

Ranking of 11 coastal halophytes from salt marshes in northwest Turkey according their salt tolerance

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Abstract: Salt-affected soils with high electrolyte contents limit the development of the majority of plants and serve as a habitat only for such species (halophytes) that can survive the conditions. To date, there is still much that is unknown about the physiological mechanisms, including ion relationships, that make plants salt-resistant. The primary aim of this study was to evaluate a method of ranking plants for their salt tolerance. A total of 11 coastal halophytes of the Kavak Delta were evaluated for their ability to cope with different soil salinities. For this, electrical conductivities of soils (of up to 135 dS m⁻¹) were recorded and a total of 100 plant samples, including plant roots, were taken from a depth of 0–15 cm in the soil. The halophytes were ranked in the following order from highest to moderate salt tolerance: *Halocnemum strobilaceum* ≥ *Salicornia fragilis* ≥ *Arthrocnemum fruticosum* = *Suaeda prostrata* ≥ *Salsola kali* = *Petrosimonia brachiata* ≥ *Juncus maritimus* = *Aeluropus litoralis* ≥ *Halimione portulacoides* = *Limonium graecum* ≥ *Artemisia santonicum*. The Na⁺/K⁺ ratios of leaves perfectly reflected the salinity tolerance ranking of all halophytic species examined. It proved possible to rank the salt tolerance of halophytes by assessment of the electrical conductivity of the soil in which they grew naturally; tolerance was well predicted by the Na⁺/K⁺ ratio in the shoots.

Key words: Coastal ecophysiology, salt marsh, halophytes, salt tolerance

1. Introduction

Salt-affected soils with high electrolyte contents limit the development of the majority of plants (Munns and Tester, 2008; Sekmen Esen et al., 2012; Hameed et al., 2013) and serve as a habitat only for such species that can tolerate the conditions caused by the effects of soil salinity. Because of a lack of competition, such habitats provide a niche for halophytes. A halophyte is a plant that completes its life cycle in a salty environment (Flowers and Colmer, 2008). The large majority of plant species, which includes virtually all major crop plants, are glycophytes and are damaged by salinity; many cannot survive even one-tenth the salt concentration found in seawater. Many halophytes, on the other hand, show optimal growth in the presence of salt in the range of 100 to 200 mM (Flowers et al., 1977; Lieth and Menzel, 1999). Some of these halophytes have specialized morphological adaptations to cope with high salinity, such as glandular hairs or succulence. Glandular hairs are one- to many-celled epidermal appendages that remove salt from the body of the plant to the exterior. Rather than remove ions, many species, such as *Salicornia fragilis* P.W.Ball & Tutin, *Suaeda prostrata* Pall., *Halocnemum strobilaceum*

Pall., *Arthrocnemum fruticosum* L., and *Salsola kali* L. (Figure 1), develop succulent leaves or stems. Succulence is mainly a result of increasing the vacuolar volume and thereby managing the cellular distribution of salts and preventing, or at least delaying, accumulation of sodium and chloride in the leaf cytoplasm (Flowers et al., 1986).

The categorization of a plant species as halophytic has proven problematic for a number of important reasons. First, the definition involves drawing an arbitrary line in a continuum of tolerance. Plant species vary in their tolerance, from those that are killed by as little as one-twentieth of the salt concentration in ocean waters to those that are found growing where the concentration can reach more than double that of seawater. Authors (Flowers et al., 1977; Aronson, 1989; Flowers and Colmer, 2008) have drawn the dividing line between glycophyte and halophyte at salt concentrations between about 80 and 200 mM. Herein lies the second difficulty: what salt? As the main source of salt on the earth is its oceans and these are dominated by a mixture of ions that make up seawater, it would be logical to use seawater in the definition. However, some soils can be dominated by salts with very

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Salicornia fragilis



Suaeda prostrata



Halimione portulacoides



Halocnemum strobilaceum



Arthrocnemum fruticosum



Limonium graecum



Salsola kali



Petrosimonia brachiata



Juncus maritimus



Artemisia santonicum



Aeluropus littoralis

Figure 1. Images of halophyte plants from the location at Kavak Delta.

different compositions from that of seawater. This brings us to the third major problem: how to test for salt tolerance. Where plants are clearly growing in seawater, there is no doubt that they are halophytes. However, it is not always easy to know if a species growing close to a seashore, for example in a dune system, is growing in a saline soil. Many experimental determinations of salt tolerance have simply added sodium chloride to the growth medium, which, while simple practically, does not take into account the complex interactions between ions that can occur at the root surface. We argue that it is better to use dilutions of seawater, or to determine the salinity in which the plants grow naturally.

If the dividing line between glycophyte and halophyte is drawn at a relatively low salt concentration, then there may be over 1500 naturally occurring salt tolerant plants

worldwide: trees (including mangroves), shrubs, grasses, and herbs, which constitute about 1% of the world's flora (Aronson, 1989). However, there may be less than 500 species that tolerate seawater (Aronson, 1989). The aim of this study was to test a method of evaluating salt tolerance by determining the salinity of soils in which plants were found growing naturally. For this, a total of 100 plant samples and corresponding soil samples (84) together with plant roots were taken from a depth of 0–15 cm at a site on the Kavak Delta in Turkey. Electrical conductivities (ECs) of soil saturation extracts (up to 135 dS m⁻¹) were matched with plant distribution. Sodium, potassium, and chloride concentrations of plant roots and shoots were measured and the interrelation between soil salinity and growth of individual halophyte species was investigated.

2. Material and methods

2.1. Site description

The plants referred to in this study grew in a naturally salt-affected habitat on the Kavak Delta on the eastern coast of the Gulf of Saros in the northeast of the Aegean Sea, Turkey (Figure 1). The delta is situated in the northwest part of the Gelibolu Peninsula at 40°39'38"N and 40°35'05"N, 26°47'45"E and 26°50'44"E, and it has an area of 2150 ha, with a coastline of 12.3 km (Özcan et al., 2009): the Çanakkale–İstanbul highway constitutes the eastern border of the delta, which is surrounded by the 3 small villages of Kocaçeşme, Kavakköy, and Evreşe (Figure 2). The flood plain of the Kavak Creek, the delta, and the coastal dunes bordering the salt marsh sediments derive from the Quaternary Period. The soils of the Kavak Delta consist of sediments carried by the Kavak Creek and by other small rivers originating in the Korudağı Mountains, extending to the northwest of the area, and can be classified within 3 taxonomic orders: Alfisol, Inceptisols, and Entisols (Özcan et al., 2009). This area has a transitional character between the Black Sea and Mediterranean climate types.

2.2. Analysis of soil and plant samples

In total, 84 soil samples were taken from depths of 0 to 15 cm in September 2009. Samples of different depths were collected using a steel cylinder. The locations of soil samples are indicated in Figure 2; sites varied by up to 10 cm in height and plants did not grow in depressions, where saline water accumulated. Plant communities were, however, present in low islets of 5–10 cm in height and 30–50 cm in radius next to these depressions. Separate soil samples were taken from areas with plants to identify differences of the soil associated with different species. Soil samples were air-dried and then passed through a sieve with a 2-mm mesh. Soil EC of the saturation extract was determined using a WTC Brand EC-meter, model LF 320 (Richards, 1954). Sodium and potassium concentrations of the soil were determined in the soil saturation extracts from the top 5-cm samples by atomic absorption spectrometry (Varian, SpectrAA 22 FS, Agilent Technologies, Santa Clara, CA, USA). Chloride was determined by potentiometric titration using silver nitrate (Chloride Titrator, American Instrument Corporation, Hartland, WI, USA).

Eleven halophyte species were collected from the soil islets: *Aeluropus littoralis* Gouan, *Artemisia santonicum* L., *Arthrocnemum fruticosum* L., *Halimione portulacoides* L., *Halocnemum strobilaceum* Pall., *Juncus maritimus* Lam., *Limonium graecum* Poir., *Petrosimonia* spp. Pall., *Salicornia fragilis* P.W.Ball & Tutin, *Salsola kali* L., and *Suaeda prostrata* Pall. Examples of these plant species and their growth stages when collected are shown in Figure 1. The roots of the plants were dug out and washed with tap water. Afterwards, the plant shoots and roots were dried in

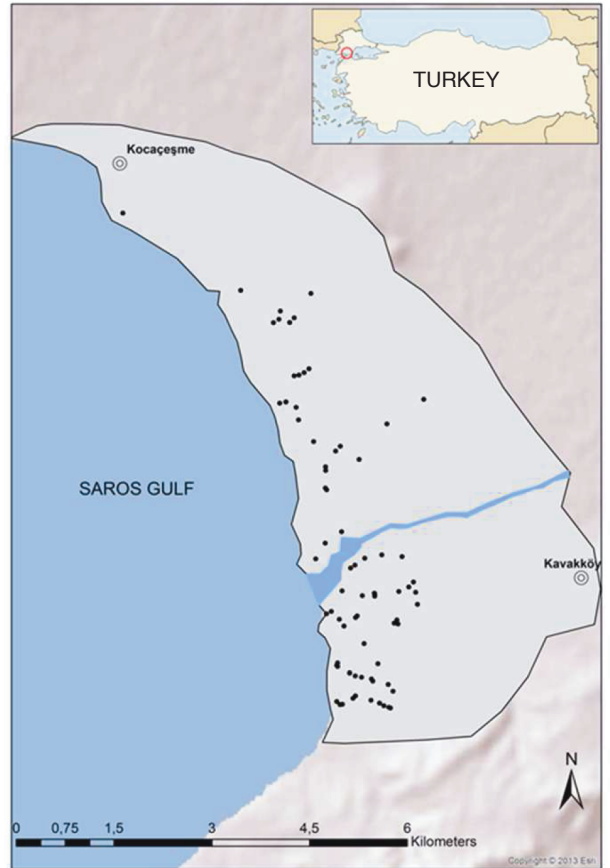


Figure 2. Location map of the study area and soil sampling points.

an oven at 80 °C until constant weight and dry weights of each plant and its parts were recorded. The plant species were sampled in 5 to 8 replications. After weighing, leaves (including stems in the cases of *Arthrocnemum*, *Halocnemum*, and *Salicornia*) and roots were ground to a fine powder using a mill (Pulverisette 14, Fritsch, Idar-Oberstein, Germany) and representative sample fractions were used to analyze ion concentrations. The dry plant material (100 mg) was ashed at 480 °C; the remnant was digested in 2 mL of 5 M HNO₃ and further diluted to a final volume of 100 mL with distilled water. After filtering, the concentrations of sodium and potassium were determined by atomic absorption spectrometry (Varian, SpectrAA 22 FS, Agilent Technologies).

For the extraction of chloride, dry, ground plant material (200 mg) was incubated in 50 mL of deionized water at 90 °C with gentle agitation in a water bath for 3 h. Chloride was then determined quantitatively by potentiometric titration using silver nitrate (Chloride Titrator, American Instrument Corporation).

Data are presented as means of all replicates ± the standard error of the mean (SE).

Statistical evaluation was carried out using the Tukey test algorithm of the Student range using SAS software (SAS Institute Inc., Cary, NC, USA). Significance was tested at the 5% level.

3. Results

3.1. Soil salinity status and halophytes growing in different salinities

We analyzed the soil in which the majority of the roots were found – from the surface to 5 cm, from 5 cm to 10 cm, and from 10 cm to 15 cm depth – and the conductivities

of the root environment of 11 species are shown as a box plot in Figure 3 (median, lowest, and highest values and 25% quartiles). Accordingly, these 11 species were ranked in terms of salt tolerance by the use of the median EC values of saline soils in which their roots were growing. *Halocnemum strobilaceum* was the most tolerant (Figure 3), having the highest median EC values of 99 dS m⁻¹ in shallow soil (depth: 0–5 cm) followed by 62 and 52 dS m⁻¹ at 5 to 10 cm and 10 to 15 cm, respectively. The species *Salicornia fragilis* and *Arthrocnemum fruticosum* (Figure 3), with similar salinity tolerance, grew at median EC

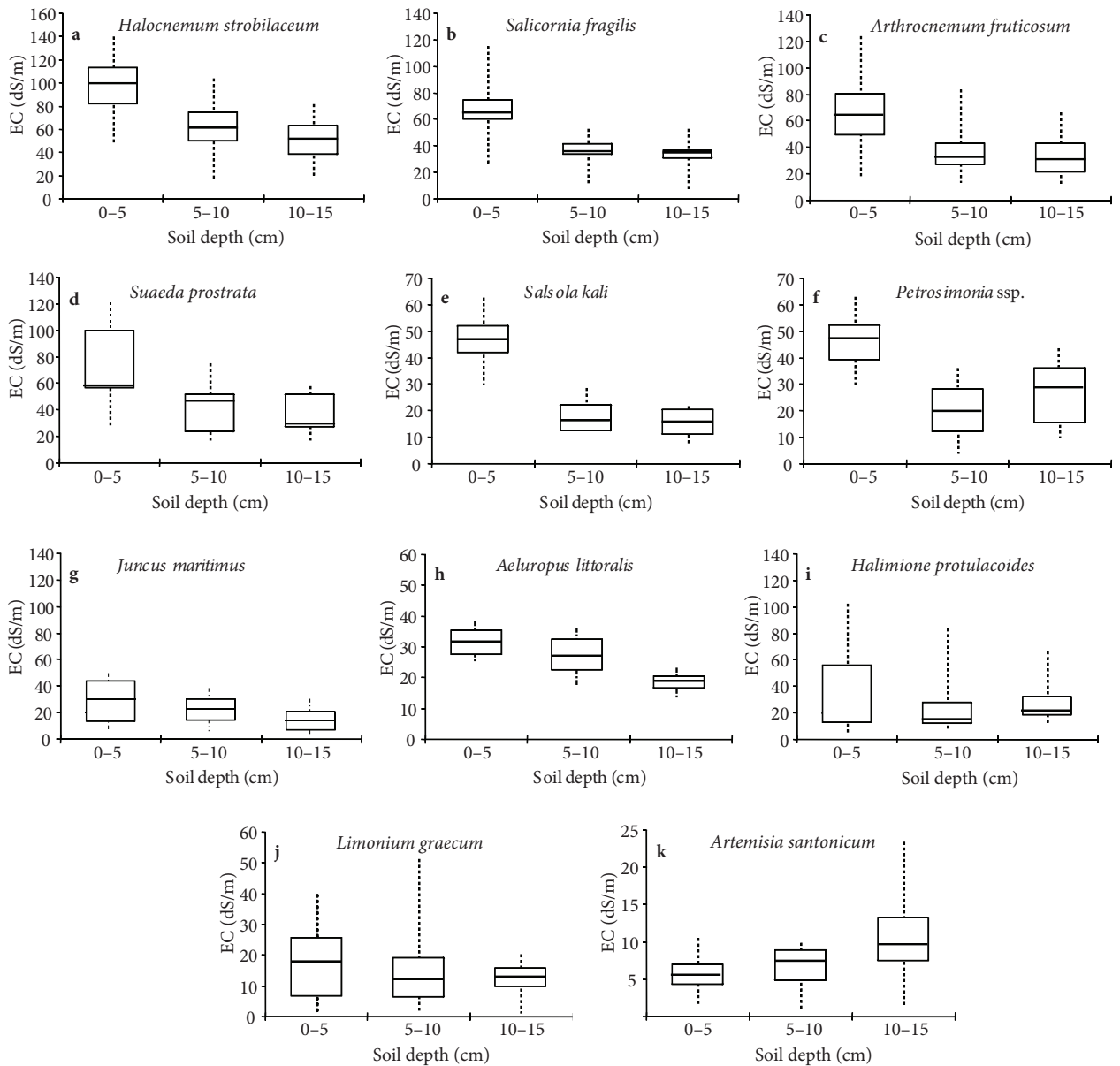


Figure 3. Ranking of species on the basis of EC values (a–k) by box-plot histograms. EC values of saturated pastes of soil were taken from depths of 0–5 cm, 5–10 cm, and 10–15 cm in which 11 halophytic species were growing. Box-plots: median, horizontal line; lowest and highest values, vertical dotted lines; 25% quartile, box.

values of 64 dS m⁻¹ in the upper soil layer and at about one-half this salinity at depths of 5–10 cm (33 dS m⁻¹) and 10–15 cm (31 dS m⁻¹). Next in the ranking was *S. prostrata*, which grew at a level of 59 dS m⁻¹ in the upper soil layer, with values decreasing the deeper the roots grew (46 and 30 dS m⁻¹). *Salsola kali* and *Petrosimonia brachiata* grew at 48–49 dS m⁻¹ at depths to 5 cm, but salinity values strongly decreased at 5 to 10 and 10 to 15 cm to values of approximately 16–28 dS m⁻¹. *Juncus maritimus* and *Aeluropus littoralis* grew at 30–32 dS m⁻¹ in the upper soil layer, with decreasing values at 5–10 cm (21–28 dS m⁻¹) and 10–15 cm (16–19 dS m⁻¹). The habitats of *Halocnemum portulacoides* and *Limonium graecum* had moderate soil salinity levels of about 12–20 dS m⁻¹. In comparison with all other halophytes at this site, *Artemisia santonicum* showed the lowest salt tolerance and the roots grew only at salinity values below 10 dS m⁻¹ (Figure 3).

NaCl is the predominant salt in saline soil of the Kavak Delta, so we analyzed sodium and chloride concentrations in soil samples derived from the root environment of each plant species separately. Table 1 shows that the sodium concentrations of the root environment of all species were higher than the chloride concentrations. Highest sodium levels were tolerated by *Halocnemum strobilaceum* (1.3 M in the saturation extract), followed by most other species ranging between about 400 and 800 mM. *Artemisia santonicum* only grew at low sodium concentrations in the root soil environment of about 200 mM. The chloride concentrations ranged between 42 and 603 mM, with the highest concentrations found in the

soil environment of *Halocnemum strobilaceum*; the soil chloride concentrations of all the other species ranged up to 603 mM soil. Some species such as *Petrosimonia* sp., *Aeluropus littoralis* and *Halocnemum portulacoides* only grew at chloride concentrations below 75 mM.

3.2. Sodium, potassium, and chloride concentrations in 11 halophytes

As shown in Table 2, root sodium concentrations of the halophytes sampled ranged between 7 and 185 µmol g⁻¹ DW: the highest concentrations in roots were measured in *Salicornia fragilis*. The sodium concentrations in leaves also varied considerably but were much higher than in the roots, ranging between 0.1 and 5.6 mmol g⁻¹ DW; *Salicornia fragilis* and *Suaeda prostrata* had the highest sodium concentrations (5.6 and 5.2 mmol g⁻¹ DW, respectively) in their leaves (the leaves of *Salicornia fragilis* are decurrent and cannot be separated from the stems). Lowest sodium concentrations were detected in *Juncus maritimus* (0.1 mmol g⁻¹) and *Aeluropus littoralis* (0.1 mmol g⁻¹).

Table 2 shows that potassium concentrations in leaves were lowest in *Aeluropus littoralis* (0.22 mmol g⁻¹ DW) and highest in *Salsola kali* (0.5 mmol g⁻¹ DW), demonstrating a low variability in leaf tissues of about 50%. Most species had root potassium concentrations in the range of 0.05 to 0.14 mmol g⁻¹ DW, but *Halocnemum strobilaceum* and *Aeluropus littoralis* showed potassium concentrations of between 0.03 and 0.02 mmol g⁻¹ DW. The potassium concentrations of roots were at least one-third to one-fourth lower than those of leaves.

Table 1. Na⁺ and Cl⁻ concentrations and corresponding Na/Cl ratios of the rooting soil medium and ranking of plant species according to their average chloride and sodium concentration and Na/Cl ratio. EC values (dS m⁻¹) and ion concentrations used were those in soil extracts taken from the region 0–5 cm below the surface. Rankings are from highest values (1) to lowest (11) values. Statistical analysis of data was performed on the basis of the 5% level using the Tukey test algorithm of the Student range and SAS software. Different letters indicate significant differences of the means.

Plant name	Na ⁺ (mM)	Rank	Cl ⁻ (g/kg)	Rank	Na ⁺ /Cl ⁻ ratio	Rank	EC* rank
<i>Halocnemum strobilaceum</i>	1344 a	1	603 a	1	1.44	8	1
<i>Salicornia fragilis</i>	820 b	2	349 b	2	1.52	7	2
<i>Juncus maritimus</i>	719 d	5	350 b	2	1.33	10	7
<i>Salsola kali</i>	731 d	5	339 bc	3	1.40	9	5
<i>Suaeda prostrata</i>	769 c	4	269 d	4	1.85	6	4
<i>Limonium graecum</i>	806 b	3	219 e	5	2.38	5	8
<i>Artemisia santonicum</i>	207 h	10	173 f	6	0.77	11	9
<i>Arthrocnemum fruticosum</i>	622 e	6	74 g	7	5.40	3	3
<i>Halimione portulacoides</i>	417 g	9	67 g	7	4.01	4	8
<i>Aeluropus littoralis</i>	476 f	8	54 h	8	5.70	2	7
<i>Petrosimonia</i> spp.	602	7	42 i	9	9.30	1	6

*: EC at 0–5 cm.

Table 2. Concentration and corresponding rankings of Na⁺, K⁺ and Cl⁻ in root and leaf of halophytes. Rankings were from highest values (1) to lowest values (11). Statistical analysis of data was performed on the basis of the 5% level using the Tukey test algorithm of the Student range and SAS software. Different letters indicate significant differences of the means. Abbreviations: *Halocnemum str.*: *Halocnemum strobilaceum*, *Arthrocnemum fr.*: *Arthrocnemum fruticosum*, *Halimione portul.*: *Halimione portulacoides*, *Limonium graec.*: *Limonium graecum*, *Artemisia sant.*: *Artemisia santonicum*, *Aeluropus littoral.*: *Aeluropus littoralis*.

Plant name	Na ⁺ (μmol g DW ⁻¹) ± SE		K ⁺ (μmol g DW ⁻¹)		Cl ⁻ (μmol g DW ⁻¹) ± SE							
	Root	Leaf	Root	Leaf	Root	Leaf						
		Rank	Rank	Rank	Rank	Rank	Rank					
<i>Salicornia fragilis</i>	185 ± 57.0 a	1	5605 ± 555 a	1	122 ± 26.8 c	3	340 ± 59.3 e	5	1241 ± 710 a	1	2912 ± 82 a	1
<i>Suaeda prostrata</i>	158 ± 11.2 b	2	5215 ± 709 b	2	141 ± 6.3 a	1	385 ± 40.4 d	4	679 ± 101 b	2	2380 ± 219 b	2
<i>Halocnemum str.</i>	46.6 ± 6.9 g	7	4658 ± 597 c	3	30.8 ± 4.0 g	9	258 ± 54.0 h	8	238 ± 11.3 h	8	2083 ± 46 c	3
<i>Petrosimonia</i> spp.	85.7 ± 14.1 de	5	4163 ± 248 d	4	125 ± 19.1 c	3	463 ± 29.9 b	2	392 ± 76.1 e	5	1113 ± 31 f	6
<i>Arthrocnemum fr.</i>	93.0 ± 13.5 d	4	3778 ± 79 e	5	55.3 ± 10.4 f	6	298 ± 8.2 f	6	479 ± 33.8 d	4	1802 ± 44 d	4
<i>Halimione portul.</i>	58.0 ± 15.7 f	6	3669 ± 118 f	6	76.9 ± 8.0 e	5	431 ± 16.3 c	3	217 ± 7.0 i	9	1687 ± 43 e	5
<i>Salsola kali</i>	102 ± 10.5 c	3	3608 ± 222 f	6	137.4 ± 9.8 ab	2	500 ± 36.3 a	1	336 ± 66.5 f	6	616 ± 54 g	7
<i>Limonium graec.</i>	16.8 ± 1.9 i	10	837 ± 188 g	7	51.4 ± 5.4 f	7	223 ± 8.3 i	9	257 ± 34.7 g	7	495 ± 36 h	8
<i>Aartemisia sant.</i>	31.5 ± 8.5 h	8	483 ± 28 h	8	87.6 ± 6.2 d	4	288 ± 26.1 fg	7	135 ± 13.1 j	10	196 ± 25 i	9
<i>Juncus maritimus</i>	19.5 ± 2.2 i	9	266 ± 74 i	9	47.7 ± 3.3 g	8	169 ± 18.2 j	10	56 ± 12.6 k	11	70 ± 11 j	10
<i>Aeluropus littoral.</i>	7.8 ± 2.1 j	11	103 ± 22 j	10	20.7 ± 2.8 h	10	121 ± 22.1 k	11	560 ± 55 c	3	196 ± 15 i	9

The potassium concentrations of the roots of many of the halophytes were higher than sodium concentrations, resulting in Na⁺/K⁺ ratios all ranging below 1. The ratios of Na⁺/K⁺ (Table 3) of roots of all species were lower than those of the leaves; however, *Halocnemum strobilaceum* (10.6) and *Salicornia fragilis* (9.7) had highest values in leaves. The highest Na⁺/K⁺ ratios in the roots were in *Arthrocnemum fruticosum* (0.99), *Salicornia fragilis*, and *Halocnemum strobilaceum* (both 0.89). K⁺/Na⁺ selectivities (S_{K,Na}), calculated from the Na⁺/K⁺ ratio in the plant divided by that in the soil (both on a molar basis), ranged from 0.09 (*Halimione portulacoides*) to 2.63 (*Juncus maritimus*) in leaves and from 1.02 (*Halocnemum portulacoides*) to 10.07 (*Juncus maritimus*) in roots (Table 3).

Chloride concentrations of plant leaves were in a range of 0.07 to 2.9 mmol g⁻¹ DW (Table 2). Highest chloride concentrations were detected in leaves of *Salicornia fragilis* (2.9 mmol g⁻¹ DW) and lowest concentrations were in *Artemisia santonicum* and *Juncus maritimus*. Roots had chloride concentrations ranging from 0.06 mol g⁻¹ DW in *Juncus maritimus* to the highest concentrations in *Salicornia fragilis* of 1.2 mmol g⁻¹ DW. Na⁺/Cl⁻ ratios were calculated (Table 3) and showed higher values in leaves compared to roots. The highest ranking species in roots and leaves were *Salsola kali* and *Petrosimonia* spp., whereas *Juncus maritimus* ranked the lowest for both parts.

4. Discussion

Resistance to NaCl appears to be the most important factor correlated with distribution of saltmarsh vegetation

(Rozema et al., 1985; Liangpeng et al., 2007). The main reason for salinity in the area studied was the capillary rise of salts in highly saline (as seawater) ground water. Evaporation of water at the soil surface then resulted in salt accumulation, especially in the upper 15 cm. A similar situation has been reported in many other studies at other saline habitats close to the sea (Schofield and Kirkby, 2003; Özcan et al., 2009). In the Kavak Delta area, the soil salinity values varied over a large range, between 5 and 135 dS m⁻¹, making them all saline and above the level of ≥4 dS m⁻¹ set by the International Soil Salinity Laboratory (Richards, 1954).

4.1. Ranking of halophytes

According to definition (Richards, 1954) all of the soil samples of the area studied would be characterized as saline or extremely saline. Nevertheless, this soil supported a range of plant species and we ranked their tolerances according to the EC of the soil in which they were growing. Among the 11 species of halophyte in the area, *Halocnemum strobilaceum* was found to grow at the highest EC values of up to 135 dS m⁻¹ in the saturation extract. The salt tolerance of the other species was, from highest to moderate salt tolerance: *Halocnemum strobilaceum* ≥ *Salicornia fragilis* ≥ *Arthrocnemum fruticosum* = *Suaeda prostrata* ≥ *Salsola kali* = *Petrosimonia brachiata* ≥ *Juncus maritimus* = *Aeluropus littoralis* ≥ *Halimione portulacoides* = *Limonium graecum* ≥ *Artemisia santonicum* (Table 1; Figure 3). To our knowledge, this is the first ranking of halophytes according to the salinity of the soil in their

Table 3. Na^+/K^+ ratio, Na^+/Cl^- ratio, and $\text{K}^+/-\text{Na}^+$ selectivities ($S_{\text{K,Na}}$) in root and leaf of halophytes. Selectivities were calculated by dividing the molar ratio of K/Na in the plant by that in the soil. The species are listed in the order of the Na concentration in the leaves as provided in Table 2.

Plant name	Na^+/K^+ ratio		Na^+/Cl^- ratio		$S_{\text{K,Na}}$	
	Root	Leaf	Root	Leaf	Leaf	Root
<i>Salicornia fragilis</i>	0.89	9.7	0.10	1.25	0.15	1.67
<i>Suaeda prostrata</i>	0.66	7.9	0.15	1.42	0.19	2.31
<i>Halocnemum strobilaceum</i>	0.89	10.6	0.13	1.45	0.17	1.99
<i>Petrosimonia</i> spp.	0.40	5.2	0.14	2.42	0.19	2.55
<i>Arthrocnemum fruticosum</i>	0.99	7.5	0.13	1.36	0.26	1.92
<i>Halimione portulacoides</i>	0.44	5.0	0.17	1.41	0.09	1.02
<i>Salsola kali</i>	0.44	4.2	0.20	3.79	0.69	6.66
<i>Limonium graecum</i>	0.19	2.2	0.04	1.10	0.24	2.79
<i>Artemisia santonicum</i>	0.21	0.9	0.15	1.60	0.54	2.51
<i>Juncus maritimus</i>	0.24	0.9	0.02	0.88	2.63	10.07
<i>Aeluropus littoralis</i>	0.22	0.5	0.09	0.95	2.03	4.61

natural habitat. In comparison to these species, moderately salt-resistant crop plants such as cotton and barley show reduced growth and yield at soil salinity levels of $\geq 8 \text{ dS m}^{-1}$ (Maas and Hoffman, 1977).

Plants with particularly succulent stems and leaves such as *Suaeda prostrata* and *Salicornia fragilis* were found in clusters in the higher salt concentrations, whereas those halophytes with salt glands (*Halocnemum portulacoides*, *Limonium graecum*, and *Artemisia santonicum*) were more common in the lower salt concentrations. Referring to Liangpeng et al. (2007), the accumulation of sodium and chloride is most significant among the major kinds of salt ions in saline soils.

4.2. Ion relations

The halophytes analyzed in this study clearly differed in the salinity of the soil in which they grew naturally. The soil EC values, which had a range from 5 to 99 dS m^{-1} in the top 5 cm of soil (given as a median in Figure 3), correlated linearly with rankings of the sodium concentrations (expressed per unit dry weight) in that soil ($R^2 = 0.91$; Table 1).

Chloride concentrations were a little more variable than those of sodium; standard deviation as a percentage of the mean [coefficient of variation (CoV)] was 72% for chloride and 48% for sodium, but sodium and chloride concentrations in the soil were linearly related ($R^2 = 0.61$), although the samples taken from the soils in which *Artemisia santonicum* and *Limonium graecum* were growing weakened the correlation. Soil potassium showed a similar degree of variation (CoV = 50%) to sodium, but it was not correlated with soil EC and hence plant salt tolerance.

Within the plant, the sodium concentrations varied considerably between species. In the leaves, where ions are eventually accumulated, the range was between 5.6 (*Salicornia fragilis*) to 0.1 (*Aeluropus littoralis*) mmol g^{-1} DW. Leaf chloride concentrations were similarly variable (CoV = 80% compared with 71% for sodium); leaf potassium was less variable (CoV = 38%), reflecting its essential role in the metabolism of all species. Yaseen and Abu-Al-Basal (2008) also reported high accumulation of sodium and chloride and lower concentrations of K^+ and Mg^{2+} in *Limonium axillare* plants. The ranking of tolerance based on the chloride concentration in the soil was, in general, a better predictor of salt tolerance (based on soil EC) than was soil sodium concentration (Table 1).

Ranking plants for their leaf sodium concentrations produced a similar order to that using leaf chloride (Table 2). The group with the highest ion concentrations (*Salicornia fragilis*, *Suaeda prostrata*, *Halocnemum strobilaceum*, and *Arthrocnemum fruticosum*) included those species growing in the soils with the highest EC values. The correlation between soil EC (0–5 cm) and leaf sodium concentration ($R^2 = 0.61$; $n = 8$) was higher than for chloride ($R^2 = 0.46$; $n = 8$) and there was no correlation between soil EC and leaf potassium concentration ($R^2 = 0$). However, Na^+/K^+ ratios of leaves reflected salinity tolerance rankings based on the EC values of the soil in which they were growing ($\text{Na}^+/\text{K}^+ \text{ ratio} = 1.7 \times \text{EC} + 2$; $R^2 = 0.85$). Root Na^+/K^+ ratios were also correlated but did not reflect salinity tolerance ranking as exactly. The selectivity for potassium over sodium (Table 3) is characteristically higher in mono- than in dicotyledonous plants (Flowers and Colmer, 2008), although there are few values in the

literature with which to make direct comparisons for the species we investigated. For *Halimione portulacoides* the value we calculated (0.1) was very much lower than that (8) determined by Harrouni et al. (2003), just as our value for *Halocnemum strobilaceum* (0.2) was lower than the values (between 2 and 4, depending on the external salt concentration) determined by Pujol et al. (2001). Our value for *Salsola kali* (0.7) was similar to that (1) calculated by Eshel (1985). We do not have explanations for these differences other than the fact that our values were calculated from plants growing in their natural soil while the other data from the literature were from experiments using some form of solution culture.

Where plants accumulate high concentrations of cations, the balancing anion concentrations are generally similar in concentration (Flowers and Colmer, 2008). *Halocnemum strobilaceum*, *Salicornia fragilis*, and *Suaeda prostrata*, the species showing tolerance to the highest soil salinities (Table 1), also tolerated the highest chloride concentrations in the leaf tissues ($>2 \text{ mmol g}^{-1}$). *Halocnemum strobilaceum* and *Suaeda prostrata* had the ability to accumulate chloride primarily in the leaves but not in roots. In general, chloride concentrations in shoots of the plants from the Kavak marsh were considerably higher than in roots (Table 2), other than in the grass *Aeluropus litoralis*. Presumably this reflects the transport of chloride (and sodium) from the roots to accumulate in the shoots. It is interesting that in the grass species *Hordeum marinum* Na^+/Cl^- was also well below 1 (Garthwaite et al., 2005),

although this is not characteristic of all grasses (Flowers and Colmer, 2008). Na^+/Cl^- ratios of all halophytes were less variable than Na^+/K^+ ratios (Table 3), suggesting that the influence of a sodium-induced potassium deficiency on potassium might be greater than that of chloride toxicity. However, the data clearly show that the amount of chloride by itself cannot achieve ion homeostasis as formerly shown in the literature (Tipirdamaz et al., 2006). This implies that other anions have to be accumulated to ensure electroneutrality at the cell level. Although high Cl^- concentrations may inhibit nitrate uptake, induced nitrogen deficiency is not likely to be an important factor in the growth depression caused by soil salinity (Marschner, 1993).

In conclusion, it is clearly possible to rank the salt tolerance of halophytes by assessment of the salinity of their natural habitat. The rankings of this survey show that halophytes such as *Halocnemum strobilaceum*, *Salicornia fragilis*, *Arthrocnemum fruticosum*, and *Suaeda prostrata* were highly salt-tolerant. Among the halophytes tested, tolerance was well predicted by the Na^+/K^+ ratio in the shoots.

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