 m from a coastline, in such a way that it included 40 m of wetland and 10 m of drier adjacent meadow (Fig. 1B). Wooden poles (1.5 m in height) were used to mark 5 m intervals.

Particular plant species were selected for the study because of their abundance: these species were present almost in all 5-m sites along the transect. The selected species were *Rumex hydrolapathum* Huds, *Bolboschoenus maritimus* (L.) Palla, *Scirpus tabernaemontani* C.C.Gmel., *Juncus compressus* Jacq. in the wetland part and *Trifolium pratense* L., *Taraxacum officinale* (L.) Weber ex F.H.Wigg. and *Festuca arundinacea* Schreb. in the drier part of the transect.

On-site measurements and collecting of soil samples and plant material for analysis were performed four times during the vegetation season: on June 6, July 2, August 8, and September 9, 2017. Soil electrical conductivity was measured in three replications at 1 m intervals along the transect using a HH2 moisture meter equipped with a WET-2 sensor (Delta-T Devices, UK). Soil samples were taken from the soil surface using a garden shovel at 5 m intervals. For every species, three leaf samples from three individual plants of each species were taken along the transect at 5-m-intervals. The plants grew not further than 0.5 m from the marker poles. In September, only leaves of *R. hydrolapathum*, which had regrown two weeks after mowing were collected. In August, three individual plants per species were sampled and used for analysis of Na<sup>+</sup> in different parts.

Plant material was dried at 60 °C in a thermostat until a constant mass. Plant tissue was crushed by hand to small pieces and a 0.2 g sample was randomly taken for analysis. After grinding with mortar and pestle to a fine powder in

presence of quartz sand, 10 mL of deionized water was added and incubated for 1 min with stirring. Homogenate was used for measurement after filtration through a nylon mesh cloth (No. 80). Concentration of Na<sup>+</sup> was measured using LAQUAtwin compact meter B-722, K<sup>+</sup> concentration with a LAQUAtwin compact meter B-731, and electrical conductivity with a LAQUAtwin conductivity meter B-771 (Horiba Scientific, Japan). Similarly, electrical conductivity, Na<sup>+</sup> and K<sup>+</sup> concentration were measured in soil solution squeezed from soil samples and filtered through nylon mesh cloth.

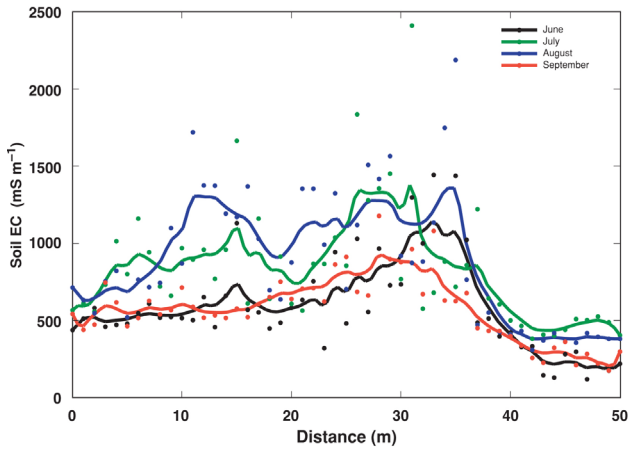
## Results

Soil electrical conductivity (EC) measured in field was highly variable on both temporal and spatial scales (Fig. 2). Soil EC was significantly higher in the more sea-affected part of wetland closer to the coastline (0 to 40 m) than in the drier part (40 to 50 m). However, in contrast to what was expected, no clear sea-affected gradient in EC was evident within the wetland. The highest average soil EC in June was at 32 – 35 m with no large peaks closer to the coastline. Similar trend with almost identical EC values was seen in September, but the highest soil EC was shifted to 28 – 32 m. The highest average EC values were evident in July and August with two distant peaks in July (at 16 and 26 – 32 m) and three peaks in August (12 – 14, 27 – 30 and 35 m).

EC of soil solution measured at 5 m intervals showed less variability than that obtained by direct soil measurements (Fig. 3A). In general, relatively lower values were found in June and September, and the highest in July. It is interesting to note that the highest EC values in July exceeded salinity of sea water at study site. Concentration of Na<sup>+</sup> in soil solution showed high temporal variability (Fig. 3B). It was lowest in June, with a clear decrease towards the drier part of the transect. Na<sup>+</sup> concentration increased in July showing a clear gradient along the transect, while it was highest in August and September, with a less pronounced



**Fig. 1.** Location of the study site in Mērsrags, Latvia (A) and placement of the transect (0 to 50 m) at the study site in respect to the sea coast (B).



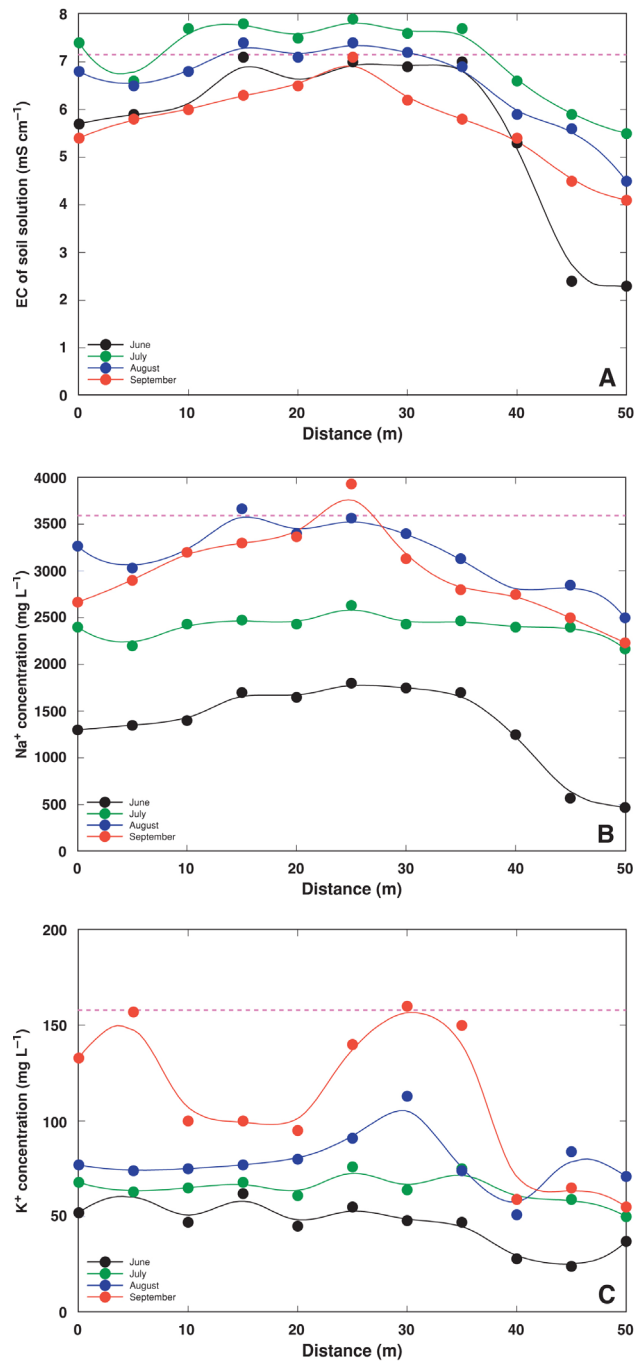
**Fig. 2.** Seasonal changes of soil electrical conductivity (EC) along the transect. Each point represents mean from 3 independent measurements.

gradient towards the drier part. K<sup>+</sup> concentration of soil solution increased during the vegetation season (Fig. 3C). In September maximum values of K<sup>+</sup> concentration at two points on the transect (at 5 and 30 m) reached that of sea water.

Na<sup>+</sup> concentration in leaf extracts of seven plant species showed a species-specific pattern with pronounced changes along a transect and during the vegetation season (Fig. 4). At the beginning of the season in June, average Na<sup>+</sup> concentration in leaves was relatively low, not exceeding 40 g kg<sup>-1</sup>, with the highest values for *R. hydrolapathum* at 0 and 35 m (Fig. 4A). Na<sup>+</sup> concentration was lower in leaves of plant species growing at the drier part of the transect. In July, Na<sup>+</sup> concentration increased in leaves of all species, especially, at 25 – 35 m (Fig. 4B). The highest values (exceeding 100 g kg<sup>-1</sup>) were found for *R. hydrolapathum* at 0 and 35 m. In August, leaf Na<sup>+</sup> concentration decreased in leaves of *B. maritimus* and *S. tabernaemontani* at 0 to 20 m, but it remained high at 25 to 40 m for these species (Fig. 4C). Na<sup>+</sup> concentration was high for *R. hydrolapathum* at 35 – 40 m, but at 10 m, Na<sup>+</sup> level in leaves of *J. compressus* was higher than that for *R. hydrolapathum*. After mowing of wetland vegetation, in September regrown leaves of *R. hydrolapathum* accumulated extremely high concentration of Na<sup>+</sup>, exceeding 160 g kg<sup>-1</sup>, at 0 m (Fig. 4D).

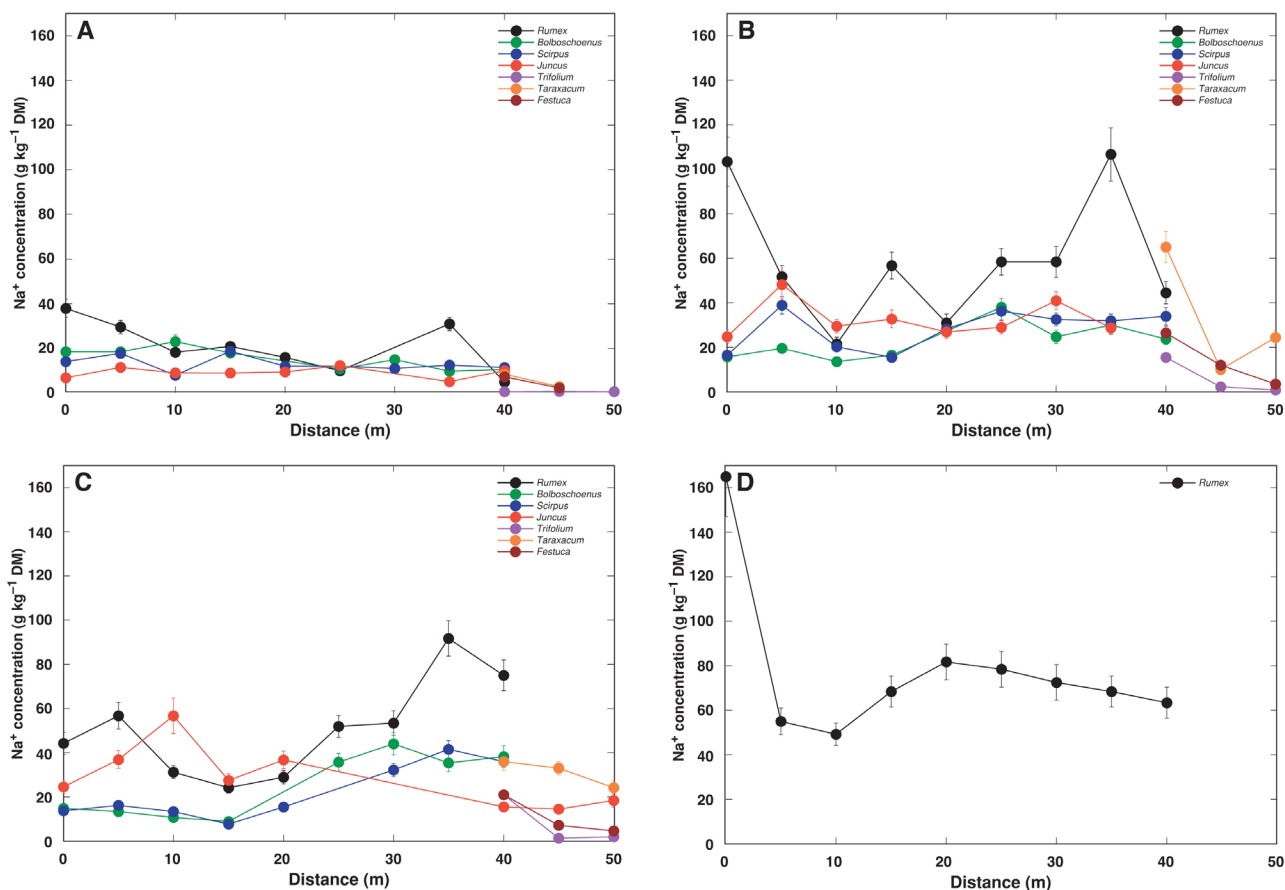
Leaf Na<sup>+</sup> concentration showed only species-specific weak to moderate correlation with Na<sup>+</sup> concentration in soil solution indicating that other factors determined rate of Na<sup>+</sup> accumulation in leaves (Fig. 5). It is also evident that *R. hydrolapathum* plants had ability to accumulate relatively larger amounts of Na<sup>+</sup> in identical conditions in comparison to other plant species.

Data on leaf K<sup>+</sup> concentration showed less season-dependent variation in comparison to Na<sup>+</sup> concentration, but species-specific spatial changes along the gradient were significant (Fig. 6). In June *B. maritimus* had higher leaf concentration of K<sup>+</sup> at 0 – 10 m and further it



**Fig. 3.** Seasonal changes of electrical conductivity (A), Na<sup>+</sup> concentration (B), and K<sup>+</sup> concentration (C) of soil solution along the transect. Dashed line represents the respective values in sea water.

decreased. *S. tabernaemontani* had high K<sup>+</sup> concentration at 0, 20 – 25 and 35 – 40 m (Fig. 6A). *R. hydrolapathum* had relatively low K<sup>+</sup> concentration. For *S. tabernaemontani* K<sup>+</sup> concentration increased towards drier part of the transect. The highest leaf K<sup>+</sup> concentration was recorded for *T. officinale*, exceeding 70 g kg<sup>-1</sup> in July and August. Leaf K<sup>+</sup> concentration had only weak positive or even negative



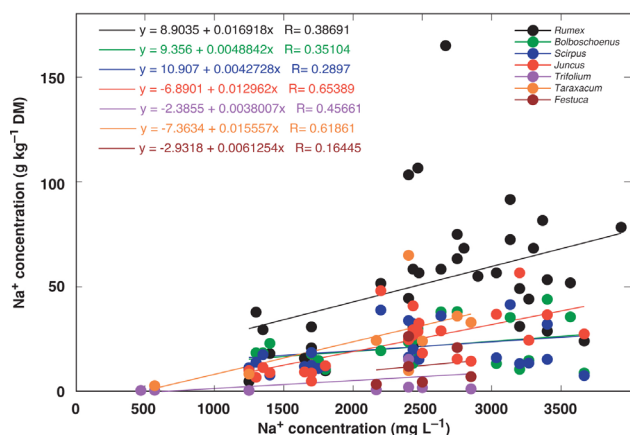
**Fig. 4.** Changes of plant tissue  $\text{Na}^+$  concentration along the transect in June (A), July (B), August (C), and September (D). Data are means from 3 replicates  $\pm$  SE per species for every point.

correlation with  $\text{K}^+$  concentration in soil solution, with exception of *J. compressus* and *T. pratense*, for which this relationship was moderately tight (Fig. 7).

Leaf  $\text{K}^+/\text{Na}^+$  concentration ratio was extremely variable. The highest values were evident in plants from the drier part of the transect, growing in soil with low  $\text{Na}^+$  concentration in soil solution, i.e. *T. pratense*, *T. officinale* and *F. arundinacea* (Table 1). In general, a positive correlation (moderate to high) between  $\text{K}^+/\text{Na}^+$  ratio and  $\text{Na}^+$  concentration in soil solution was characteristic for all plant species (Fig. 8).

In June electrical conductivity of leaf tissues showed only small differences between species and moderate changes along the transect (Fig. 10A). At 0 – 5 m EC level in *J. compressus* was significantly lower in comparison to other species. In July, *T. hydrolapathum* had higher tissue EC at 0 – 5 and 25 – 35 m (Fig. 10B). In August, leaf EC for *R. hydrolapathum* peaked at 5 and 35 m, for *J. compressus* at 10 m, *B. maritimus* at 25 m, and for *S. tabernaemontani* at 35 – 40 m (Fig. 10C). Leaf EC of *T. hydrolapathum* showed only minor spatial differences except at 0 m (Fig. 10D). Correlation between EC in leaf tissues and that in soil solution was relatively weak (Fig. 10). For *B. maritimus* and *S. tabernaemontani* this correlation was negative. Similarly, moderate negative correlation was found between leaf

tissue EC and  $\text{Na}^+$  concentration in soil solution for *B. maritimus*, *S. tabernaemontani* and *F. arundinacea* (Fig. 11). It was expected to find a tight positive correlation between EC in leaf tissues and summed concentration of  $\text{K}^+$  and  $\text{Na}^+$  in leaf tissue, but this relationship was confirmed only in



**Fig. 5.** Relationship between  $\text{Na}^+$  concentration in leaves of different plant species and  $\text{Na}^+$  concentration in soil solution at the time and point of sampling. The same data as in Fig. 3B and Fig. 4 are used.



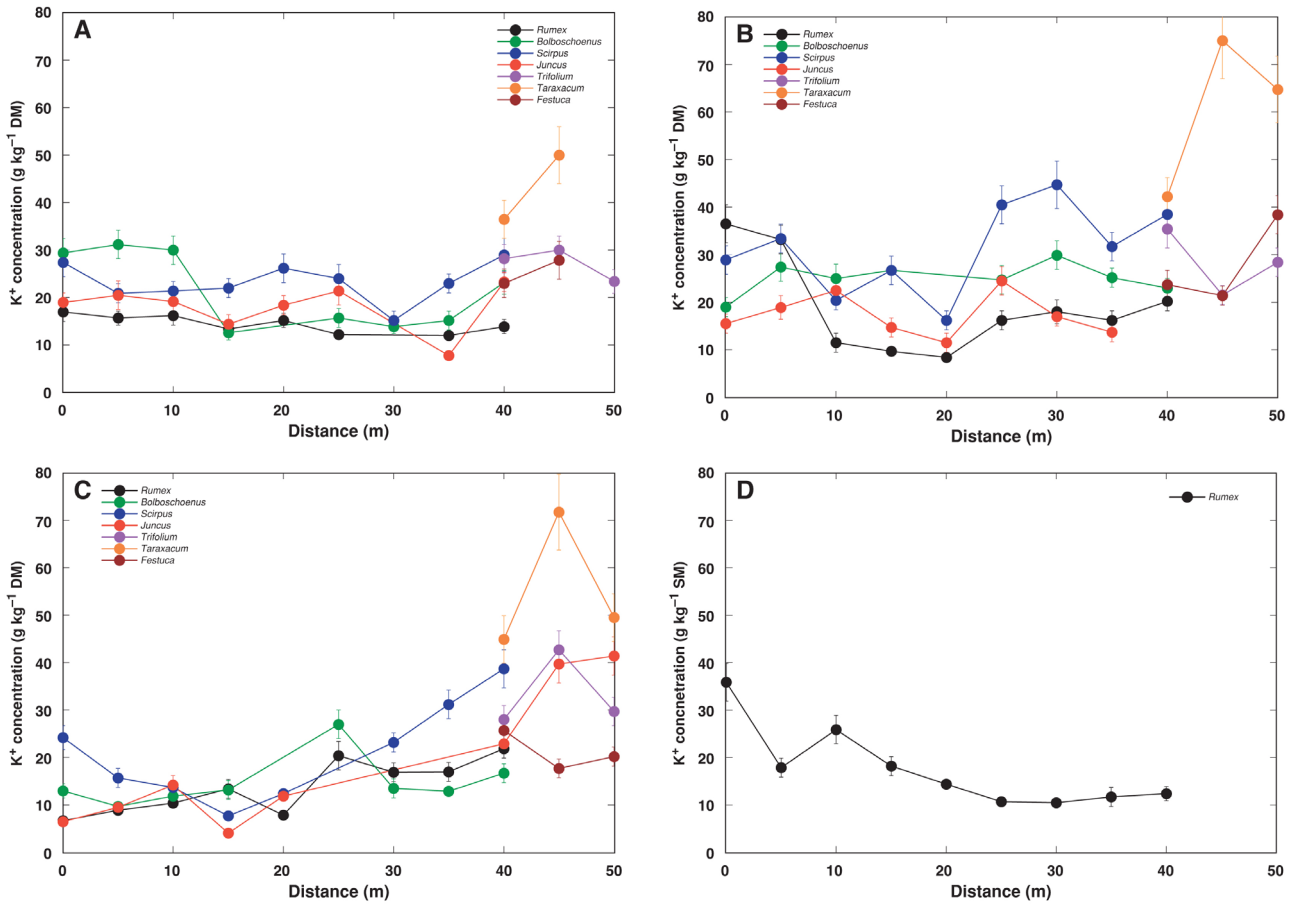


Fig. 6. Changes of plant tissue K<sup>+</sup> concentration along the transect in June (A), July (B), August (C), and September (D). Data are means from 3 replicates ± SE per species for every point.

the case of *R. hydrolapathum* (Fig. 12). For other species, the correlation was less tight and diminished in the order *S. tabernaemontani* > *J. compressus* > *B. maritimus* > *T. pratense* > *T. officinale* > *F. arundinacea* suggesting that other ions besides Na<sup>+</sup> and K<sup>+</sup> significantly contributed to

electrical conductivity in these plant species.

Distribution of Na<sup>+</sup> among various organs was determined for several plant species collected in August. For *R. hydrolapathum*, Na<sup>+</sup> was excluded from both roots and flowers, and preferentially accumulated in the oldest leaves

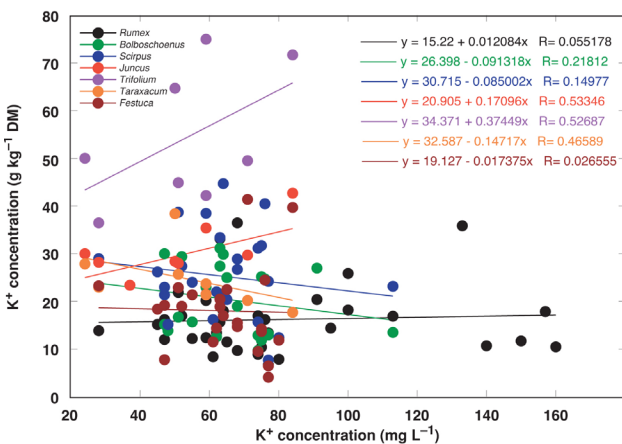


Fig. 7. Relationship between K<sup>+</sup> concentration in leaves of different plant species and K<sup>+</sup> concentration in soil solution at the time and point of sampling. The same data as in Fig. 3C and Fig. 6 are used.

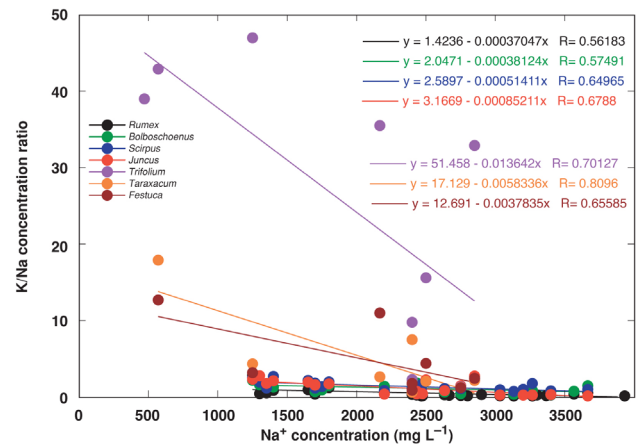


Fig. 8. Relationship between K<sup>+</sup>/Na<sup>+</sup> concentration ratio in leaves of different plant species and Na<sup>+</sup> concentration in soil solution at the time and point of sampling. The same data as in Fig. 3B are used.

**Table 1.** Changes of  $K^+/Na^+$  concentration ratio in leaves of different plant species along the transect during a vegetation season. The data are calculated from these in Fig. 4 and Fig. 5. nd, not determined

Species	Distance (m)	Month			
		June	July	August	September
<i>Rumex hydrolapathum</i>	0	0.45	0.35	0.15	0.22
	5	0.53	0.64	0.16	0.33
	10	0.89	0.54	0.33	0.53
	15	0.64	0.17	0.55	0.27
	20	0.96	0.27	0.27	0.18
	25	1.23	0.28	0.39	0.14
	30	nd	0.31	0.32	0.15
	35	0.39	0.15	0.19	0.17
	40	2.84	0.45	0.29	0.20
	<i>Bolboschoenus maritimus</i>	0	1.59	1.21	0.87
5		1.69	1.41	0.72	nd
10		1.30	1.85	0.96	nd
15		0.70	1.63	1.48	nd
20		nd	nd	nd	nd
25		1.47	0.65	0.76	nd
30		0.93	1.21	0.31	nd
35		1.57	0.84	0.37	nd
40		2.20	0.97	0.44	nd
<i>Scirpus tabernaemontani</i>		0	1.96	1.76	1.77
	5	1.18	0.86	0.97	nd
	10	2.71	1.00	1.02	nd
	15	1.18	1.73	1.00	nd
	20	2.18	0.58	0.81	nd
	25	2.00	1.12	nd	nd
	30	1.38	1.38	0.72	nd
	35	1.84	0.99	0.75	nd
	40	2.54	1.14	1.08	nd
	<i>Juncus compressus</i>	0	2.79	0.63	0.27
5		1.78	0.39	0.26	nd
10		2.13	0.76	0.25	nd
15		1.62	0.45	0.15	nd
20		1.96	0.43	0.32	nd
25		1.74	0.85	nd	nd
30		nd	0.42	nd	nd
35		1.56	0.48	nd	nd
40		2.33	nd	1.48	nd
45		nd	nd	2.74	nd
<i>Trifolium pratense</i>	40	47.00	2.30	1.33	nd
	45	42.90	9.80	32.90	nd
	50	39.00	35.50	15.60	nd
<i>Taraxacum officinale</i>	40	4.35	0.65	1.25	nd
	45	17.90	7.50	2.17	nd
	50	nd	2.65	2.05	nd
<i>Festuca arundinacea</i>	40	3.19	0.90	1.22	nd
	45	12.70	1.78	2.46	nd
	50	nd	11.00	4.39	nd

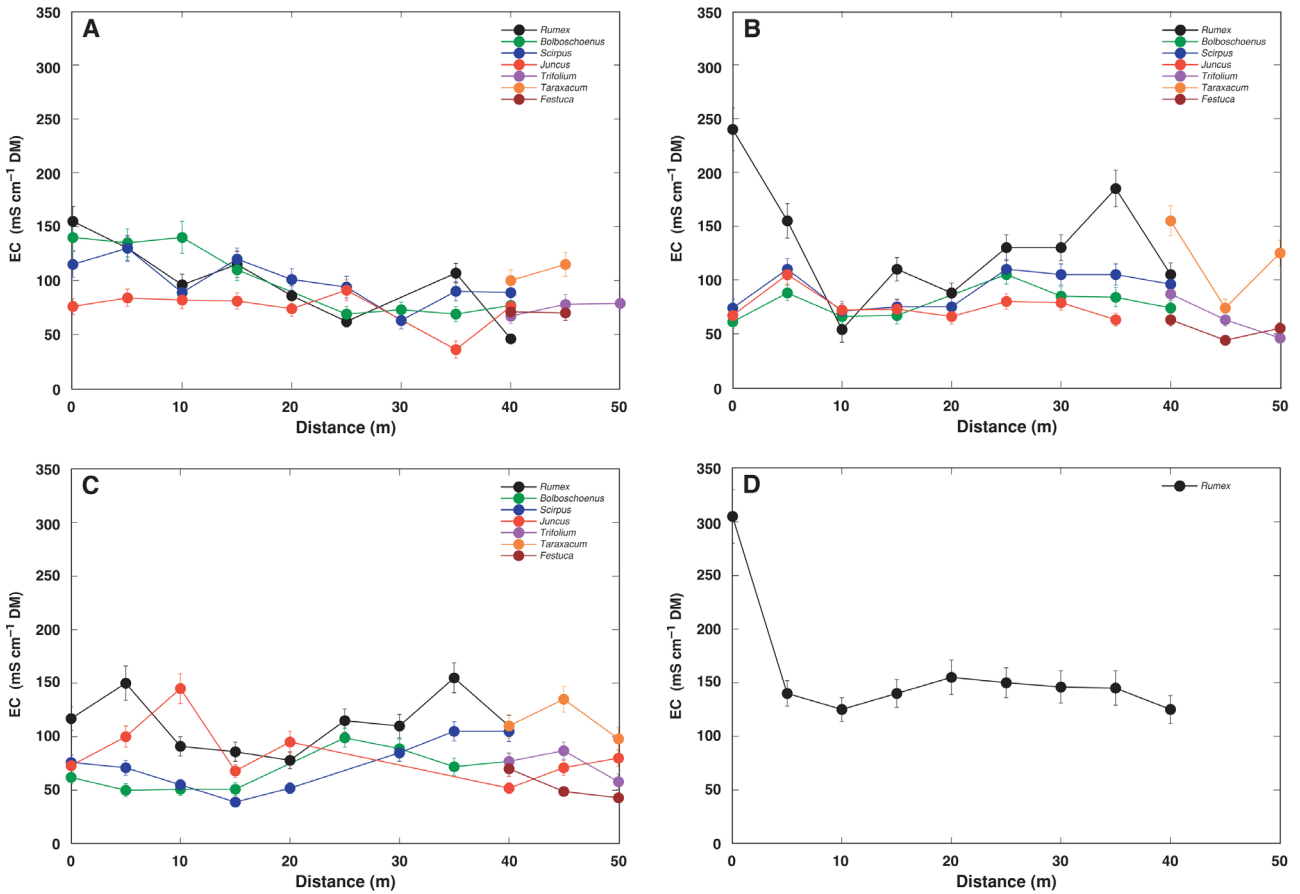


Fig. 9. Changes of leaf extract electrical conductivity (EC) along the transect in June (A), July (B), August (C), and September (D). Data are means from 3 replicates ± SE per species for every point.

and their petioles (Fig. 13). Other typical wetland species, *B. maritimus* and *S. tabernaemontani*, also accumulated Na<sup>+</sup> in leaves and excluded it from flowers (Table 1). A similar pattern of Na<sup>+</sup> distribution was characteristic for *F.*

*arundinacea*, but in *T. officinale* plants the largest amount of Na<sup>+</sup> was accumulated in leaf petioles. Interestingly, for *T. pratense* Na<sup>+</sup> was excluded from inflorescences, was low in both leaves and petioles, and accumulated in stolons.

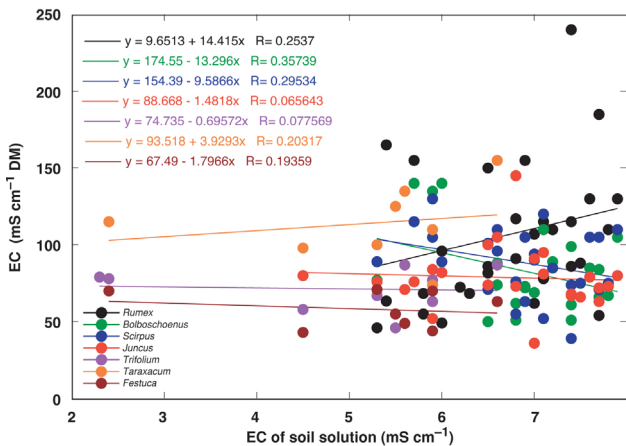


Fig. 10. Relationship between electrical conductivity (EC) in leaf extracts of different plant species and electrical conductivity in soil solution at the time and point of sampling. The same data as in Fig. 3B and Fig. 9 are used.

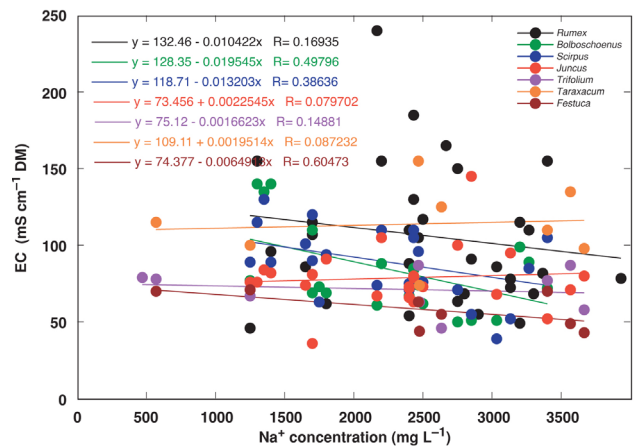
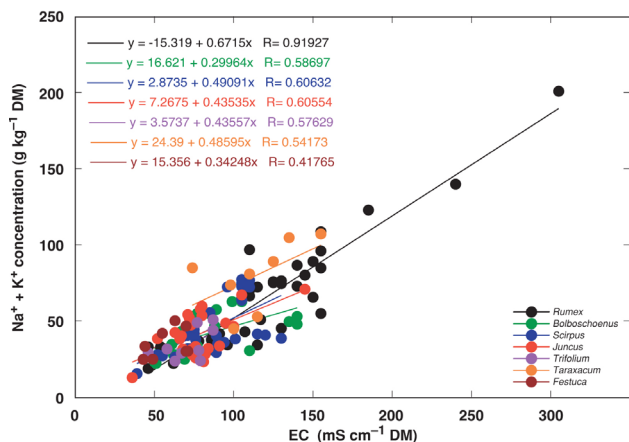


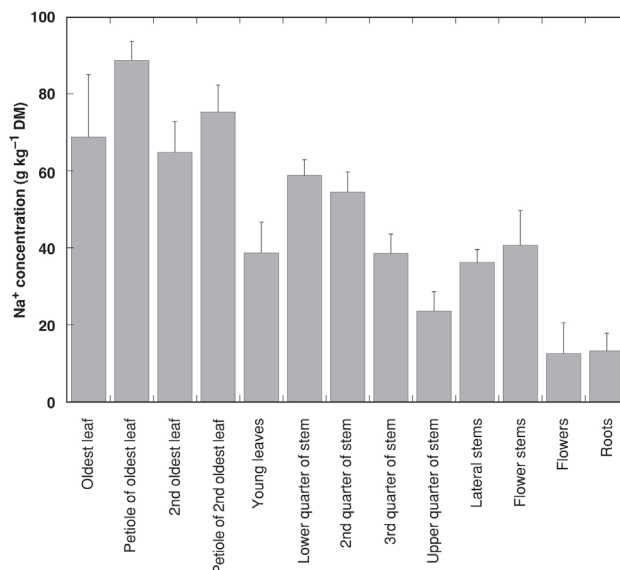
Fig. 11. Relationship between electrical conductivity (EC) in leaf extracts of different plant species and Na<sup>+</sup> concentration in soil solution at the time and point of sampling. The same data as in Fig. 3A and Fig. 9 are used.



**Fig. 12.** Relationship between electrical conductivity (EC) in leaf extracts of different plant species and summed concentration of  $\text{Na}^+$  and  $\text{K}^+$  in leaves.

## Discussion

We did not aim to study factors affecting soil chemical heterogeneity in a coastal wetland, but rather to test whether the spatial and temporal heterogeneity found can differentially affect accumulation of  $\text{Na}^+$  and  $\text{K}^+$  in tissues of different native plant species. Studies comparing ion accumulation in tissues of different plant species in natural saline-affected conditions are rarely described in the literature, especially those that examined seasonal effect. In a study of phreatophytic desert plants in a hyperarid desert, it was found that four adjoining plant species employed different salt adaptation strategies: dilution of salts by succulence, exclusion by salt glands together with low constant shoot  $\text{K}^+/\text{Na}^+$  ratio, low shoot  $\text{Na}^+$  concentration with high  $\text{K}^+/\text{Na}^+$  ratio, and low shoot  $\text{Na}^+$  concentration with high  $\text{K}^+$  and  $\text{Ca}^{2+}$  concentration (Arndt et al. 2004). In conditions of sea-affected coastal vegetation, the typical saline wetland species *Aster tripolium*, *Glaux maritima*, *Triglochin maritima*, *Trifolium fragiferum* and *Plantago maritima* showed typical features of salt accumulators, as these species had concentrations of 80 to 110  $\text{g kg}^{-1} \text{Na}^+$  in leaves during the peak of soil  $\text{Na}^+$  (3.5  $\text{g L}^{-1}$ ) in June. This concentration sharply decreased to steady state level of 20  $\text{g kg}^{-1} \text{Na}^+$  in *Aster tripolium*, *Glaux maritima*, *Trifolium fragiferum* and 40  $\text{g kg}^{-1} \text{Na}^+$  in *Triglochin maritima*, *Plantago maritima*, when soil  $\text{Na}^+$  concentration declined



**Fig. 13.** Gradient of  $\text{Na}^+$  concentration in different parts of *Rumex hydrolapathum* plants in August. Data are means from 3 replicates  $\pm$  SE.

from 1.4 to 0.5  $\text{g L}^{-1}$  in the period from July to September (Karlsons et al. 2017). In the present study, comparable levels of  $\text{Na}^+$  in soil solution were attained in both August and September (Fig. 3B), but high concentration of  $\text{Na}^+$  in leaves (above 100  $\text{g kg}^{-1}$ ) was reached only for *R. hydrolapathum* at some points along the transect in July, August and September (Fig. 4). In general, correlation between leaf  $\text{Na}^+$  concentration and that in soil solution was comparably low, even for *R. hydrolapathum* (Fig. 5), indicating that factors other than soil  $\text{Na}^+$  concentration affected intensity of  $\text{Na}^+$  accumulation in leaves.

In light of the present study, one could be tempted to ask whether all halophyte species represent  $\text{Na}^+$  hyperaccumulators? Of course, there are no accepted criteria for hyperaccumulation of  $\text{Na}^+$ , but for biogenous heavy metals, like plant nutrients Zn and Mn, the critical concentration in tissue is 1% (10  $\text{g kg}^{-1}$ ; Baker, Brooks 1989). Another criterion is shoot to root concentration ratio, which needs to be  $> 1$  (Macnair 2003). Comparative data on maximum  $\text{Na}^+$  accumulation in different halophyte species cannot be easily found in the literature, therefore, only some examples are mentioned further (data are recalculated in g per kg dry mass). Halophyte *Sesuvium*

**Table 2.** Concentration of  $\text{Na}^+$  ( $\text{g kg}^{-1} \text{DM}$ ) in various parts of different plant species in August. Data are means from 3 replicates  $\pm$  SE

Plant part	<i>Bolboschoenus maritimus</i>	<i>Scirpus tabernaemontani</i>	<i>Trifolium pratense</i>	<i>Taraxacum officinale</i>	<i>Festuca arundinacea</i>
Leaves	25.1 $\pm$ 3.0	22.0 $\pm$ 4.3	8.0 $\pm$ 0.4	31.1 $\pm$ 5.7	10.9 $\pm$ 0.9
Inflorescences	3.8 $\pm$ 0.4	2.9 $\pm$ 0.4	1.8 $\pm$ 0.2	–	2.1 $\pm$ 0.2
Leaf petioles	–	–	7.3 $\pm$ 0.6	45.9 $\pm$ 5.9	3.0 $\pm$ 0.4
Stolons	–	–	21.2 $\pm$ 4.4	–	–
Leaf sheaths	–	–	–	–	8.8 $\pm$ 0.7



*portulacastrum* accumulated maximum concentration 22 g kg<sup>-1</sup> Na<sup>+</sup> growing in field and greenhouse conditions at 12 to 20 mS cm<sup>-1</sup> soil EC (Muchate et al. 2016). In another study, however, *Sesuvium portulacastrum* and *Mesembryanthemum crystallinum* accumulated up to 110 and 130 g kg<sup>-1</sup> Na, respectively, in a hydroponic system in greenhouse conditions in the presence of 100 mM NaCl (Ghnaya et al. 2007). Moreover, when cultivated in greenhouse in sand culture under 400 mM NaCl, *Sesuvium portulacastrum* and *Tecticornia indica* accumulated 218.5 and 184.0 g kg<sup>-1</sup> Na in shoots, respectively (Rabhi et al. 2012). The coastal species *Centaurea ragusina* accumulated 138 g kg<sup>-1</sup> Na in shoots when treated with 300 mM NaCl (Radić et al. 2013). *Salicornia europaea* and *Suaeda maritima* in greenhouse conditions accumulated 103.8 and 52.0 g kg<sup>-1</sup> Na in shoots, respectively, when treated with 510 mM NaCl (Moghaieb et al. 2004).

Even salt tolerant cultivated plants, like sugar beet cultivars, can accumulate 25 to 40 g kg<sup>-1</sup> Na<sup>+</sup> in leaves in a treatment range 50 to 200 mM NaCl (Ghoulam et al. 2002). In the same range, sheaths of sorghum leaves subjected to 100 mM NaCl treatment accumulated up to 34.5 g kg<sup>-1</sup> Na<sup>+</sup> (de Lacerda et al. 2003). As sorghum is a grass species, which are usually considered as Na<sup>+</sup> excluders that control translocation of Na<sup>+</sup> from roots to shoots or possess leaf salt glands for NaCl secretion to leaf surface (Hester et al. 2001), it seems interesting to provide some examples of Na<sup>+</sup> accumulation in selected species of the grass family. Among grasses, the rhizomatous perennial halophyte *Spartina alterniflora* accumulated up to 41.4 g kg<sup>-1</sup> fresh mass Na<sup>+</sup> in leaves when treated with 600 mM NaCl plus Na<sub>2</sub>SO<sub>4</sub> (Li et al. 2010). Shoots of *Phragmites karka* from saline wetlands accumulated 18.4 g kg<sup>-1</sup> of Na at 300 mM NaCl (Abideen et al. 2014). In natural conditions of a salt-affected area, grass species *Cynodon dactylon* and *Thinopyrum ponticum* accumulated only up to 4.5 and 3.1 g Na<sup>+</sup> kg<sup>-1</sup> in shoots, respectively (Bhuiyan et al. 2015). Salt-tolerant ecotype *Festuca rubra* ssp. *litoralis* accumulated 65 and 80 g kg<sup>-1</sup> Na<sup>+</sup> in leaves and roots, respectively, when cultivated at 500 mM NaCl in hydroponics (Diédhiou et al. 2009). In spite of some relatively highly-accumulating grass species, in general, they can be hardly designated as Na<sup>+</sup> hyperaccumulators, because, even at high accumulation rates, plant roots usually have higher concentration of the element in comparison to shoots. In the present study, leaves of *F. arundinacea* accumulated as high as 21.0 g kg<sup>-1</sup> Na<sup>+</sup> in August at the point nearest to the wetland part of the transect (Fig. 4C).

In the present study, there were clear season-dependent changes of average Na<sup>+</sup> concentration in leaves of the studied wetland-adapted species, showing increase from 14.6 ± 1.3 in June to 36.1 ± 3.7 in July and 33.9 ± 3.6 in August. Na<sup>+</sup> concentration increased further in September to 72.4 ± 13.0 g kg<sup>-1</sup> (Fig. 4), which could be in part related to leaf development-related characteristics,

as ion concentrations increase with increasing leaf age (Albert 1975). The highest Na<sup>+</sup> concentration (165 g kg<sup>-1</sup>) was found in *R. hydrolapathum* leaves in September at the point closer to the coastline (Fig. 4D). In comparison to the examples mentioned above, *R. hydrolapathum* appears among the strongest Na<sup>+</sup> accumulators. In this context, it is interesting to note, that so far no *Rumex* species has been described as a halophyte, but there are some studies indicating a potential of some species for reclamation of saline soil (Chen et al. 2004).

Typical glycophyte species, like different wheat varieties, are considered to be salinity tolerant if the ratio of K<sup>+</sup>/Na<sup>+</sup> concentration is at least 2.5 (Chhipa, Lal 1995). A relatively tolerant sorghum cultivar under 100 mM NaCl treatment has observed to have K<sup>+</sup>/Na<sup>+</sup> ratio 1.41, compared to only 0.43 for sensitive cultivar (de Lacerda et al. 2003). However, the data on actual K<sup>+</sup>/Na<sup>+</sup> ratio are rather contradictory. One of the reasons for high variability of K<sup>+</sup>/Na<sup>+</sup> concentration ratio might be related to the ability of some plant species to substitute K<sup>+</sup> with Na<sup>+</sup>, which is thought to be one of the salinity tolerance mechanisms of halophytes (Flowers, Colmer 2008). Consequently, halophyte species can have highly variable K<sup>+</sup>/Na<sup>+</sup> ratio in relation to actual soil salinity. For a salt marsh halophyte, *Sesuvium portulacastrum*, K<sup>+</sup>/Na<sup>+</sup> ratio decreased from 1.25 in control conditions to 0.33 at 20 mS cm<sup>-1</sup> salinity (Muchate et al. 2016). Grass species *Cynodon dactylon* and *Thinopyrum ponticum* from salt-affected native soil showed extremely high K<sup>+</sup>/Na<sup>+</sup> ratio, reaching 22.06 and 7.40 for shoots, and 11.18 and 3.99 for roots, respectively (Bhuiyan et al. 2015). In salt-tolerant *Festuca rubra* ssp. *litoralis*, K<sup>+</sup>/Na<sup>+</sup> ratio decreased from 10 in control conditions to 0.37 and 0.21 in leaves and roots, respectively, under treatment with 500 mM NaCl in hydroponics (Diédhiou et al. 2009). In *Salicornia europaea* and *Suaeda maritima*, K<sup>+</sup>/Na<sup>+</sup> ratio in shoots decreased from 1.6 and 3.9 in control conditions to 0.6 and 1.3 in 510 mM NaCl treatment, respectively (Moghaieb et al. 2004).

It is rather erroneous to conclude that low K<sup>+</sup>/Na<sup>+</sup> tissue ratio automatically reflects a low ratio in cytoplasm, as in halophytes the larger part of Na<sup>+</sup> can be stored in cell vacuole (Flowers, Colmer 2008). Based on the results of the present study, it can be concluded that K<sup>+</sup>/Na<sup>+</sup> ratio in the natural sea-affected wetland is highly variable and has low informative value by itself. The highest ratio (47.0) was characteristic for leaves of *T. pratense* in June at the point near the wetland part of the transect, but declined to 2.3 and even 1.3 in July and August at the same site, respectively.

Given that there is a large chemical similarity between Na<sup>+</sup> and K<sup>+</sup> (Subbarao et al. 2003), would it be possible that K<sup>+</sup> could be more toxic in comparison to Na<sup>+</sup>? Indeed, for a Mediterranean species *Cynara cardunculus*, KCl treatment resulted in more deleterious effect on plant growth than the same concentration of NaCl (Benlloch-González et al. 2005). It is interesting to note that 100 mM KCl-treated plants accumulated 300 mM (11.7 g kg<sup>-1</sup>) K<sup>+</sup> in shoots

in comparison to 180 mM (4.14 g kg<sup>-1</sup>) Na<sup>+</sup> in 100 mM NaCl-treated plants, and this difference was suggested as a main reason for increased toxicity of KCl. However, for the majority of species tested so far, NaCl usually was observed to be more inhibitory in comparison to KCl or Na<sub>2</sub>SO<sub>4</sub>, as in a study with *Trifolium alexandrinum*, where plant relative fresh mass at 200 mM was 47.9, 72.2 and 69.5% of the control, respectively (Abogadallah 2010). In the present study, leaves of *T. officinale* accumulated maximum of 75.0 and 71.7 g kg<sup>-1</sup> K<sup>+</sup>, in July and August, respectively (Fig. 5B and C), with no evident toxicity symptoms. K<sup>+</sup>/Na<sup>+</sup> concentration ratio in these samples were 7.5 and 2.2. Interestingly, *T. officinale* has been used in phytoextraction studies of Zn and Cd and showed relatively high accumulation potential (Muhammad et al. 2012). It seems that K<sup>+</sup>/Na<sup>+</sup> interactions cannot be described only based on positive influence of high K<sup>+</sup>/Na<sup>+</sup> concentration ratio, as it has been experimentally shown that low levels of K<sup>+</sup> can indeed relieve Na<sup>+</sup> toxicity, and that low levels of Na<sup>+</sup> enhance K<sup>+</sup> toxicity (Kinraide 1999).

Typical wetland species (*R. hydrolapathum*, *B. maritimus*, *S. tabernaemontani*) were not found in the drier part of the transect indicating that regular soil flooding rather than salinity can be the limiting factor of distribution. Xerophytic species from Cyperaceae (*B. maritimus* and *S. tabernaemontani*) are known to use a salt dilution mechanism by increasing water content during leaf maturation (Albert 1975). It can be proposed that *R. hydrolapathum* represents a typical basal rosette species, similar to *Aster tripolium* and *Triglochin maritima* (Albert 1975), is being able to initiate development of new leaves when Na<sup>+</sup> concentration in maturing leaves increases. It is interesting that leaf Na<sup>+</sup> concentration of individuals of both “wetland” and “dryland” plant species growing on the border between the two parts of the transect was similar, and it significantly decreased only for “dryland” individuals located further away from the wetland (Fig. 4).

In conclusion, both spatial and temporal, as well as species-specific changes in tissue Na<sup>+</sup> concentration were found in a sea-affected wetland. From a practical point of view, *R. hydrolapathum* emerged as a potential Na<sup>+</sup> accumulator species, as leaf Na<sup>+</sup> concentration of this plant growing in the sea-affected wetland was constantly higher than that of other adjacent species. Moreover, Na<sup>+</sup> was relatively low both in roots (13.2 g kg<sup>-1</sup>) and generative organs (12.5 g kg<sup>-1</sup>), reaching the highest concentration in older leaves (69.2 g kg<sup>-1</sup>) and their petioles (88.6 g kg<sup>-1</sup>) (Fig. 7). These characteristics might indicate potential of *R. hydrolapathum* in metal accumulation and as a useful model species for phytoremediation studies. So far, only some *Rumex* species have been described as efficient metallophytes: *Rumex acetosa* as a Cu accumulator (Ye et al. 2012), *Rumex crispus* as a Zn and Cd accumulator (Zhuang et al. 2007), *Rumex obtusifolius* as an Al hyperaccumulator (Vondráčková et al. 2015) and *Rumex hastatus* as a Cu accumulator (Tang, Fang 2001).

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