

# Effects of sodium on nitrate uptake and osmotic adjustment of *Suaeda physophora*

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**Abstract:** Na<sup>+</sup> ions play an important role in the growth of halophyte. The effect of Na<sup>+</sup> ions on nitrate uptake and osmotic adjustment in the euhalophyte *Suaeda physophora* was investigated under glasshouse conditions. Seedlings were exposed to 1 mmol/L NaCl (control), 300 mmol/L NaCl, 150 mmol/L NaCl plus 150 mmol/L KCl or 300 mmol/L KCl treatments for 24 d. Dry weight was not affected greatly by different salt treatments, but water content and succulence in leaves of *S. physophora* were significantly increased at 300 mmol/L NaCl and 150 mmol/L NaCl plus 150 mmol/L KCl treatments. The concentrations of Na<sup>+</sup> and NO<sub>3</sub><sup>-</sup> in leaves of *S. physophora* were the highest at 150 mmol/L NaCl plus 150 mmol/L KCl, but lowest at 300 mmol/L KCl treatment. Moreover, the increase of NO<sub>3</sub><sup>-</sup> concentration did not result in the decrease of Cl<sup>-</sup> concentration at 150 mmol/L NaCl plus 150 mmol/L KCl treatments. The estimated contribution of NO<sub>3</sub><sup>-</sup> to osmotic potential (C<sub>NO<sub>3</sub></sub>) in leaves of *S. physophora* was 9.8% at 150 mmol/L NaCl plus 150 mmol/L KCl, and C<sub>Na</sub> and C<sub>Cl</sub> were 31.0% and 23.3%, respectively. However, C<sub>NO<sub>3</sub></sub>, C<sub>Na</sub> and C<sub>Cl</sub> were respectively 1.6%, 7.9% and 11.9% at 300 mmol/L KCl treatment. It is concluded that Na<sup>+</sup> stimulates NO<sub>3</sub><sup>-</sup> absorption and the stimulation is independent on the internal or the external Cl<sup>-</sup> concentration in the euhalophyte *S. physophora*. These characteristics may explain the high levels of N in leaves of saline desert plants in arid ecosystem.

**Keywords:** euhalophyte; *Suaeda physophora*; NaCl; KCl; NO<sub>3</sub><sup>-</sup>

## 1 Introduction

High concentration of salts in soils is the basic environmental factor accounting for decreased crop productivity in many geographic areas, mainly in arid and semi-arid regions (Greenway and Munns, 1980). The injurious effects of salinity are associated with water deficit, ionic imbalance, mineral nutrition, stomata behavior, photosynthetic efficiency, and carbon allocation and utilization (Greenway and Munns, 1980; Bohnert *et al.*, 1995). The physiological mechanisms involved in nutrient deficiencies by salinity, however, have not been completely resolved.

Sodium is an important microelement for halophyte growth, and it participates in the process of photosynthesis (Ohta *et al.*, 1987), osmotic adjustment (Yeo and Flowers, 1980; Blumwald *et al.*, 2000) and maintaining water potential gradient (Balnokin *et al.*, 2005). In addition, although it has been proposed that both

Na<sup>+</sup> and Cl<sup>-</sup> are involved in the osmotic adjustment of halophytes in response to high soil salinity, it showed that Na<sup>+</sup> ions contribute more efficiently than Cl<sup>-</sup> ions to perform this function (Ramos, 2004). And phenomenon which stress effects imposed by Na<sup>+</sup> on seedlings were weaker than those by Cl<sup>-</sup> ions was observed in soybean (Chen and Yu, 2007) and *Citrus* species (Romero-Aranda *et al.*, 1998). Nutrition deficiency could be caused by over dominance of specific ions (Bernstein *et al.*, 1974). However, much of the recent research focus on the suppression to Cl<sup>-</sup> antagonism of NO<sub>3</sub><sup>-</sup> absorption (Bar *et al.*, 1997; Cerezo *et al.*, 1999), while the role of Na<sup>+</sup> ions, its frequently occurring counter-ion, has been relatively ignored. Little information is available on the role of Na<sup>+</sup> ions in the nitrate uptake and osmotic adjustment

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process in euhalophytes. Therefore, the present study was designed to test the hypothesis that the effect of  $\text{Na}^+$  ions on the nitrate uptake and osmotic adjustment was more pronounced than those  $\text{Cl}^-$  ions in the leaf-succulent euhalophyte *Suaeda physophora* (Chenopodiaceae). In addition, we want to determine if *S. physophora* plants are able to grow well in the absence of significant  $\text{Na}^+$  amounts.

## 2 Materials and methods

### 2.1 Plant material

Seeds of *Suaeda physophora* Pall. were collected from plants growing in a saline land (44°9'N, 87°50'E) in Xinjiang, northwestern of China. Seeds were stored in refrigerator at  $< 4^\circ\text{C}$  before use.

### 2.2 Plant culture and experimental design

Seedlings of *S. physophora* were raised from seeds in plastic pots, 15 cm in diameter and 15 cm in depth, filled with acid-rinsed quartz sand in April 2007. There were 10 seedlings in each pot. The seedlings were cultured in greenhouse in Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences. The temperatures range between 18–23°C at night and 25–30°C during the day, and the relative humidity was maintained at 65% approximately. The plants were irrigated every two days with full-strength Hoagland's nutrient solution.

After 7 weeks of pre-culture, seedlings of *S. physophora* were divided into four groups for treatments: (1) 1 mmol/L NaCl (control); (2) 300 mmol/L NaCl; (3) 150 mmol/L NaCl plus 150 mmol/L KCl; (4) 300 mmol/L KCl. NaCl and KCl concentrations were increased every two days in equal increments for two weeks to the final concentrations. The experiment was terminated at 24 d after final salt concentrations were reached. The shoots and roots were harvested separately. Fresh plant samples were frozen in liquid N before use. Osmotic potential and concentrations of  $\text{Cl}^-$ ,  $\text{NO}_3^-$ , amino acid and proline were measured on fresh samples, while the concentrations of  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$ , and  $\text{Mg}^{2+}$  were determined on dry samples.

### 2.3 Determination of water content, fresh weight, dry weight and succulence in plant

Plant materials were first cleaned with distilled water. After the water on the plant was absorbed by tissue

paper, fresh weight (FW) was measured. Dry weight (DW) was then measured after the fresh material was dried at 80°C for 72 h. Water content of leaves was determined as  $\text{WC} = (\text{FW} - \text{DW}) / \text{DW} \times 100\%$ . Succulence was calculated as  $\text{FW} / \text{DW}$ .

### 2.4 Determination of inorganic ions and organic solutes in plant tissues

Frozen plant materials were extracted with boiling distilled water, and the concentrations of  $\text{Cl}^-$  and  $\text{NO}_3^-$  were determined. The  $\text{NO}_3^-$  concentration was determined (UV-120-02 Spectrophotometer, Shimadzu, Kyoto, Japan) by the colorimetric method (Cataldo *et al.*, 1975), and the concentration of  $\text{Cl}^-$  was determined by the 0.03 mM  $\text{AgNO}_3$  titration method, with 5%  $\text{K}_2\text{CrO}_4$  as an indicator. The frozen plant tissues were ground in 10% acetic acid, and the ninhydrin colorimetric method was used for the determination of the concentration of amino acids (Moore and Stein, 1948) and the concentration of proline (Troll and Lindsley, 1955). A 25 mg of dried plant material was placed in a muffle furnace to be ashed. The ash was dissolved with concentrated nitric acid and then diluted to a volume of 100 ml with deionized water. The  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  were determined with an atomic absorption spectrophotometer (Thermo Solaar M, Thermo Electron, American). Three replicates were set up for each treatment.

### 2.5 Determination of osmotic potential

The frozen plant tissues were put into a syringe to thaw. The liquid squeezed from the plant tissues was put into a freezing point osmometer (Osmomat 030, Gonotec, Berlin, Germany) to determine osmotic potential.

### 2.6 Statistic analysis

Data were subjected to One-way analysis of variance (ANOVA) using SAS<sup>TM</sup> software. Treatment means were compared by least significant differences (LSD) at  $P = 0.05$ .

## 3 Results

### 3.1 Effects of different salt treatments on the dry weight, water content, succulence and root shoot ratio of *S. physophora*

Dry weight (DW) in shoot and water content (WC) in

root were not significantly different among various salt treatments, while water content in shoot, dry weight in root and succulence of *S. physophora* were respectively 20.3%, 75.0% and 39.4% higher at 150 mmol/L NaCl plus 150 mmol/L KCl than that in control. A similar trend was observed at 300 mmol/L NaCl. However, dry weight, water content and succulence were the same as control in the case of plants growing in the presence of 300 mmol/L KCl except for the root shoot ratio (Table 1).

### 3.2 Effects of different salt treatments on the concentrations of $\text{Na}^+$ , $\text{K}^+$ , $\text{Cl}^-$ , $\text{NO}_3^-$ , $\text{Ca}^{2+}$ and $\text{Mg}^{2+}$ in shoots and roots of *S. physophora*

Ion concentrations were calculated on a tissue water basis. The concentration of  $\text{Na}^+$  in shoots of *S. physophora* had no significant difference at 300 mmol/L KCl compared with 1 mmol/L NaCl, while the values were 128.4% higher at 300 mmol/L NaCl and 198.0% higher at 150 mmol/L NaCl plus 150 mmol/L KCl treatments, respectively. The concentration of  $\text{Na}^+$  in roots of *S. physophora* was the highest at 300 mmol/L NaCl, followed by the treatment of 150 mmol/L NaCl plus 150 mmol/L KCl. However, the concentrations of  $\text{Na}^+$  were not different between 300 mmol/L KCl and 1 mmol/L NaCl treatments (Fig. 1a).

There were no differences in  $\text{K}^+$  concentrations at different salt treatments in shoots of *S. physophora*. However, the  $\text{K}^+$  concentration at 150 mmol/L NaCl plus 150 mmol/L KCl treatments was about 1.5 times that of 300 mmol/L KCl treatment. The  $\text{K}^+$  concentration in the root increased by 192.0% at 150 mmol/L NaCl plus 150 mmol/L KCl compared with the control (Fig. 1b).

The concentrations of  $\text{Cl}^-$  in the shoots and roots of *S. physophora* was significant higher at various salt levels, especially at 150 mmol/L NaCl plus 150

mmol/L KCl and 300 mmol/L KCl treatments, and the values were 71.2% and 36.5% higher than that in control in the shoots (Fig. 1c).

The concentration of  $\text{NO}_3^-$  in shoots of *S. physophora* was 88.5% higher at 150 mmol/L NaCl plus 150 mmol/L KCl treatments than that in control, while the values decreased by about 21.2% at 300 mmol/L KCl. The concentrations of  $\text{NO}_3^-$  in roots of *S. physophora* were not significant differences at all salt treatments (Fig. 1d).

There were no significant differences in  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  concentrations at different salt treatments in shoots and roots of *S. physophora* (Fig. 1e, f).

### 3.3 Effects of different salt treatments on the concentrations proline and amino acid in shoots of *S. physophora*

There was no significant difference in proline concentration at 300 mM KCl, while these values increased by 243.1% at 300 mmol/L NaCl and 387.1% higher at 150 mmol/L NaCl plus 150 mmol/L KCl treatments compared with the 1 mmol/L NaCl treatment, respectively, in shoots of *S. physophora* (Fig. 2a). Amino acid concentrations in shoots of *S. physophora* decreased by 33.4% and 35.5% at 300 mmol/L NaCl and 300 mmol/L KCl compared with plants at 150 mmol/L NaCl plus 150 mmol/L KCl (Fig. 2b).

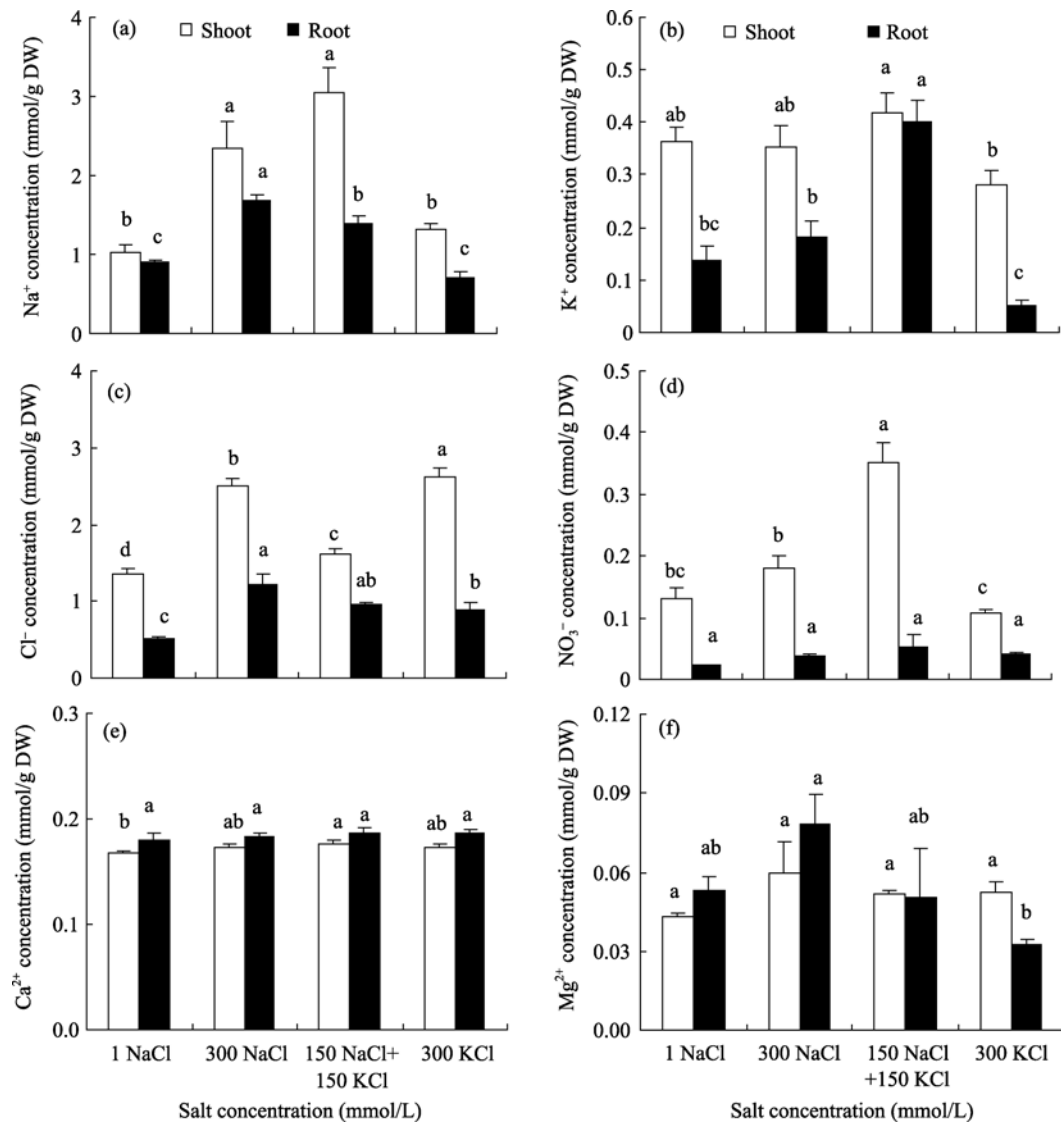
### 3.4 Effects of different salt treatments on osmotic potential and the estimated contributions of $\text{Na}^+$ , $\text{K}^+$ , $\text{Cl}^-$ , $\text{NO}_3^-$ , $\text{Ca}^{2+}$ , $\text{Mg}^{2+}$ , proline and amino acid to $\Psi_s$ in leaves of *S. physophora*

There were no significant differences in osmotic potential in leaves of *S. physophora* at 300 mmol/L NaCl and 150 mmol/L NaCl plus 150 mmol/L KCl treatments, while it progressively decreased at 300 mmol/L KCl (Table 2).

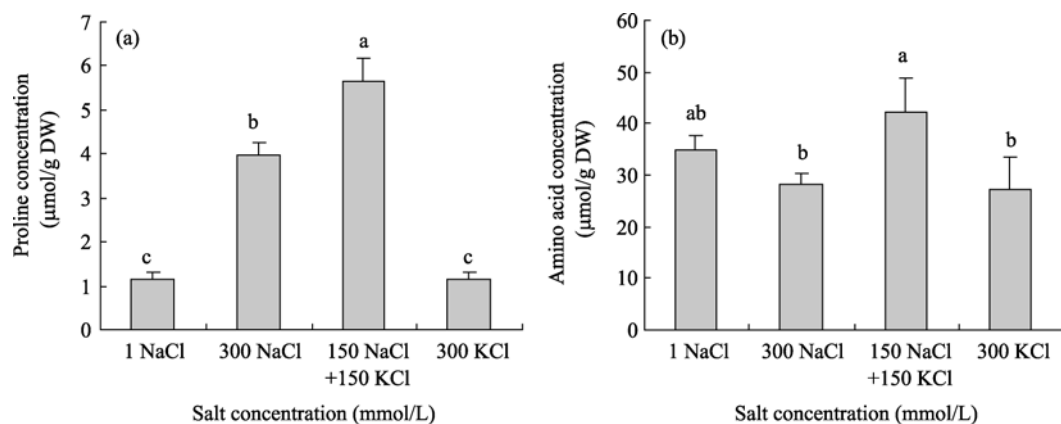
**Table 1** Effects of different salt treatments on the dry weight, water content, succulence and root shoot ratio of *Suaeda physophora*

Treatments (mmol/L)	Shoot		Root		Succulence FW/DW	Root/shoot
	DW (g/plant)	WC (ml/g FW)	DW (g/plant)	WC (ml/g FW)		
1 NaCl	1.05a	0.59c	0.28b	0.67a	2.46c	0.26b
300 NaCl	1.00a	0.67b	0.37ab	0.71a	3.07b	0.37ab
150 NaCl + 150 KCl	1.14a	0.71a	0.49a	0.67a	3.43a	0.43ab
300 KCl	0.97a	0.59c	0.46ab	0.67a	2.48c	0.47a

Within each column, values with different letter are significantly different at  $P < 0.05$  level. DW, WC and FW mean dry weight, water content and fresh weight, respectively.



**Fig. 1** Effects of different salt treatments on the concentrations of  $\text{Na}^+$  (a),  $\text{K}^+$  (b),  $\text{Cl}^-$  (c),  $\text{NO}_3^-$  (d),  $\text{Ca}^{2+}$  (e) and  $\text{Mg}^{2+}$  (f) in the shoots and roots of *Suaeda physophora*. Means of the different salt treatments with different letter are significantly different at  $P < 0.05$  level. Vertical bars represent standard errors ( $n = 3$ ).



**Fig. 2** Effects of different salt treatments on the concentrations of proline (a) and amino acid (b) in shoots of *Suaeda physophora*. Means with different letter are significantly different at  $P < 0.05$  level. Vertical bars represent standard errors ( $n = 3$ ).

**Table 2** Effects of different salt treatments on the osmotic potential ( $\Psi_s$ ) and the estimated contribution of  $\text{Na}^+$  ( $C_{\text{Na}}$ ),  $\text{K}^+$  ( $C_{\text{K}}$ ),  $\text{Cl}^-$  ( $C_{\text{Cl}}$ ),  $\text{NO}_3^-$  ( $C_{\text{NO}_3}$ ),  $\text{Ca}^{2+}$  ( $C_{\text{Ca}}$ ),  $\text{Mg}^{2+}$  ( $C_{\text{Mg}}$ ), proline ( $C_{\text{pro}}$ ) and amino acid ( $C_{\text{AA}}$ ) to the osmotic potential in leaves of *Suaeda physophora*

Treatments (mmol/L)	$\Psi_s$ (MPa)	$C_{\text{Na}}$	$C_{\text{Cl}}$	$C_{\text{K}}$	$C_{\text{NO}_3}$ (%)	$C_{\text{Ca}}$	$C_{\text{Mg}}$	$C_{\text{pro}}$	$C_{\text{AA}}$
1 NaCl	-4.5a	14.3c	13.6b	15.1ab	4.5b	2.8a	3.6a	0.04c	1.2a
300 NaCl	-4.3a	21.3b	15.4b	18.2a	3.7b	1.8b	3.0ab	0.08b	0.6b
150 NaCl + 150 KCl	-3.8a	31.0a	23.3a	14.5ab	9.8a	2.5a	3.6a	0.16a	1.2a
300 KCl	-6.9b	7.9d	11.9b	10.6b	1.6c	1.3c	2.0b	0.02d	0.4b

Within each column, values with different letter are significantly different at  $P < 0.05$  level.

The estimated contribution of  $\text{Na}^+$  to  $\Psi_s$  ( $C_{\text{Na}}$ ) increased by 116.8% and 49.0% at 150 mmol/L NaCl plus 150 mmol/L KCl and 300 mmol/L NaCl treatments, but it was decreased significantly at 300 mmol/L KCl. Similar trends were found in the estimated contribution of  $\text{NO}_3^-$  to  $\Psi_s$  ( $C_{\text{NO}_3}$ ) and proline to  $\Psi_s$  ( $C_{\text{pro}}$ ). And the estimated contribution of  $\text{NO}_3^-$  to  $\Psi_s$  ( $C_{\text{NO}_3}$ ) was not affected by the  $\text{Cl}^-$  to  $\Psi_s$  ( $C_{\text{Cl}}$ ). Compared with plants at 1 mmol/L NaCl, 300 mM KCl significantly reduced the estimated contribution of  $C_{\text{Na}}$ ,  $C_{\text{NO}_3}$ ,  $C_{\text{pro}}$  and  $C_{\text{AA}}$  to the osmotic potential in leaves of *S. physophora* (Table 2).

#### 4 Discussion and conclusion

Succulence minimizes the toxic effects of excessive ion accumulation and has been reported to be associated with accumulation of osmotically active solutes for maintenance of cell turgor pressure (Lüttge and Smith, 1984). Compared to 300 mmol/L NaCl, 150 mmol/L NaCl plus 150 mmol/L KCl treatment led to the higher of water content and succulence in shoots of *S. physophora*. However, *S. physophora* had no significant shoot growth, water content and succulence increasing at 300 mM KCl (Table 1). This implied that high concentrations of KCl inhibited the growth of even salt-growing species, which might be due to the toxic effect of  $\text{K}^+$  or increased crucial osmotic pressure at which the plant under stress would not be able to uptake required water. The results are consistent with the reports for *Atriplex prostrata* (Egan and Ungar, 1998), *Atriplex nummularia* (Ramos *et al.*, 2004) and *Suaeda salsa* (Qi *et al.*, 2005).

Analysis of ions accumulation revealed that *S. physophora*, similar to most halophytes (Lüttge and Smith, 1984), accumulates  $\text{Na}^+$  as a primary osmoticum. The concentration of  $\text{Na}^+$  measured in shoots of

*S. physophora* at 300 mmol/L NaCl, 150 mmol/L NaCl plus 150 mmol/L KCl treatments were estimated to contribute 21.3% and 31.0% of the  $\Psi_s$ , respectively. However, the value was about 7.9% at 300 mmol/L KCl (Table 2). A similar trend was found in  $\text{NO}_3^-$  concentrations for different salts treatments. The estimated contribution of  $\text{NO}_3^-$  to  $\Psi_s$  was the highest (9.8%) at 150 mmol/L NaCl plus 150 mmol/L KCl, while it was lowest (1.6%) at 300 mmol/L KCl (Table 2), indicating that sodium concentration may be linked with nitrate uptake and accumulation in shoots of *S. physophora*.

However, the result is not in agreement with the data of Ivashikina and Feyziev (1998), who showed that nitrate uptake in maize was stimulated by cations in the order  $\text{K}^+ \gg \text{Mg}^{2+} > \text{Na}^+ > \text{Ca}^{2+}$ . A high  $\text{K}^+/\text{Na}^+$  selectivity due to the preferential uptake of  $\text{K}^+$  over  $\text{Na}^+$  appears to be an important mechanism of combating salt stress in glycophytes or salt-tolerant crops (Rus *et al.*, 2001; Chen *et al.*, 2007). The  $\text{Na}^+$  ions accumulation significantly reduced  $\text{K}^+$  ions content in shoots of *S. physophora* at 150 mmol/L NaCl plus 150 mmol/L KCl treatments in the present study (Fig. 1).  $\text{Na}^+$  and  $\text{K}^+$  accumulations in plant tissues have an antagonistic relationship. In other words, they have a negative correlation, so that increasing  $\text{Na}^+$  content would lead to a decrease in the content of  $\text{K}^+$  (Flower *et al.*, 1986). On the other hand, *Suaeda*, represents an extreme in terms of  $\text{Na}^+/\text{K}^+$  selectivity, where the ability to maintain  $\text{Na}^+$  uptake for growth and osmotic adjustment at high external salt concentrations is essential for the nutrient and water uptake (Eshel, 1985a, b). Therefore, the present results, especially the correspondence indicated by data presented in Fig. 1 and Table 2, clearly established that compared to  $\text{K}^+$  ions,  $\text{Na}^+$  ions influx plays more useful role in  $\text{NO}_3^-$  uptake and osmotic adjustment in the

euhalophyte of *S. physophora*. Moreover, *S. physophora* exposed to  $K^+$  salts, in contrast to  $Na^+$  salt treatments, was not able to use  $K^+$  as an osmoticum to adjust the vacuolar water potential, causing specific ion toxicity in the cytoplasm that inhibited both  $NO_3^-$  uptake and growth of *S. physophora*.

Aslam (1984) proposed that both  $K^+$  and  $Na^+$  salts inhibited  $NO_3^-$  uptake similarly and the anionic salinity is more sensitive to cationic salinity. Meanwhile, a strong inhibition of  $NO_3^-$  uptake by  $Cl^-$  has been found in barley. Using different species and experimental conditions many researchers reported that the presence of  $Cl^-$  suppressed  $NO_3^-$  uptake, indicating a direct competition effect between these ions (Bottacin *et al.*, 1985; Cerezo *et al.*, 1997; Abdelgadir *et al.*, 2005). In the present experiment, leaf  $NO_3^-$  concentration significantly increased at 150 mmol/L NaCl plus 150 mmol/L KCl treatments, while the  $Cl^-$  concentration was not accordingly decreased (Fig. 1), which may indicate that the concentration of  $Cl^-$  was not related to  $NO_3^-$  uptake. Moreover, the antagonism is considered not to be strong as the relation between  $Na^+$  accumulation and  $NO_3^-$  absorption in *S. physophora*. These results consist with Prasad and Willia (1976) who proposed that anions ( $Cl^-$ ,  $Br^-$  and  $SO_4^{2-}$ ) had only small effect on the absorption of  $NO_3^-$ . The differences between the contribution of  $NO_3^-$  to  $\Psi_s$  in the presence and absence of  $Na^+$  were significant, and the addition of NaCl more than doubled the  $NO_3^-$  osmotic contribution than the addition of KCl. However, the contribution of  $Cl^-$  to  $\Psi_s$  had no difference between NaCl and KCl treatments (Table 2).

Desert shrubs have relatively high N content in leaves despite the low levels of N in most desert soils

(Whittaker *et al.*, 1979). However, the factors involved in higher leaf nutrient levels of halophytes are not well documented. In the present experiment, uptake and accumulation of  $NO_3^-$  was found to correlate with  $Na^+$  concentration in shoots of *S. physophora*, indicating a  $Na^+$  coupled symport mechanism. We proposed that  $Na^+$ -coupled  $NO_3^-$  cotransporter maybe responsible for the high N accumulation under salt stress in the euhalophyte of *S. physophora*. Dependence of  $NO_3^-$  uptake on  $Na^+$  has been previously reported in a marine diatom, *Phaeodactylum tricornutum* (Rees *et al.*, 1980) and marine angiosperm, *Zostera marina* (Garcá-sánchez *et al.*, 2000). However, little is known about molecular mechanisms of  $NO_3^-$  acquisition under salt stress in euhalophytes. Therefore, it is to be hoped that future studies can contribute to this issue.

In conclusion,  $Na^+$  has been shown to be an essential micronutrient not only for  $C_4$  plants (Ohta *et al.*, 1988) but also for some halophytes (Eshel, 1985; Naidoo and Rughunanan, 1990). However, the physiological mechanism for the  $Na^+$  requirement of  $NO_3^-$  uptake has never been elucidated. This is the first report of a possible role of  $Na^+$  in  $NO_3^-$  uptake and osmotic adjustment in the euhalophyte of *S. physophora*. The results of this study showed that  $Na^+$  stimulates  $NO_3^-$  absorption and the stimulation is independent on the internal and the external  $Cl^-$  concentration in the euhalophyte of *S. physophora*.

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