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Effect of salinity on tissue nutrient contents of the four dryland tree species of Indus flood plains

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ABSTRACT

Salinity is a common issue of semi-arid and arid lands rendering them unfit for agriculture. Saline wastelands can be converted into productive ecosystems by rehabilitating them with salt tolerant native tree species. The objective of this work was to study the effect of NaCl salinity on tissue nutrient contents of the four dryland tree species. Saplings were grown in pots under nonsaline and high salinity conditions. After eighteen weeks the plants were harvested and their tissue nutrient contents were analyzed. Results revealed that all species accumulated high amounts of Na^+ under saline conditions, while concentrations of N, P and Mg^{2+} decreased in their tissues. Concentrations of K^+ and Ca^{2+} showed more variable trend in various tissues in response to increase in soil salinity. Na^+: K^+ ratios of roots (1.57), stems (1.27), and leaves (1.66) of salinized *Salvadora oleoides* plants were lowest among all the four species. Root Na^+: K^+ ratio of salinized plants was significantly higher for *Prosopis cineraria* (7.10), while these ratios for stem (1.85) and leaf (3.42) were highest for T*amarix aphylla*. Plants of *P. cineraria* showed lowest Stem-Na^+/root-Na^+ ratio (0.30) when subjected to salinity. Results showed that salinity induces nutrient deficiency in all species. Salinity tolerance of these species can be attributed to their ability to (i) restrict translocation of Na^+ from roots to stem; (ii) keeping low tissue Na^+: K^+ ratios; and (iii) selectivity of K^+ and Ca^{2+} over Na^+, and can be used for the screening of salt-tolerant ecotypes for the rehabilitation of saline wastelands.

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Ion homeostasis; mineral nutrition; salt tolerance; secondary salinity; thorn forest community

Introduction

More than 3% of the world's total land is affected by salinity (Corbishley and Pearce 2007). Most of this salinity is primary but human activities are causing loss of productive land from secondary salinization (Munns 2011). One of the major reasons of secondary salinity, especially in arid and semi-arid areas is the conversion of land covered by deep rooted natural vegetation to other land uses like agriculture (Barrett-Lennard 2002). It has been estimated that worldwide almost 25% of the irrigated land is affected by salinity to various degrees from which 1.4 M ha has been abandoned (World Bank 2006).

Approximately 6.3 M ha area is estimated to be salt affected in Pakistan, most of which is due to the presence of excess amounts of NaCl in the soil (Qureshi and Barrett-Lennard 1998). Salinity is one of the major reasons of land degradation in Pakistan (Dregne

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2002), where secondary salinity is causing a loss of 40,000 ha area each year (Ansari, Khan, and Gul 2007). Larger dryland areas of Indus flood plains (above the flood line) were once covered by plain thorn forests having the climax community comprising of *Prosopis cineraria* L. (Druce.) and *Salvadora oleoides* Decne. (Champion, Seth, and Khattak 1965). The bi-species climax is associated with *Tamarix aphylla* (L.) Karst. and *Capparis decidua* (Forssk.) Edgew. as subclimax species (Khan 1994, 2010). This once widespread plain thorn forest community is now under threat, and it has either been removed due to large scale clearance of land for agricultural purposes, or has been replaced by economically more important species (Khan 1994, 1996; Wikramanayake et al. 2002).

All the four thorn forest species are salt tolerant to varying degrees with *S. oleoides* being the most salt resistant and *C. decidua* the least (Sharif and Khan 2009). *T. aphylla* has salt secreting glands and concentration of Na^+ and Cl^- in the salts excreted by *T. aphylla* increase with the increase in NaCl concentration of the rooting medium (Hagemeyer and Waisel 1988). All the four thorn forest species are drought tolerant and contribute towards increasing soil fertility and stability (Gates and Brown 1988; Deans et al. 2003; Khan and Qaiser 2006; Khan 2010). They provide wildlife habitat (Nazir et al. 2013, 2014), and are a source of food, fodder, fuel wood, construction material and medicine to local communities (Khan 1994, 1996).

Plants are affected from salinity through complex interaction of ionic, osmotic, and nutritional imbalances (Shannon 1997). Plants show two types of salt tolerance mechanisms i.e., by minimizing salt entry and by reducing salt concentration in the cytosol (Munns 2002). Many physiological processes controlled by a group of genes are involved in plant salt tolerance (Mansour and Salama 2004). Species differ in their abilities to exclude, accumulate and tolerate the harmful effects of specific ions (Flowers and Yeo 1986; Shannon, Grieve, and Francois 1994). Salinity tolerance exhibited by a particular species is dependent on its anatomical and physiological complexity. The synthesis and accumulation of low molecular weight organic molecules such as sugars, glycinebetaine, proline, and other organic solutes for osmotic balance and protecting enzyme denaturation is one of the ways to combat the harmful effects of ionic toxicity (Greenway and Munns 1980). Poor osmotic adjustment in plants results in loss of cell turgor and stomatal closure that leads to reduced gas exchange and photosynthesis, ultimately affecting their growth (Shannon 1997). Plant growth is also reduced because of the harmful effects of turgor loss on cell division and elongation.

Maintenance of growth in the presence of high cellular Na^+ in halophytes is an indication of their capability to compartmentalize excess ions in vacuoles or to confine them to apoplast (Zheng et al. 2009). High salinity decreases concentration of leaf proteins, total carotenoids, chlorophyll, soluble sugars, starch and phenolic contents (Migahid 2003). Decrease in leaf protein contents reduces the grazing value of the species. With the increase in uptake of Na^+ and Cl^- concentrations of N, Ca^{+2}, K^+, and Mg^{+2} decrease in both glycophytic and halophytic plant species upsetting the nutritional balance of plants, which ultimately reduces their growth (Zhong and Läuchli 1994; Koyro 2006; Nandy et al. 2007). Improved N and P nutrition has reported to increase plant salinity tolerance of the four thorn forest species (Sharif and Khan 2009). For activation of enzymatic reactions and maintenance of plant growth, an optimal cytoplasmic K^+/Na^+ ratio is required (Wakeel 2013). Supplemental K^+ has been reported to help maintain high K^+/Na^+ ratios in leaf tissues and highest photosynthetic and plant growth rates were achieved with leaf K^+/Na^+ ratios of 1.0–2.0 (Rodrigues et al. 2013).

The response of plants to salinity varies at different growth stages and with time of exposure to salinity (Zeng and Shannon 2000). Most of the previous studies on the effects of salinity on tissue nutrient contents of thorn forest species have been conducted at the seedling stage when the plants are very young and fragile, or were exposed to salinity for shorter periods of time (Ramoliya and Pandey 2002; Ramoliya et al. 2006; Hardikar, Panchal, and Pandey 2011). The objectives of the current study were to: (i) determine the effects of long-term exposure of NaCl salinity on tissue nutrient contents of the four thorn forest species, and (ii) find out the possible mineral nutrient concentration related salt tolerance mechanisms involved. On the basis of the previously mentioned literature it was hypothesized that high soil salinity will increase tissue Na^+ concentrations that will result in reduced uptake and accumulation of other nutrients in tissues of thorn forest species. It was expected that when subjected to salinity species with higher salinity tolerance will be able to maintain their tissue nutrient concentrations through ion homeostasis.

Materials and methods

An eighteen-week (April 15 to August 30) pot experiment was set-up at the Botanic Garden of GC University, Lahore to see the effect of NaCl salinity on the tissue nutrient contents of the four tree species.

Soil used in the experiment was sandy loam in texture with 7.5 pH and value of the electrical conductivity of saturated extract (EC_e) 0.65 mS cm^{-1}. Soil fertility was low with respect to nitrogen and phosphorus (Table 1). Soil with low N and P was used in the experiment because soils of natural habitat of the thorn forest community are low in organic matter and deficient in plant available nutrients, especially P (Muhammad, Müller, and Joergensen 2008). Plants were provided with different salinity treatments (EC_e mS cm^{-1} 0.65, 5.80, 10.69, 20.71, 30.40) and their growth and survival were regularly monitored. *T. aphylla, P. cineraria* and *S. oleoides* plants survived salinity up to 30.4 mS cm^{-1} while none of the *C. decidua* plants survived at this salinity by the end of the study period. As a result, the highest salinity treatment for this species was 20.71 mS cm^{-1}. Tissue analyses were carried-out for only control plants (EC_e mS cm^{-1} 0.65) and plants under highest salinity treatments (EC_e mS cm^{-1} 30.4 for *T. aphylla, P. cineraria* and *S. oleoides* and 20.71 for *C. decidua*).

Salinized treatments were prepared by mixing NaCl in the air dried and sieved soil to get required EC_e (mS/cm) values. The plants grown in the soil without salt addition acted as control. The soil of all treatments was filled in plastic lined clean earthen pots of 30 cm diameter. Ten-month old saplings of *P. cineraria, S. oleoides*, and *C. decidua* (raised from seeds) and 6-month old saplings of *T. aphylla* (propagated from stem cuttings) were transferred to the labeled treatment pots. Both salinized and control treatments were provided to five healthy replicate plants of each species that were of almost equal height (one plant/pot). There were a total of forty plants of the four species (ten plants/species) under both

Table 1. Physico-chemical characteristics of soil used in the experiment.

		Soluble Ions (mg kg^{-1})					N	P		Soil Texture			Textural
ECe mS cm^{-1}	pH	Cl^-	Ca^{2+}	Mg^{2+}	Na^+	K^+	(%)	mg kg^{-1}	SAR	Sand (%)	Silt (%)	Clay (%)	class
0.65	7.5	63	44	21.6	36.5	76	0.01	4.6	6.37	78	17	5	Loamy Sand

control and high salinity treatments. The pots were randomly placed in a thick transparent plastic covered fenced enclosure under natural light for 18 weeks. The saplings were watered once a week with deionized water. Mean maximum temperature during the study period was 36.42 ± 2.2°C, mean minimum temperature was 26.28 ± 2.03°C, while percentage relative humidity remained 59.4 ± 17.33%.

At the termination of the experiment all plants were harvested and were dried separately in an oven at 65°C for 48 h to determine their dry biomass. Salinity tolerance index was determined to see the effect of salinity on their biomass accumulation as (salinized plant biomass/mean plant biomass of control plants). Dried tissues of plants of the same treatment were pooled separately and were ground in grinding mill (IKA Werke MF10) using a sixty-mesh sieve. Mineral analyses were carried out after performing two kinds of wet digestions and adopting procedures described in (Ryan, Estefan, and Rashid 2001). For N estimation conc. H_2SO_4 was used and for other minerals (2:1) HNO_3: $HClO_4$ *v/v* was used. Jenway Flame Photometer was used to determine Na^+ and K^+. Atomic absorption spectrophotometer was used to determine Ca^{2+} and Mg^{2+}, while P was detected by using Spectroscan 80D Spectrophotometer. Nitrogen was determined by using Nitrogen assembly Behr Inkjel M for digestion and S3 for distillation.

To test the effects of salinity, tissues, and species on mineral nutrient accumulation, Na^+: K^+ ratios of root, stem, leaf and Stem-Na^+/root-Na^+ ratios, two-way ANOVAs were applied using SPSS software version 19. Tukey H.S.D. multiple comparison test was used to distinguish groups. Statistical differences between the two salinity treatments were analyzed by independent sample *t*-test.

Results

There was a significant difference ($P < 0.01$) in tissue nutrient contents of the four tree species with respect to salinity level, tissue type, species, and the interaction between tissue × species (Table 2). The interaction of salinity × tissues was significant for all nutrients except N and Mg^{2+}. Interactions between salinity × species and salinity × tissue × species were also significant for all except N and P. Concentrations of all nutrients were significantly ($P < 0.01$) higher in leaf, followed by stem and root tissues in all species (Figures 1–4). The results revealed a decline in N, P and Mg^{2+} (except in the roots of *S. oleoides*) and an increase in Na^+ concentrations in tissues of all salinized plants as compared to their controls (Figures 1–4). This decline in tissue nutrient concentrations of all species was

Table 2. Univariate ANOVA with salinity treatment ($n = 2$), tissue type ($n = 3$) and plant species ($n = 4$) as factors and tissue nutrient concentrations of the four thorn forest species as variables.

		F – value					
Variables	df	N	P	K	Ca	Mg	Na
Salinity	1	224.098**	49.219**	12.455**	11.387**	162.875**	1861.104**
Tissue	2	215.503**	94.137**	120.645**	45.544**	235.489**	55.413**
Species	3	18.809**	17.840**	63.687**	41.727**	262.799**	37.161**
Salinity × Tissue	2	2.729	4.744*	17.956**	21.961**	3.167	37.755**
Salinity × Species	3	0.987	0.576	9.465**	29.532**	60.342**	65.471**
Tissue × Species	5	15.625**	12.411**	14.011**	20.053**	89.022**	54.799**
Salinity × Tissue × Species	5	0.500	0.793	12.306**	23.698**	6.573**	41.925**

*Significant difference at $P < 0.05$. **Significant difference at $P < 0.01$.

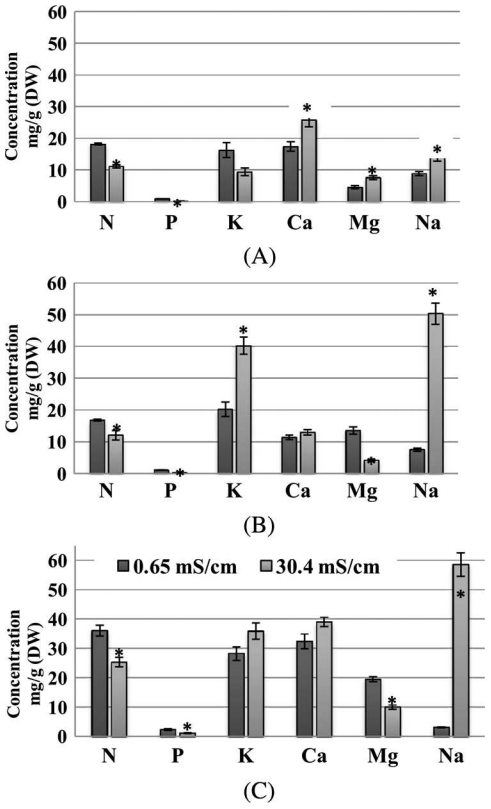

Figure 1. Nutrient concentrations in (A) root, (B) stem, and (C) leaf tissues of nonsalinized and salinized *S. oleoides* plants. Means ± 1 *S.E.* on (DW) dry weight basis. *, Significant difference at $P < 0.05$ (*t*-test).

statistically significant ($P < 0.05$) for N and Mg^{2+}, while decrease in P was significant for all tissues of *S. oleoides* and roots of *C. decidua* only. Na^+ accumulation was significantly ($P < 0.05$) higher in all salinized plant tissues except leaves of *S. oleoides*. Ca^{2+} concentrations significantly decreased ($P < 0.05$) in all tissues of *P. cineraria, C. decidua* and in the stems of *T. aphylla*, while it increased significantly in both roots and leaves of *T. aphylla* and roots of *S. oleoides* in response to the increase in soil salinity. Salinized plants showed a decline in K^+ concentrations in all tissues of *P. cineraria*, stems and leaves of *T. aphylla* and roots of *S. oleoides* and *C. decidua*, but this decline was statistically significant ($P < 0.05$) in the root tissues of *P. cineraria* and *C. decidua* only. The concentration of K^+ increased significantly ($P < 0.05$) in the stem tissues of salinized *S. oleoides* and *C. decidua* and nonsignificantly in the leaves of *S. oleoides* and roots of *T. aphylla* as compared to their controls.

Salinity, species, and the interaction of both factors (except stem Na^+: K^+) significantly ($P < 0.05$) affected Na^+: K^+ ratios of root, stem, and leaf tissues of the four species (Table 3). All the tissue nutrient ratios of the salt-treated plants (except for root Na^+: K^+ ratio of *S. oleoides*) were significantly ($P < 0.05$) higher as compared to their controls, while Stem-Na^+/Root-Na^+ ratios of *P. cineraria* and *T. aphylla* declined significantly in response to exposure to salinity (Table 4). Salinized *T. aphylla* and *S. oleoides* plants showed the lowest root Na^+: K^+ ratios while the highest value (7.10) was shown by

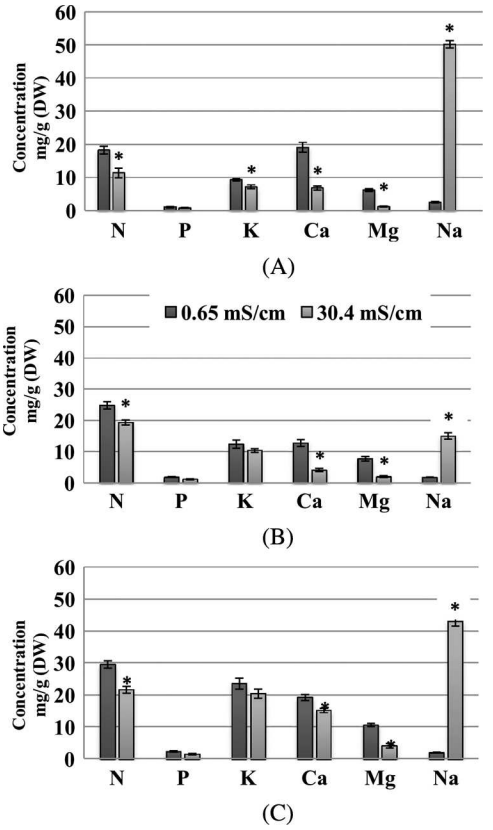

Figure 2. Nutrient concentrations in (A) root, (B) stem, and (C) leaf tissues of nonsalinized and salinized *P. cineraria* plants. Means ± 1 *S.E.* on (DW) dry weight basis. *, Significant difference at $P < 0.05$ (*t*-test).

P. cineraria. Both stem and leaf Na^+: K^+ ratios of the salinized plants were lowest for *S. oleoides* (1.27 and 1.66 for stem and leaf, respectively). Lowest Stem-Na^+/root-Na^+ ratio of the salinized plants was shown by *P. cineraria* (0.33) followed by *T. aphylla* (0.90), *C. decidua* (2.98), and *S. oleoides* (3.58).

Exposure to salinity significantly reduced the dry biomass accumulation in all plant species ($t = 4.095$, 8.742, 22.883, and 12.288 for *S. oleoides, P. cineraria, T. aphylla*, and *C. decidua*, respectively, $P < 0.01$). Plant biomass was not compared across species because *T. aphylla* plants were raised from stem cuttings giving them higher biomass, while the remaining three species were raised from seeds. Salinity tolerance index remained highest for salinized *S. oleoides* plants (0.46).

Discussion

All four plant species accumulated high amounts of Na^+ in their tissues in response to the increase in soil salinity while concentrations of N, P, and Mg^{2+} (except in the roots of *S. oleoides*) decreased in tissues of all plant species. Ca^{2+} decreased in tissues of all plants except in the roots and leaves of *T. aphylla* and roots of *S. oleoides*. Concentrations of Ca^{2+} in the root tissues of *S. oleoides* and *T. aphylla* were, respectively, 45 and 25% greater than Na. Change in K^+ concentration remained nonsignificant in leaf and stem tissues of all

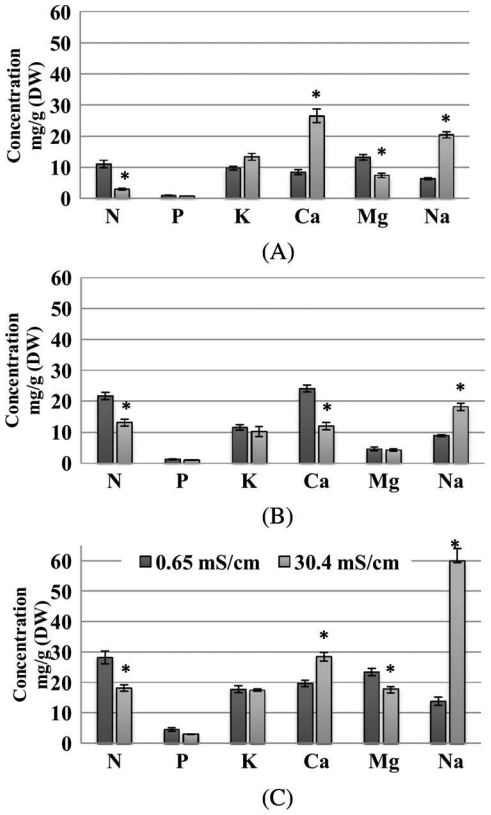

Figure 3. Nutrient concentrations in (A) root, (B) stem, and (C) leaf tissues of nonsalinized and salinized *T. aphylla* plants. Means ± 1 *S.E.* on (DW) dry weight basis. *, Significant difference at $P < 0.05$ (*t*-test).

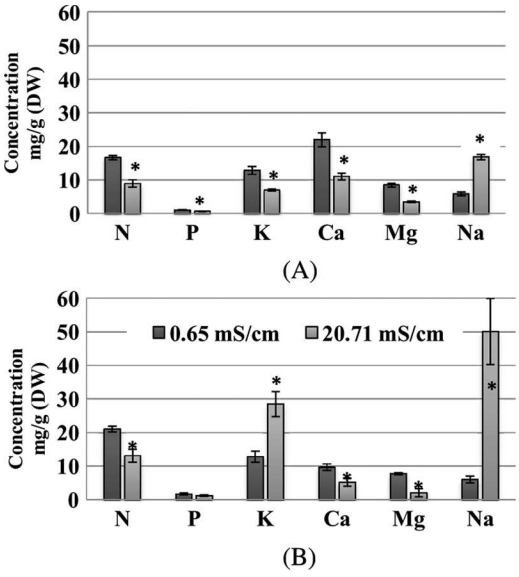

Figure 4. Nutrient concentrations in (A) root and (B) stem tissues of nonsalinized and salinized *C. decidua* plants. Means ± 1 *S.E.* on (DW) dry weight basis. *, Significant difference at $P < 0.05$ (*t*-test).

Table 3. Two-way ANOVA with salinity level ($n = 2$) and species ($n = 4$) as factors and Na^+: K^+ ratios of root, stem and leaf and Stem-Na^+/Root-Na^+ ratios of four thorn forest species as variables.

Variable	Source	df	*F*	Sig.
Na:K Root	Salinity	1	177.11	0.000
	Species	3	39.22	0.000
	Salinity × Species	3	49.74	0.000
Na:K Stem	Salinity	1	171.46	0.000
	Species	3	8.39	0.001
	Salinity × Species	3	1.22	0.335
Na:K Leaf	Salinity	1	244.00	0.000
	Species	2	31.89	0.000
	Salinity × Species	2	5.56	0.020
Stem-Na:Root-Na	Salinity	1	79.87	0.000
	Species	3	56.34	0.000
	Salinity × Species	3	63.36	0.000

plants in response to the increase in soil salinity except in the stems of *S. oleoides* and *C. decidua* where its concentration increased by 50 and 55%, respectively, as compared to unsalinized plants. Tissue Na^+: K^+ ratio of all plant species significantly increased in response to salinity as compared to their controls (except in the roots of *S. oleoides*) indicating that all thorn forest species similar to most other halophytes accumulate Na^+ as primary osmoticum (Flowers, Hajibagheri, and Clipson 1986).

Tissue Na^+: K^+ ratios of salinized *S. oleoides* plants were lowest among all the four thorn forest species. This probably could be the reason for it being the most salt tolerant species among four studied species showing minimum reduction in dry matter production in response to the increase in soil salinity. Stem-Na^+/root-Na^+ ratio significantly increased in *S. oleoides* and *C. decidua* plants in response to the increase in soil salinity while it decreased significantly in *P. cineraria* and *T. aphylla*. Increased Stem-Na^+/root-Na^+ ratio shows that in these plants roots transfer the major part of absorbed Na^+ to stem, while its decrease shows the presence of some restriction mechanism for controlling the transfer of Na^+ from the root to shoot.

Table 4. Comparison between tissue nutrient contents of plants of the four tree species grown under non-saline and saline conditions.

		Mean ± *S.E.*			
Variable	Source	*S. oleoides*	*P. cineraria*	*T. aphylla*	*C. decidua*†
Na:K Root	C	$0.58^{a} \pm 0.12$	$0.27^{b} \pm 0.04$	$0.66^{a} \pm 0.05$	$0.47^{ab} \pm 0.08$
	S	$1.57^{b} \pm 0.34$	$7.10^{a**} \pm 0.68$	$1.54^{b**} \pm 0.12$	$2.40^{b**} \pm 0.15$
	Sp	$1.08^{b} \pm 0.27$	$3.69^{a} \pm 1.56$	$1.10^{b} \pm 0.21$	$1.44^{b} \pm 0.44$
Na:K Stem	C	$0.38^{bc} \pm 0.03$	$0.15^{c} \pm 0.01$	$0.78^{a} \pm 0.04$	$0.49^{b} \pm 0.13$
	S	$1.27^{b**} \pm 0.14$	$1.45^{ab**} \pm 0.08$	$1.85^{a*} \pm 0.26$	$1.76^{ab**} \pm 0.08$
	Sp	$0.82^{b} \pm 0.21$	$0.80^{b} \pm 0.29$	$1.32^{a} \pm 0.27$	$1.13^{ab} \pm 0.29$
Na:K Leaf	C	$0.11^{b} \pm 0.02$	$0.09^{b} \pm 0.01$	$0.79^{a} \pm 0.12$	–
	S	$1.66^{b**} \pm 0.20$	$2.13^{b**} \pm 0.21$	$3.42^{a**} \pm 0.24$	–
	Sp	$0.89^{b} \pm 0.36$	$1.11^{b} \pm 0.47$	$2.11^{a} \pm 0.60$	–
Stem-Na:Root-Na	C	$0.85^{b} \pm 0.02$	$0.75^{b} \pm 0.13$	$1.40^{a} \pm 0.09$	$1.03^{b} \pm 0.17$
	S	$3.58^{a**} \pm 0.09$	$0.30^{d*} \pm 0.03$	$0.90^{c*} \pm 0.11$	$2.98^{b**} \pm 0.32$
	Sp	$2.22^{a} \pm 0.61$	$0.53^{c} \pm 0.12$	$1.15^{b} \pm 0.13$	$2.01^{a} \pm 0.46$
Total plant biomass (g)	C	5.92 ± 0.52	6.78 ± 0.45	50.21 ± 1.70	3.61 ± 0.19
	S	$2.75** \pm 0.58$	$2.42** \pm 0.22$	$10.51** \pm 0.36$	$0.92** \pm 0.11$
	Sp	4.34 ± 0.64	4.60 ± 0.76	30.36 ± 6.67	2.26 ± 0.46
Salinity tolerance index		$0.46 \pm 0.10\%$	$0.36 \pm 0.03\%$	$0.21 \pm 0.07\%$	$0.25 \pm 0.03\%$

Means of C, control; S, salinized; Sp, species. *Significant treatment difference at $P < 0.05$. **Significant at $P < 0.01$ (*t*- test). Means followed by different letters in a row are significantly different at $P < 0.05$ (Tukey HSD). † Salinity level for *C. decidua* was 20.71 mS/cm.

Root: stem: leaf ratio of Na^+ in the salinized *S. oleoides* plants was 1: 3.6: 4.2 which showed that the accumulation of Na^+ is minimum in roots and is maximum in leaves. This is in contrast with the findings of Hardikar, Panchal, and Pandey (2011) who found maximum accumulation in stem tissues as well as an increase in tissue N concentrations in response to the increase in soil salinity. This could be because of the fact that in their study the maximum salinity treatment provided to the seedlings was only 11.9 dSm^{-1}. Absorbed Na^+ is transferred from roots to stems and leaves in the transpiration stream where it finally accumulates to toxic levels in the older leaves. The leaves of *S. oleoides* are succulent and toxic effects of high Na^+ concentration is perhaps reduced by dilution. Many halophytic plant species regulate their internal ion concentrations by increasing leaf water contents as an adaptive mechanism to cope with saline conditions (Short and Colmer 1999). Hardikar, Panchal, and Pandey (2011) found 50% biomass reduction in different tissues of salinized *S. oleoides* seedlings at EC (dSm^{-1}) values of 8.9–10.8, while the same reduction in biomass of 1-year old plants was found by the authors at 28.55 dSm^{-1}(Sharif and Khan 2009), showing an increased salinity tolerance with age. Concentration of proline in the tissues of *S. oleoides* plants is reported to increase as a result of exposure to salinity showing its use for cell osmoregulation (Vaghela et al. 2009; Hardikar, Panchal, and Pandey 2011). High K^+ accumulation in stem and Ca^{2+} in the root tissues in response to exposure to salinity shows that this species has high selectivity for both ions, but seems to lack effective mechanism to control transport of sodium from roots to shoots.

Root: stem: leaf ratio of Na^+ in the salinized *P. cineraria* plants was 3.3:1:2.9, which shows that accumulation of Na^+ is minimum in stem and maximum in roots. Avoidance of sodium accumulation in shoots is suggested to confer tolerance to salt stress in salt tolerant plants (Zhang and Shi 2013). This is in accordance with the findings of Ramoliya et al. (2006) who found that stem tissues act as a barrier for translocation of Na^+ from roots to leaves in *P. cineraria* seedlings subjected to moderate salinity.

Root: stem: leaf ratio of Na^+ in the salinized *T. aphylla* plants was 1.1:1:3.3, which shows that the accumulation of Na^+ is minimum in stems and roots and is maximum in leaves. Despite of having a non-succulent character and salt secreting glands, leaves of *T. aphylla* were found to accumulate considerably high amounts of Na^+. Leaf succulence and presence of secretory structures allow the plants to tolerate high soil salinity conditions (Naz et al. 2013). *T. aphylla* plants regulate their internal ion concentration by increasing secretion rates with increasing salinity. Moreover, the composition of the secretion in *T. aphylla* is highly dependent on the composition of the salts in the root environment (Waisel 1960; Berry 1970). With increasing salinity higher secretion rates have also been found to maintain the internal leaf ion concentration in other salt secreting tree species (Suárez and Medina 2008) where the selective character of the secretion is reported to maintain favorable Na/K and Cl^- ratios in leaf cells. *Tamarix* spp. are salt tolerant and leaf-level physiological parameters of *T. ramosissima* (photosynthesis at 2000 μ mol m^{-2} s^{-1}, intercellular CO_2 concentration, stomatal conductance, and leaf $\delta^{13}C$) showed little change over surface-soil salinities from 0.5–17.65 mS/cm (Carter and Nippert 2012). However, higher salinity levels negatively affect their growth (Sharif and Khan 2009; Cui et al. 2010).

Root: stem ratio of Na^+ in the salinized *C. decidua* plants was 1:3, which shows that the accumulation of Na^+ is minimum in roots and is maximum in stems. High Ca^{2+} accumulation in the roots shows high selectivity for this ion as an adaptation to salt stress, while

high Na^+ concentration of the stem shows that there lacks a mechanism for restricting the translocation of Na^+ ions from roots to stem. Very low Na^+ concentration in the roots of *S. oleoides, T. aphylla*, and *C. decidua* plants suggest the selectivity of uptake of ions from the soil solution. The presence of exclusion mechanisms operating at the roots of halophytes explain the occurrence of a lower Na^+ concentration in the roots of salt tolerant plants (Munns 2002).

Salinity and sodicity reduce soil potential to support native plant communities by altering their structure and reducing N and soil organic C (Day et al. 2015). They affect N accumulation in plants along with the concentrations of P, Mg^{2+} and Ca^{2+} (Greenway and Munns 1980). Phosphorus concentration in the cell is related to the rate of photosynthesis and decrease of P in leaves reduces shoot growth (Overlach, Diekmann, and Raschke 1993). Magnesium does not only play important roles in plants as part of chlorophyll and as an enzyme co-factor, but it is also reported to be important for the export of photosynthates, that is impaired in the case of Mg deficiency (Marschner and Cakmak 1989). Calcium also plays important roles in salinity stress, as it affects K/Na selectivity (Cramer et al. 1987; Läuchli and Grattan 2007), preserves integrity of membranes (Rengel 1992) and is important for osmoregulation signaling (Mansfield, Hetherington, and Atkinson 1990). Application of supplemental Ca^{2+} improves plant salinity tolerance and supports growth (Vaghela et al. 2009; Yousaf and Sharif 2013). Salinity affects plant growth by changing permeability of plasma membranes that happens before the appearance of morphological symptoms of salt stress. Plant adaptation to saline conditions is dependent upon the integrity of plasma membranes under saline conditions (Mansour and Salama 2004).

The accumulation, and Na^+ and K^+ partitioning both in tissues and organs are important physiological processes leading to salt tolerance. Interaction between internal K^+ and Na^+ has been suggested as an important factor in the determination of salt tolerance in many plant species (Rascio et al. 2001; Silveira et al. 2001). Halophytes are able to use sodium as an osmoticum and their selective uptake of K^+ over Na^+ is reported to be associated with stability of photosynthetic pigments and PSII functioning (Debez et al. 2010). Accumulation of Na^+ as a primary osmoticum can generate Na^+/K^+ ratios in tissues of dicotyledonous halophytes often in excess of 10 (Flowers, Hajibagheri, and Clipson 1986).

Ion exclusion and other physiological criteria are effectively used for the screening of salt tolerant crop varieties (Noble and Rogers 1992; Munns and James 2003). Different plant ecotypes have found to be different in their ability to exclude Na^+ from shoot, tissue tolerance to Na^+ and tolerance to osmotic effects, which are due to varying expressions of several genes that control many ion channels and transporters (Labidi et al. 2002; Jha et al. 2010). Screening of more salt tolerant ecotypes of native tree species based on physiological criteria will remain helpful before large-scale plantation for the rehabilitation of saline sites. The poor establishment and low survival rates of transplants of comparatively less salt tolerant ecotypes can result in the waste of time, effort and money of already constrained rehabilitation projects.

Conclusions

Existing literature and the results of present study both suggest that plants of the thorn forest community show salt tolerance mechanisms by both minimizing the entry of salts into plants, and by reducing their concentration in the cytoplasm through exclusion, ion

homeostasis, succulence, and salt excretion via salt glands. Adoption of these physiological mechanisms is certainly at the cost of energy that is diverted from growth. It is also evident from the results that salinity induces nutrient deficiency in all the four tree species. *S. oleoides* was found to be the most salt tolerant species that showed the lowest biomass reduction under saline conditions as compared to other three species because of its ability to maintain low tissue Na^+: K^+ ratios of the root, stem, and leaf tissues. Addition of organic and inorganic fertilizers along with other amendments such as soil replacement and gypsum may remain helpful in establishing these plant species on saline wastelands converting them into productive ecosystems that will yield economic, social, and biological benefits.

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