Tropical Ecology **58**(4): 705-716, 2017 ISSN 0564-3295

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Root exudates reduce electrical conductivity and water potential of rhizospheres and facilitate non-halophytes to survive in dry land saline soils

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Abstract: High amount of salts in dry-land soils (high ECe) reduces water potential which causes plasmolysis in agricultural crops and result in food grain yield reduction. Salt tolerant non-halophytic trees and shrubs, however, survive the highly saline soils as they extrude Na^+ from their cell cytoplasm by an active Na^+/H^+ antiport and/ or compartmentalize it into vacuoles and adjust osmotic pressure of the cytoplasm and also uptake water from that part of rhizosphere and soil depth, which contain a relatively lower amount of salts. But, how they change electrical conductivity and water potential in their rhizospheres is not yet known. Aims of this study were to know root distribution in different soil depths; changes in salt concentrations in the soil depths across seasons; and to understand how glucose exuded from roots changes pHs, ECe, salt concentrations and water potential in rhizospheric soils of the trees and shrubs in highly dry-land saline soils. Distribution of fine roots of two salt-tolerant non-halophytic trees (i.e. *Acacia nilotica, Tamaryx aphylla)* and a shrub (i.e. *Prosopis juliflora*) species in different soil depths (0–15, 15–30, 30–45, 45–60, 60–75, 75–90 and 90–105 cm) and changes in salt concentrations across the soil depths between two seasons (i.e. rainy: rainfall 400 mm, temp. 10 °C; summer: rainfall 0 mm, temp. 46 °C) were examined. To test the effect of glucose on ECe, pHs and salt concentrations, an ex-situ experiment was conducted where soils from the rhizospheres of the species and open plots were treated with three doses of dextrose (0 g + 1 g soils, 0.25 g + 1 g soils, 0.50 g + 1 g soils). The study revealed that fine roots were found in all depths of soils under the trees and shrub species. Maximum (32 to 60%) salts were located in to 0–15 cm during the summer season, which declined to 20 to 40% during rainy season. During raining season reverse was observed, which created vertical heterogeneity in salt concentrations across the seasons. In the *ex-situ* experiment, the dextrose (0.25 g + 1 g^{-1} and 0.50 g + 1 g^{-1} rhizospheric soils) was found to form gluconic acid, which lowered pHs, proportionately greater in the soils treated with higher amount of the dextrose. In the presence of gluconic acid / dextrose, Cl^- probably formed OCl_4^-, and Na^+ and K^+ formed their gluconates with some amount of gluconic acid; these changes lowered ECe, which dropped water potential of the rhizospheric soils and created horizontal heterogeneity in salt concentrations. These horizontal and vertical heterogeneities likely facilitated water uptake to the non-halophytic tree-shrub species. The decline in ECe and pHs due to addition of dextrose sheds a new light on how glucose, exuded through roots, helps the non-halophytic trees to survive in the highly dry-land saline soils; these declines are a major target for development of techniques for reclamation of salt affected soils.

Key words: Rhizospheric soils, root biomass, salt concentration, salt movement, soil profile.

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Introduction

The world loses about 1.6 million hectare of fertile land every year due to salinization (Buringh 1978; UNEP 2009) which causes food grain loss by 20% (UNEP 2009). High salts in soils decrease water potential of soil solution to the extent which draws down water from plant cells to the soils through reverse osmosis and causes water deficit in the plant cells (Salisbury & Ross 1986); and high salts in cell cytoplasm on the other hand affect biochemical activities (Wyn Jones 1981; Wyn Jones & Gorham 2002), and these both processes together reduce growth and productivity of non-halophytic agricultural crops (Apse *et al.* 1999). Salt tolerant non-halophytes, however, adjust water potential of their leaf, stem and root cells by compartmenttalization of salts (Na^+ and Cl^-) in their vacuoles through Na^+/H^+ antiport system (Barkla & Pantoja 1996; Blumwald & Gelli 1997; Niu *et al.* 1995; Salisbury & Ross 1986); this helps to keep the salts away from the sites of metabolism (Wyn Jones 1981) and also develops a gradient of lower water potential from roots to leaves, which help flow of water from soil solution to the leaves (Glenn *et al.* 1999). Salt tolerant non-halophytes, however, require energy to osmoregulate the uptake of water using the antiport system (Higinbotham 1973; Macklon 1975; Pierce & Higinbotham 1970; Poole 1978), because it is an active process and transports Na^+ into plant vacuole by using an electrochemical gradient of protons generated by the vacuolar H^+-translocating enzymes like H^+-adenosine triphosphate (ATPase) and H^+- inorganic pyrophosphate (PPase) (Blumwald & Poole 1985; Rea & Sanders 1987). Recently, an isotopic water (^{18}O) study demonstrates that *Rhizophora mangle* in an estuary in USA utilizes fresh water from shallow soil profile during wet season, but uptakes water from deeper ground-water during dry season when the water in shallow soil profile turns hypersaline due to evaporation and intrusion of brackish water from the Florida Bay (Ewe *et al.* 2007). This indicates a strategy of roots to reduce or avoid excess uptake of salts (Ewe *et al.* 2007). Like the vertical heterogeneity in salt concentrations across the seasons in the estuary, horizontal heterogeneity also exists in saline soils, and salt tolerant plants uptake water from that side of rhizospheres, which contains relatively lower amount of salts (Bazihizina *et al.* 2012). The horizontal and vertical variations in the salinity of soil solution occur because of the interplay between soil leaching events triggered by rainfall / irrigation and water infiltration, and evapo-concentrations of solutes, caused by evaporation from moist soil surfaces and root-water extraction (Bennett *et al.* 2009; Tanji 2002). One of the common causes of upward ion movement is the development of shallow water-tables as a result of over-irrigation or other factors like loss of deep-rooted perennial vegetation. In these landscapes water and ions move from the shallow ground-water to the soil surface, especially at the times when evaporative demand is high (Bleby *et al.* 1997; Ghassemi *et al.* 1995; Northey *et al.* 2006). Heterogeneity is further exacerbated by the fact that dissolved salts can interact with soil matrix of the soil (eg. through adsorption) and also precipitate when their concentrations exceed their solubility (eg. common in soils with high gypsum) (Hillel 1980; Robbins *et al.* 1980).

In India, salt affected dry-lands are found in 6.3 million hectare (Mandal *et al.* 2010), where vegetation other than saline tolerant herb like *Suaeda salsa* does not survive. However, some non-haline *Acacia nilotica* and *Tamaryx aphylla* tree and *Prosopis juliflora* shrub species tolerate high soil salinity in the dry-lands and grow well. This prompted us to understand how the tree-shrub species influence salt concentrations in soils under their canopies, which help survive the tree-shrub species in the highly saline soil milieu. The study was also aimed to examine distribution of fine roots and salt concentrations in different depths of soils; and to know movement of salts across the depths in relation to seasons and tree-shrub species. Ultimate objective of the study, however, was to know the mechanisms which help the tree-shrub species to survive the high dry-land saline soil conditions. We hypothesize that the tree species add glucose through root exudates, which reduces electrical conductivity (electrolyte concentrations) and water potential in the rhizospheric soils of the species and thus facilitates their survival in the dry-land saline soils. Plants are well known to add glucose in their rhizospheres and substantially more in saline soils (Marschner 1995; Sacchi *et al.* 2000).

Materials and Methods

Study sites

The study was conducted in a research farm (>50 ha) of Central Institute for Research on Buffaloes (CIRB) (29.17 N lat. and 75.72 E long.), at Hisar, India. The soils of the farm were entisols with high proportion of fine particles (50 %), hence were poorly drained and characterized with high

ECe (129 dS m^{-1}). Three seasons: rainy (July–Sept.), winter (December–Feb.) and summer (March-June), with October as a transition month between rainy and winter seasons, prevail at the site. Mean monthly temperature ranges from 10 to 46 °C. January is the coolest (1.5 to 4 °C) and May the hottest (40 to 46 °C) month. Rainfall at the study site is 400 mm, maximum (85%) occurring during the rainy season (CIRB 2012). Natural vegetation in the salt affected soils is comprised of only two salt tolerant non-halophytic trees (*Acacia nilotica, Tamaryx aphylla*) and a shrub (*Prosopis juliflora*) species.

Experimental design and soil sampling

A tree of each salt-tolerant non-halophytic trees (i.e. *Acacia nilotica*: height 7.3 ± 0.98 m, canopy radius 3.6 ± 0.54 m, bole diameter (dbh) 32.2 ± 0.78 cm; *Tamaryx aphylla*: height 6.73.3 ± 1.07 m, canopy radius 4.56 ± 0.93 m, bole diameter (dbh) 43.1 ± 1.02 cm) and a shrub species (i.e. *Prosopis juliflora*: height 1.2 ± 0.21, canopy radius 2.6 ± 0.34 m, bole diameter (dbh) 12.4 ± 0.46 cm) and an open plot having no trees, 30 m apart from one another were selected in a field (≈ 1 ha); this treatment was replicated three times in the research farm. To know the distribution of salts in soil depths, rhizospheric soils were sampled from 10 random places from different depths (0–15, 15–30, 30–45, 45–60, 60–75, 75–90 and 90–105 cm) under the canopies of the tree-shrub species and the open plot as well in September 2012 and composited depth-wise for a tree-shrub species and an open plot. To know the salt movement pattern across the soil depths due to season, another sampling was done in the same soil depths and in the same manner in April 2012. To understand if the tree-shrub species influence salt concentration, rhizospheric soils (0–15 cm) were sampled from 10 random places from under the canopies of the tree-shrub species in January 2012 and composited for a tree-shrub species and an open plot. To understand how root exudates of the salt tolerant non-halophyte tree-shrub species regulate salts and water potential in their rhizospheric soils, we sampled rhizospheric soils (0–15 cm) further in April 2012 from 20 places underneath the trees and the open plots as well, and were composited for a tree and an open plot.

For chemical analyses, each composited soil sample was subjected to saturation paste (s) extraction (e). The saturation paste was prepared by adding 100 ml distilled water in 250 g composited soils and mixing them thoroughly in a beaker with stainless steel spatula. The beaker was covered and saturation paste was stored at room temperature for about 12 hours and then extracted using vacuum pump. To understand how do root exudates of the salt-tolerant non-halophytic tree-shrub species affect ECe, pHs, Cl^-, SO_4^{--}, Na^+, K^+, Ca^{++} and Mg^{++} in their rhizospheres, an *ex-situ* experiment was conducted where the composited rhizospheric and open plot soils, sampled in April 2012, were treated with dextrose. This was done because plant roots are known to exude 40% of the net carbon fixed during photosynthesis in their rhizospheres (Whipps & Lynch 1985) in the form of root exudates, which contain glucose and other carbon compounds (Marschner 1995; Newman & Romheld 2007; Sacchi *et al.* 2000; Whipps & Lynch 1985). For this, each composited rhizospheric and open plot soil sample was divided into three parts; first part was treated with dextrose at 0.25 g dextrose + 1 g soil, the second part at 0.50 g dextrose + 1 g soil and the third part at 0 g dextrose + 1 g soil. Both, with (0.25 g dextrose + 1 g soil, 0.50 g dextrose + 1 g soil) and without (0 g dextrose + 1 g soil) dextrose treated samples were subjected to saturation paste (s) extraction (e) as stated before. To understand if the changes in the concentrations of salts (Cl^-, SO_4^{--}, Na^+, K^+, Ca^{++} and Mg^{++}), ECe and pHs in response to the dextrose are chemical or biological in nature, we did another experiment where a set of composited soils sampled in April 2012 was autoclaved and another set was not autoclaved before addition of the dextrose.

ECe, pHs, Na^+, K^+, Ca^{++}, Mg^{++}, Cl^- and SO_4^{--} were determined following Richards (1954). ECe and pHs of the saturation paste extract were determined using water quality analyzer (Elico-PE-136, India), and Na^+ and K^+ by atomic absorption spectrophotometer (AA-41, Electronics Corporation of India). Sulphate was determined gravimetrically by treating 10 ml of the extract with $BaCl_2$ and washing the precipitate on Whatman 42 filter paper till it was free of chloride. Weight of the precipitate was then estimated by making it's ash in a silica crucible at 500°C. Ca^{++} and Mg^{++} were estimated in the extract by titrating it with EDTA; 5 ml of the extract was used for Ca^{++} and 1 ml for Mg^{++}. Gluconic acid and gluconates were determined by HPLC (YL9100, YL Instruments Korea; column: Hypersil C-18, Dia 250×4.6 mm, solvent 108% acetonitrile in 0.0035 M H_2SO_4; flow 0.5 ml min^{-1}, Temperature 35 °C, UV detector at 210 nm, injection volume 20 µL, starting pressure 480 psi) after filtration with 13 mm dia nylon membrane (0.22 µm mess) filters (Agela Technologies, USA).

Table 1. ECe, pHs, cations (Na^+, K^+, Ca^{++}, Mg^{++}), anions (Cl^- and SO_4^{--}) and soil organic carbon (SOC, %) in the soils (0–15 cm) from the open plots and rhizospheres of three salt-tolerant non-halophytes (i.e. two non-halophytic trees, *Acacia nilotica* and *Tamaryx aphylla*; and a shrub species, *Prosopis juliflora*) growing in the saline dry lands at the research farm of CIRB, Hisar, India.

Parameter	Open plot	Rhizospheric soils		
		A. nilotica	*T. aphylla*	*P. juliflora*
ECe (dS m^{-1})	^{a}118	^{b}75.6	^{c}24.5	^{d}20.1
pHs	^{a}8.2	^{b}7.8	^{c}7.5	^{c}7.3
Na^+ (me L^{-1})	^{a}1241	^{b}631	^{c}115	^{d}63.5
K^+ (me L^{-1})	^{a}3.2	^{b}8.3	^{c}5.4	^{d}12.1
Ca^{++} (me L^{-1})	^{a}52	^{b}61	^{b}56	^{c}65
Mg^{++} (me L^{-1})	^{a}45	^{b}60	^{b}55	^{c}65
Cl^- (me L^{-1})	^{a}919	^{b}780	^{c}104	^{d}67
SO_4^{--} (me L^{-1})	^{a}495	^{b}230	^{c}43	^{d}73
SOC (%)	^{a}0.028	^{b}0.038	^{b}0.040	^{c}0.115

Values in a row superscript with the same letter is not significant at $P<0.05$;

To confirm the formation of gluconic acid in the studied soils, another *in-situ* experiment was conducted where NaCl (analytical AR grade) solutions (1000 ppm and 2000 ppm) were treated with two doses of dextrose (6 ml NaCl + 1 g dextrose, and 6 ml NaCl + 2 g dextrose).

For measurement of fine live root biomass a monolith, 25 × 25 cm, from each 0–15, 15–30, 30–45, 45–60, 60–75, 75–90 and 90–105 cm depth, was excavated from beneath the selected tree-shrub species in October 2012. The monoliths were washed with a fine jet of water using successive 2 mm and 0.5 mm mesh screens. Fine live roots (< 2 mm diameter) were shorted out and dried at 60 °C in an oven to a constant weight and weighed.

Statistical analysis

Data of glucose treated soils were subjected to two way ANOVA using SPSS statistical package where treatment included three tree-shrub species and three doses of glucose, and number of tree-shrub (three) served as replicates. Two way ANOVA was also performed to test significance in differences in salt distribution among soil depths and seasonality in their movement across the depths. However, to test the significance of difference in root biomass distribution across the soil depths, one way ANOVA was performed. To compare significance of difference between two means LSD ($P < 0.05$) is used.

Results

Change in salts in response to non-haline trees

Chemical characteristics of rhizospheric saline soils under the studied tree-shrub species are given in Table 1. The tree-shrub species lowered ECe, pHs, Cl^-, SO_4^{--} and Na^+, and increased K^+, and to a limited extent Ca^{++} and Mg^{++} in their rhizospheres than open plot (Table 1). The decline, however, was the highest under *Prosopis juliflora* and the lowest under *Acacia nilotica*. Soil organic carbon also increased under the tree and shrub species, but the increase was the highest (311%) under *P. juliflora* and lowest (36–43%) under *A. nilotica* and *Tamaryx aphylla*.

Distribution of salts (Na^+, K^+, Ca^{++}, Mg^{++}, Cl^- and $SO4^{--}$) across the soil depths under the tree-shrub species and open plot are given in Table 2. Amount of the salts was the highest on the uppermost layer (0–15 cm) and declined with depths. Amount of salts in all depths under the studied tree-shrub species declined compared to corresponding depths in open plot. This decline, however, was the highest under the *P. juliflora* and lowest under *A. nilotica*. Since, all cations and anions showed similar pattern of their distribution and movement across the depths in relation to season, only values of NaCl (Na^+ + Cl^+) are presented here to show salt dynamics across the depths (Table 3). Movement of the salts occurred only within 45 cm depths under all tree-

Table 2. ECe, pHs, cations (Na^+, K^+, Ca^{++}, Mg^{++}) and anions (Cl^- and SO_4^{--}) in the soils from different depths of the open plots and rhizospheres beneath three salt-tolerant non-halophytes (i.e. two non-halophytic trees, *Acacia nilotica* and *Tamaryx aphylla*; and a shrub species, *Prosopis juliflora*) growing in the saline dry lands at the research farm of CIRB, Hisar, India.

Depth (cm)	ECe (dS m^{-1})				pHs			
	Open plot	*A. nilotica*	*T. aphylla*	*P. juliflora*	Open plot	*A. nilotica*	*T. aphylla*	*P. juliflora*
0–15	102.0	79.6	26.7	24.3	$^{xy}8.0^{a}$	$^{x}8.1^{a}$	$^{x}7.3^{a}$	$^{y}7.8^{a}$
15–30	68.5	46.9	21.9^{ab}	12.5^{b}	$^{x}7.7^{a}$	$^{x}7.7^{a}$	$^{x}7.8^{a}$	$^{x}7.9^{a}$
30–45	42.6	29.9	22.0^{ac}	11.6^{b}	8.3^{ab}	8.0^{ab}	$^{x}7.7^{a}$	$^{x}7.7^{a}$
45–60	$^{x}26.0^{a}$	$^{x}25.3^{a}$	20.4^{b}	11.7^{b}	9.0^{b}	8.0^{ab}	$^{x}7.0^{a}$	$^{x}7.5^{a}$
60–75	$^{x}18.2$	25.3^{a}	$^{x}19.1^{c}$	11.0^{b}	8.7^{ab}	$^{x}7.7^{b}$	$^{x}7.3^{a}$	$^{x}7.0^{a}$
75–90	25.3^{a}	22.8^{b}	20.2^{b}	12.6^{b}	8.5^{ab}	$^{x}7.7^{b}$	$^{x}7.4^{a}$	$^{x}7.1^{a}$
90–105	26.5^{a}	22.9^{b}	18.5^{c}	11.1^{b}	8.5^{ab}	$^{x}7.7^{b}$	$^{x}7.1^{a}$	$^{x}7.5^{a}$
	Na^+ (me L^{-1})				K^+ (me L^{-1})			
0–15	1361	588	168^{a}	87	$^{x}3.1^{a}$	$^{x}4.3$	$^{y}8.4$	$^{x}4.1$
15–30	805	413	168^{a}	69^{a}	$^{x}1.9$	$^{x}3.7$	5.8	$^{x}2.9$
30–45	483	234	168^{a}	69^{a}	$^{x}0.9^{b}$	$^{x}2.5$	$^{x}2.6$	x1.6
45–60	263	199	161	64^{a}	$^{x}0.^{3b}$	$^{y}1.1$	$^{y}1.0^{a}$	$^{x}0.5^{a}$
60–75	239^{a}	191	148	64^{a}	$^{x}0.3^{b}$	$^{y}0.8^{a}$	$^{y}1.1^{a}$	$^{xy}0.4^{a}$
75–90	244^{a}	$^{x}175^{a}$	$^{x}168^{a}$	74	$^{x}0.3^{b}$	0.8^{a}	1.3^{a}	$^{x}0.5^{a}$
90–105	244^{a}	168^{a}	148	42	2.6^{a}	$^{x}0.6^{a}$	1.7^{a}	$^{x}0.6^{a}$
	Ca^{++} (me L^{-1})				Mg^{++} (me L^{-1})			
0–15	64	70	65	81	30	65	35	70^{a}
15–30	40	48	45	61	16	33^{a}	43	67^{a}
30–45	10	26^{a}	24	33	7.5^{a}	$^{x}31^{a}$	62	$^{x}28$
45–60	2^{a}	23^{ab}	$^{x}19^{a}$	$^{x}23^{a}$	1.8^{b}	27^{b}	48^{a}	37
60–75	2^{a}	$^{x}19^{bc}$	$^{x}17^{a}$	28^{b}	1.8^{b}	28^{b}	47^{a}	23
75–90	2^{a}	$^{x}15^{cd}$	$^{x}18^{a}$	30^{b}	3.8^{bc}	$^{x}27^{b}$	41^{b}	$^{x}27^{b}$
90–105	4^{a}	12^{d}	16^{a}	21^{a}	6.8^{ac}	$^{x}26^{b}$	41^{b}	$^{x}27^{b}$
	Cl^- (me L^{-1})				SO_4^{--} (me L^{-1})			
0–15	1000	153^{a}	726	91	543	216	63	35
15–30	591	150	509	75^{a}	321	152	55^{a}	29^{a}
30–45	354	143	288	72^{a}	192	86	51^{a}	26^{ab}
45–60	193	45^{bc}	245	63	105	73^{a}	17^{b}	23^{bc}
60–75	175^{a}	46^{b}	235	70^{a}	95^{a}	70^{a}	18^{b}	25^{bc}
75–90	179^{a}	$^{x}40^{c}$	215	$^{x}43$	92^{a}	64	15^{b}	28^{b}
90–105	162	$^{x}32$	206	$^{x}31$	81	28	8	20^{c}

Data in a column and a row with same superscript letter are not significant at $P<0.05$.

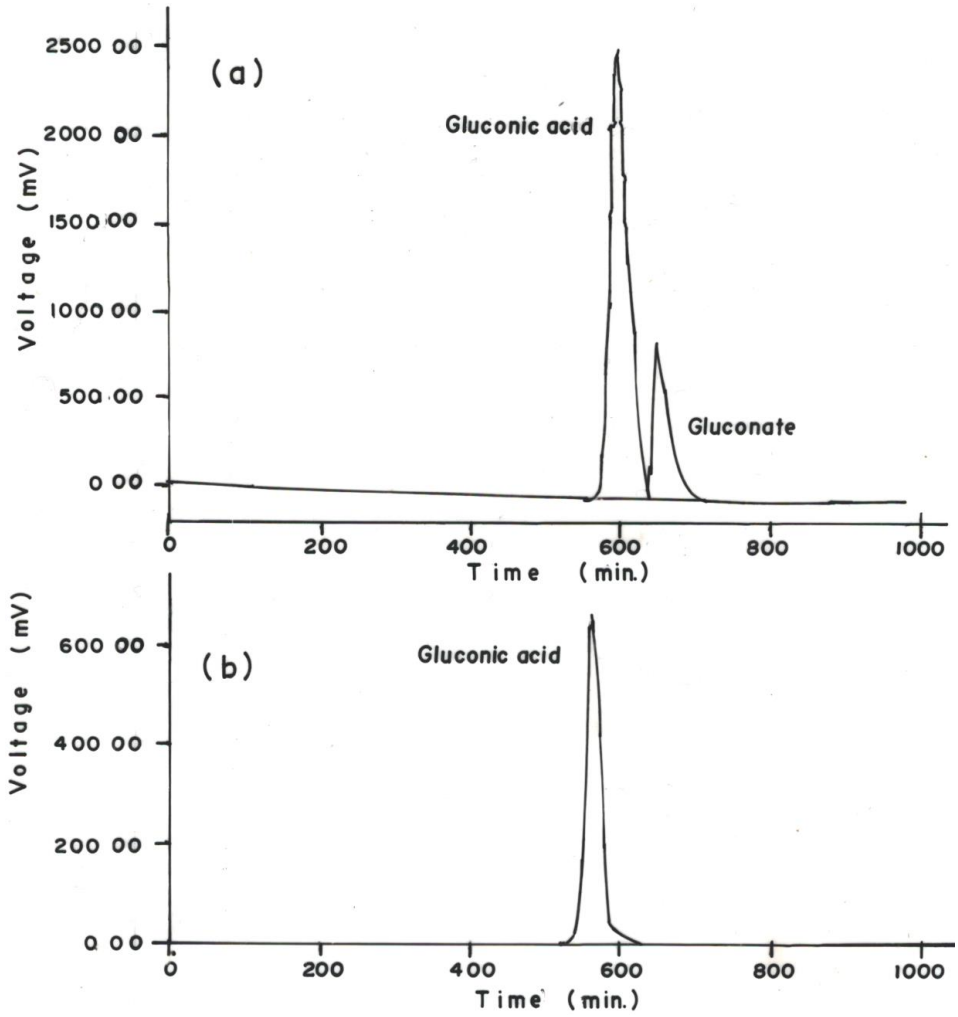

Fig. 1. Chromatograms of (a) standard solution, (b) rhizospheric soils of *Prosopis juliflora*.

shrub species. Maximum (32 to 60%) salts were located in to 0–15 cm during the summer season which declined to 20 to 40% during rainy season. During the summer season 2 to 13% salt increased in 15 to 30 cm and 3 to 12% in 30–45 cm. The highest increase in the salt in 15–30 cm occurred in open plot, whereas in 30–45 cm depth it was under *P. juliflora.*

Ex-situ experiment

In the *ex-situ* experiment, concentrations of all salts, other than K, were influenced by the tree-shrub species, the amount (dose) of dextrose and their interactions (Table 4). ECe, pHs, Cl^- and SO_4^{--} declined (21 to 64%, 0.1 to 0.7 unit, 19 to 77 %, 10 to 48 %, respectively) in the rhizospheric as well as open plot soils due to addition of the dextrose (Table 5). The decline was, however, greater in the soils treated with higher amount of the dextrose. Ca^{++} and Mg^{++} did not change; both Na^+ declined (8 to 18%, respectively), however, decline in the K^+ occurred only at the high dose of dextrose. The dextrose formed gluconic acid in the extracts of the saline soils sampled from under the tree-shrub species and open plots. In the soils of the open plots, amount of gluconic acid increased linearly with the amount of dextrose, however, in the soils from under the tree-shrub species, increase in the amount of gluconic acid occurred when treated with dextrose at moderate dose (0.25 g dextrose + 1 g soil), but declined when amount of the dextrose was increased further (0.50 g dextrose + 1 g soil) (Table 5, Fig. 1). The gluconic acid was found maximum in the rhizospheric soils from under the *A. nilotica* and lowest under *P. juliflora*. The amount of the gluconic acid, however, was always greater in the open plot soils than in the rhizospheric soils from under the tree-shrub species. In the autoclaved

Table 3. Dynamics of salts (Na + Cl; me L^{-1}) across seasons (summer season, S; rainy season, R) and soil depths beneath three salt-tolerant non-halophytes (i.e. two non-halophytic trees, *Acacia nilotica* and *Tamaryx aphylla*; and a shrub species, *Prosopis juliflora*) growing in the saline dry lands at the research farm of CIRB, Hisar, India.

Depth (cm)	Open plot		*Acacia nilotica*		*Tamaryx aphylla*		*Prosopis juliflora*	
	S	R	S	R	S	R	S	R
0–15	$^{q}3868^{a} \pm 418$	$^{r}2115^{a} \pm 97$	$^{s}1161^{a} \pm 256$	$^{t}859^{a} \pm 62$	$^{u}318^{a} \pm 11$	$^{v}233^{a} \pm 13$	$^{w}180^{a} \pm 16$	$^{x}110^{a} \pm 8$
15–30	$^{q}1585^{b} \pm 70$	$^{r}1999^{a} \pm 79$	$^{s}866^{a} \pm 79$	$^{t}1017^{b} \pm 20$	$^{u}294^{b} \pm 12$	$^{v}350^{a} \pm 33$	$^{w}146^{b} \pm 9$	$^{x}188^{b} \pm 13$
30–45	$^{q}950^{c} \pm 53$	$^{r}1140^{b} \pm 136$	$^{s}443^{b} \pm 48$	$^{t}528^{c} \pm 83$	$^{u}365^{c} \pm 7$	$^{v}426^{b} \pm 25$	$^{w}136^{c} \pm 8$	$^{x}196^{b} \pm 14$
45–60	$^{q}517^{d} \pm 28$	$^{q}523^{c} \pm 43$	$^{r}407^{c} \pm 24$	$^{r}473^{c} \pm 56$	$^{s}314^{d} \pm 7$	$^{t}367^{c} \pm 7$	$^{u}124^{c} \pm 5$	$^{v}155^{c} \pm 12$
60–75	$^{q}470^{d} \pm 38$	$^{q}463^{c} \pm 76$	$^{q}383^{c} \pm 105$	$^{q}378^{c} \pm 42$	$^{r}291^{d} \pm 48$	$^{r}284^{d} \pm 17$	$^{s}121^{c} \pm 7$	$^{s}126^{d} \pm 10$
75–90	$^{q}480^{d} \pm 19$	$^{q}469^{c} \pm 127$	$^{r}355^{c} \pm 55$	$^{r}315^{d} \pm 29$	$^{r}310^{d} \pm 5$	$^{r}311^{d} \pm 11$	$^{s}154^{b} \pm 7$	$^{s}150^{c} \pm 18$
90–105	$^{q}457^{d} \pm 9$	$^{q}461^{c} \pm 61$	$^{qr}341^{c} \pm 40$	$^{r}332^{d} \pm 13$	$^{r}335^{d} \pm 5$	$^{r}325^{d} \pm 15$	$^{s}88^{d} \pm 8$	$^{s}86^{e} \pm 10$

Data in a row prefixed with same letter are not significant at $P<0.05$.
Data in a column prefixed with same letter are not significant at $P<0.05$.

Table 4. Summary of ANOVA results (F value) on ECe, pHs, cations (Na^+, K^+, Ca^{++}, Mg^{++}), anions (Cl^- and SO_4^{--}), gluconic acid and water potential of dextrose treated soils from an open plot and rhizospheres of three salt-tolerant non-halophytes (i.e. two non-halophytic trees, *Acacia nilotica* and *Tamaryx aphylla*; and a shrub species, *Prosopis juliflora*) growing in the saline dry lands at the research farm of CIRB, Hisar, India.

Source	*df*	Na	pH	ECe	K	Ca	SO4	Cl	Mg	Gluconic acid	Water potential
Species (spp.)	3	3009*	3.14***	7909*	1176*	28041*	2910*	117007*	15247*	752148*	65322*
Glucose (Gl)	2	36*	5.41***	12740*	28.7*	8.9*	260*	33931*	91*	5327*	6543*
Spp. × Gl	6	21815*	2.70**	417*	1.67NS	9.8*	47*	2308*	185*	8875*	2872*
Error	108										

*<0.001**<0.01; ***<0.05.

(sterilized) soil extracts, ECe, pHs, Cl^- and SO_4^{--} did not differ significantly ($P < 0.05$) with that in the no-sterilized soils (Table 6).

Tree root distribution

Fine root biomass was found in all soil depths under the tree-shrub species; it was the highest in 0–15 cm and declined with the depths (Table 7). Amount of the root biomass was the highest under the *P. juliflora* and lowest under *Acacia nilotica*.

Discussion

The concentrations of salts found in the study were well within the range reported from different continents of the world (Szabolcs 1994). Reduction in pH in both rhizospheric (from under the trees) and non-rhizospheric soils (open plot) treated with dextrose could be due to formation of gluconic acid. In our study glucose is not measured directly in the rhizospheric soils, because it is well known that root exudates contain glucose and other compound (Barkla & Pantoja 1996; Bazihizina *et al.* 2012; Salisbury & Ross 1986; Wyn Jones 1981). Plants are known to exude about 40% of the net carbon fixed during photosynthesis in their rhizosphere in the form of glucose and other water soluble carbon compounds (Bazihizina *et al.* 2012), which is almost doubled in saline soil conditions (Wyn Jones 1981). One may argue that amount of dextrose used in our study was pharmaceutical rather than biological dose, but concentration of glucose at the point of exudation in the rhizospheres may be assumed to be at relatively higher concentration. Reduction in ECe, however, in the rhizospheric soils treated with the dextrose may be attributed to decline mainly in Cl^- and partly in Na^+. In the presence of gluconic acid or glucose, Cl^- was probably converted into oxychlorides (OCl_4^-) (Andreassen 2009), which reduced the number of ions carrying charges. Though we expected, but the decline in Cl^- did not

Table 5. ECe, pHs, cations (Na^+, K^+, Ca^{++}, Mg^{++}), anions (Cl^- and SO_4^{--}), gluconic acid and water potential of dextrose treated soils from the open plots and rhizospheres of three salt-tolerant non-halophytes (i.e. two non-halophytic trees, *Acacia nilotica* and *Tamaryx aphylla*; and a shrub species, *Prosopis juliflora*) growing in the saline dry lands at the research farm of CIRB, Hisar, India.

Parameter	Non-halophytic tree-shrub species									Open plot (without tree)		
	Acacia nilotica			*Tamaryx aphylla*			*Prosopis juliflora*					
	SPERS			SPERS			SPERS			SPENRS		
	Dextrose (g g^{-1} soil)			Dextrose (g g^{-1} soil)			Dextrose (g g^{-1} soil)			Dextrose (g g^{-1} soil)		
	0	0.25	0.50	0	0.25	0.50	0	0.25	0.50	0	0.25	0.50
†ECe	96.3	64.9	35.6	78.5	61.7	28.6	49.1	25.6	18.6	128.8	84.1	56.8
pH	8.1	7.6	7.4	7.6	7.5	7.3	7.5	7.3	7.1	8.2	6.7	6.4
*Na^+	1066	[a]948	[a]933	607	560	496	240	219	198	[a]1782	[a]1771	1582
*K^+	[a]33.5	[a]31.8	28.1	[a]16.8	[a]15.3	13.3	[a]4.6	[a]3.3	1.8	[a]7.2	[a]6.3	5.4
*Ca^{++}	[a]31.4	[a]34.7	[a]34.4	[a]39.6	[a]39.9	[a]40.1	[a]91.5	[a]91.2	[a]91.9	[a]22.0	[a]21.6	[a]21.9
*Mg^{++}	[a]153	[a]156	[a]157	[a]255	[a]258	[a]264	189	151	127	[a]40	[a]38	[a]36
*Cl^-	973	752	453	750	607	533	252	134	58	1320	972	864
*SO_4^{--}	399	210	198	224	196	202	272	241	183	711	661	599
**Gluconic acid	0	99	68	0	76	54	0	64	15	0	1083	1429
Water potential#	-2094	-3078	-3821	-1877	-2726	-3611	-835	-2670	-3071	-1264	-2236	-2691

SPERS = saturation paste extract of rhizospheric soils; SPENRS = saturation paste extract of non- rhizospheric soils (open plot); †(dS m^{-1});* (me L^{-1});** (mg L^{-1}); # = m mol Kg^{-1};
Values with same prefixed letter in a row for a plant species and open plot are not significant. Data were subjected to one way ANOVA analysis using SPSS statistical package to know significance in the difference due to the dextrose treatment.

lead to equivalent decline in cations (i.e. Ca^{++}, Mg^{++}, Na^+, K^+). Decline in Cl^- was four times greater than the decline in all cations together, which suggested OCl_4^- as a probable compound, which only explained the disproportionate decline of cations and anions in our study. A little decline in Na^+ and K^+, however, indicated that Na^+ and K^+ could have reacted with some amount of gluconic acid and their gluconates might have been formed (Buttrworth 1997), but these were not detected in chromatograms likely due to their quick conversion into some other organic compounds. We were not able to find out factors, which caused the formation of the gluconic acid. Some studies, however, reports conversion of glucose to gluconic acid in alkaline medium (Ewe *et al.* 2007; Niu *et al.* 1995). To confirm the formation of gluconic acid in the rhizospheric and non-rhizospheric soils, another *in-situ* experiment was conducted where NaCl (analytical AR grade) solutions (1000 ppm and 2000 ppm) were treated with two doses of glucose (6 ml NaCl + 1 g glucose, and 6 ml NaCl + 2 g glucose). In the NaCl solutions, EC and pH declined and gluconic acid was formed. The decline in EC and pH, however, was higher in the solution treated with the greater amount of glucose. We did not find correlation between the ECe and amount of gluconic acid, but the formation of greater amount of gluconic acid in the non-rhizospheric than rhizospheric soils suggested that high electrical conductivity of the rhizospheric soils could be the driver. Among the studied tree-shrub species, the greatest amount of gluconic acid in the rhizospheric soils of *A. nilotica*, which contained the highest ECe, corroborates our prediction. Insignificant differences in ECe, pHs, Na^+, Ca^{++}, Mg^{++}, Cl^- and SO_4^{--} between sterilized [autoclaved the extracts for 1hr at psi (121 °C) and then cooled to room temperature] and no-sterilized soil extracts, however, indicated that decline in ECe was chemical rather than biological in nature. The decline in ECe seemed to have moderated the harsh conditions of the rhizospheric soils.

The decline in water potential in the rhizospheric soils may be attributed to the addition

Table 6. Effect of sterilization on ECe (dS m^{-1}), pHs, cations and anions (me L^{-1}) of saturation paste extracts of dextrose treated soils from the rhizospheres of three salt-tolerant non-halophytes (i.e. two non-halophytic trees, *Acacia nilotica* and *Tamaryx aphylla*; and a shrub species, *Prosopis juliflora*) growing in the saline dry lands at the research farm of CIRB, Hisar, India.

Tree	No sterilized			Sterilized		
	Dextrose (g g^{-1} soil)			Dextrose (g g^{-1} soil)		
	0	0.25	0.50	0	0.25	0.50
			ECe			
A. nilotica	^{a}96.3	^{b}64.9	^{c}35.6	^{a}94.7	^{b}62.4	^{c}36.1
T. aphylla	^{a}78.5	^{b}61.7	^{c}28.7	^{a}76.2	^{b}60.3	^{c}28.2
P. juliflora	^{a}49.1	^{b}25.6	^{c}18.6	^{a}48.7	^{b}26.1	^{c}18.7
			pHs			
A. nilotica	^{a}8.4	^{b}7.9	^{c}7.7	^{a}8.3	^{b}7.8	^{c}7.6
T. aphylla	^{a}7.9	^{b}7.8	^{c}7.6	^{a}7.8	^{b}7.8	^{c}7.7
P. juliflora	^{a}7.8	^{b}7.6	^{c}7.4	^{a}7.7	^{b}7.7	^{c}7.5
			Na^{+}			
A. nilotica	^{a}1066	^{b}948	^{c}933	^{a}1062	^{b}950	^{c}931
T. aphylla	^{a}607	^{b}560	^{c}496	^{a}610	^{b}557	^{c}492
P. juliflora	^{a}240	^{b}219	^{c}198	^{a}241	^{b}220	^{c}196
			Cl^{-}			
A. nilotica	^{a}973	^{b}752	^{c}453	^{a}969	^{b}750	^{c}451
T. aphylla	^{a}750	^{b}606	^{c}533	^{a}747	^{b}610	^{c}530
P. juliflora	^{a}252	^{b}134	^{c}58	^{a}250	^{b}133	^{c}56
			SO_4^{--}			
A. nilotica	^{a}399	^{b}210	^{c}198	^{a}396	^{b}208	^{c}199
T. aphylla	^{a}224	^{b}196	^{c}186	^{a}220	^{b}198	^{c}176
P. juliflora	^{a}272	^{b}241	^{c}183	^{a}270	^{b}240	^{c}181

Values with same superscript letter in a row are not significantly different at $P<0.05$.

Table 7. Fine root biomass in different soil depths under three salt-tolerant non-halophytes (i.e. two non-halophytic trees, *Acacia nilotica* and *Tamaryx aphylla*; and a shrub species, *Prosopis juliflora*) growing in the saline dry lands at the research farm of CIRB, Hisar, India.

Depth (cm)	Fine root biomass (g m^{-2})		
	A. nilotica	*T. aphylla*	*P. juliflora*
0–15	168.9	235.6	360.0
15–30	102.2	186.7^{a}	288.9
30–45	80.0	182.2^{a}	275.6^{a}
45–60	35.6	168.9	271.1^{a}
60–75	26.7^{a}	164.4	266.7
75–90	22.2^{a}	135.3	253.3
90–105	13.3	120.0	222.2

Values suffixed with same superscript letter in a column and in a row are not significantly different at $P<0.05$.

of dextrose. Plant roots are known to exude glucose more than two times greater in saline than non-saline soils (Sacchi *et al.* 2000). The decline in water potential in the extracts of the rhizospheric soils due to addition of the dextrose indicated that the non-halophytic tree-shrub species probably drew water through osmosis from nearby places having relatively greater water potentials (Salisbury & Ross 1986) and thereby generated patches of low salt water; this way the exudates seem to have generated horizontal heterogeneity in salt distribution. Salt distribution pattern along soil depths in our study indicated that maximum salts (44 to 77%) were distributed in upper depths (0–45 cm) and 23 to 55% in deeper depths (45 to 105 cm) of the soils. This clearly generated low salt and high salt zones and thereby vertical heterogeneity in salt distribution. Salts in the deeper depths did not vary

due to season probably due to consistency in soil-moisture, but it was otherwise in the upper depths. In the upper depths evaporative demands pulled the greater amount of salts in uppermost depth during the summer and vice-versa in rainy season and likely generated seasonal heterogeneity in upper depths in our dryland saline soils. Horizontal and vertical variations in the salinity of the soil solution are known to occur because of the interplay between soil leaching events triggered by rainfall / irrigation and water infiltration, and evapo-concentration of solutes, due to evaporation from moist soil surface and root water extraction (Bennett *et al.* 2009; Tanji 2002). At our study site 400 mm rainfall seems to have pushed down the salts up to 45 cm depth likely due to clayey nature of the soils, which causes low infiltration. CAZRI (2014) reported very low infiltration rate in dry-land saline soils in Bikaner, India. Though not studied, we speculate that the horizontal and vertical heterogeneity helped the studied to tree-shrub species to uptake water from the soils having relatively low amount of salts. In split root studies, where horizontal and vertical heterogeneous salinity were created, and the most of the water uptake (73 to 90%) by non-haline plants in saline environment was reported to have occurred from the lower-salt sides of root zones (Ewe *et al.* 2007; Bazihizina *et al.* 2012). Though vertical and horizontal heterogeneity in salinity reduces water potential, water uptake from high saline zones does not cease and it accounts for 9 to 30% of total water uptake (Bazihizina *et al.* 2012) this uptake of water from high salt zone increases shoot ion concentrations. During summer season when salts concentrates in upper depths is high, the studied tree-shrub species seem to have used water from deeper depths where concentration of salts is lower. In coastal Everglades of Southern Florida, where salinity in shallow and ground-water vary with season, the shallow water being the less saline than ground water in winter and vice versa in summer, *Cladium jamaicense, Sesuvium portulacastrum*, and Rhizophora mangle used non-saline shallow water in winter, but in summer reverse in the water uptake pattern occurs (Ewe *et al.* 2007).

Root distribution pattern in the studied tree-shrub species in our study was similar to glycophytes; this indicates that salt tolerant non-halophytes are well adapted to the saline soil conditions. Srivastava *et al.* (1986) and Pandey & Singh (1992) have found that trees and grasses in dry deciduous forests and dry tropical savannas allocate the highest amount of root biomass in upper depths, and the allocation, however, decline with depths. Greater amount of root biomass in *Prosopis juliflora* and *T. aphylla* could be due to greater tolerance of the species for salts in the soil profile, and reverse was true for the *Acacia nilotica.* Bazihizina *et al.* (2012) argued that in a heterogeneous soil profile, root allocation by non-halophytes to saline zones can be expected to decrease with increasing salinity, but salinity tolerant species may make it otherwise. They are of the further view that root biomass allocation in non-halophytes depend upon their ability to tolerate salts (Bazihizina *et al.* 2012). For example, root growth in two non-halophytes like *Phaseolus vulgaris* and *Gossypium hirsutum* was similar in non-saline soil column. In soil column with increasing salinity experiment, however, relatively less tolerant *P. vulgaris* was able to grow a few roots in a column with moderate salt, but it did not grow even a single root in the part of the column with high salts. Contrary to this a more salt tolerant non-halophyte *G. hirsutum* grew roots in all saline soil columns. A substantial decline in salts in all depths of soils under *P. juliflora* than in open plot in our study suggests their removal, but our study is unable to explain decline in total salt amount from the soil profile.

Conclusions

Our study concludes that the salt-tolerant non-haline tree-shrub species exude glucose in their rhizospheres, which form gluconic acid in the saline soil environment and drops pHs; and also causes decline in ECe, and salts (Na^+, Ca^{++}, Mg^{++}, Cl^- and SO_4^{--}). Decline in Cl^- is, however, four times greater than decline in total cations suggesting that OCl_4 could be the compound, which caused disproportionate decline in cations and Cl^-. The reduced ECe decreases water potential of the soils and generates horizontal heterogeneity in salt concentrations, whereas the seasonal movement of salts across the soil depths creates vertical heterogeneity in salt concentrations. Both, horizontal and vertical heterogeneity in the salt concentrations facilitate uptake of water in the highly saline soil environment. The decline in ECe and pHs due to addition of the dextrose in the saline soils has a great bearing for reclamation of over 800 m ha salt affected lands (Song *et al.* 2009), which cause food grain production loss globally about ≈11,400 million US$ every year (Pitman & Lauchli 2002).

Acknowledgements

The study was funded under Institute Research program by Indian Council of Agricultural Research, New Delhi, India. Technical assistance of Mr. Rameshwar Ram and Mr. Rajesh Kumar is thankfully acknowledged.

References

Andreassen, T. 2009. *New Methods for Preparation of Optically Active Unsaturated Amines*. Ph.D. Thesis. Department of Chemistry, Faculty of Natural Science and Technology, Norwegian University of Science and Technology, NTNU-Trykk.

Apse, M. P., G. S. Aharon, W. A. Snedden & E. Blumwald. 1999. Salt tolerance conferred by overexpression of a vacuolar Na^+ / H^+ antiport in Arabidopsis. *Science* **285:** 1256–1258.

Barkla, B. J. & O. Pantoja. 1996. Physiology of ion transport across the tonoplast of higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **47**: 159–184.

Bazihizina, N., E. G. Barrett-Lennard & T. D. Colmer. 2012. Plant growth and physiology under heterogeneous salinity. *Plant and Soil* **354**: 1–19.

Bennett, S. J., E. G. Barrett-Lennard & T. D. Colmer. 2009. Salinity and waterlogging as constraints to salt land pasture production: a review. *Agriculture Ecosystems and Environment* **129:** 349–360.

Bleby, T. M., M. Aucote, A. K. Kennett-Smith, G. R. Walker & D. P. Schachtman. 1997. Seasonal water use characteristics of tall wheatgrass (*Agropyron elongatum* (Host) Beauv) in a saline environment. *Plant Cell & Environment* **20:** 1361–1371.

Blumwald, E. & A. Gelli. 1997. Secondary in organic ion transport at the tonoplast. *Advances in Botanical Research* **25:** 401–417.

Blumwald, E. & R. J. Poole. 1985. Na+ / H+ antiport in isolated tonoplast vesicles from storage tissue of *Beta vulgaris*. *Plant Physiology* **78**: 163-167

Buringh, P. 1978. Food production potential of the world. pp. 477–485. *In*: R. Sinha (ed.) *The World Food Problem: Consensus and Conflict*. Pergamon Press.

Buttrworth, H. 1997. *Biotechnological Innovations in Chemical Synthesis*. Reed Educational and Professional Publishing, Oxford.

CAZRI. 2014. *Annual Report*. Central Arid Zone Research Institute, Jodhpur, India.

CIRB. 2012. *Annual Report*. Central Institute for Research on Buffaloes, India.

Ewe, S. M. L., L. S. L. Sternberg & D. L. Childers. 2007. Seasonal plant water uptake patterns in the saline southeast Everglades ecotone. *Oecologia* **152**: 607–616.

Ghassemi, F., A. J. Jakeman & H. A. Nix. 1995. *Salinisation of Land and Water Resources: Human Causes, Extent, Management and Case Studies*. University of New South Wales Press Ltd, Canberra.

Glenn, E., J. J. Brown & E. Blumwald. 1999. Salt tolerance and crop potential of halophytes. *Critical Reviews in Plant Sciences* **18**: 227–255.

Higinbotham, N. 1973. Electropotentials of plant cells. *Annual Review of Plant Physiology* **24:** 25–46.

Hillel, D. 1980. *Fundamentals of Soil Physics*. Academic, New York.

Macklon, A. E. S. 1975. Cortical fluxes and transport to the stele in excised root segments of *Allium cepa* L. *Planta* **122:** 109–130.

Mandal, A. K., R. C. Sharma, Gurbachan. Singh & J. C. Dagar. 2010. *Computerized Database on Salt Affected Soils in India*. Technical Bulletin. Central Soil Salinity Research Institute, Karnal, Haryana, India.

Marschner, H. 1995. *Mineral Nutrition of Higher Plants*. Academic Press, London.

Newman, G. & V. Romheld. 2007. The release of root exudates as affected by the plant physiological status. pp. 23–72. *In*: R. Pinton, Z. Varanini & P. Nannipieri (eds.) *The Rhizosphere: Biochemistry and Organic Substances at the Soil Plant Interface*. CRC Press.

Niu, X., R. A. Bressan, P. M. Hasegawa & J. M. Pardo. 1995. Ion homeostasis in NaCl stress environments. *Plant Physiology* **109:** 735–742.

Northey, J. E., E. W. Christen, J. E. Ayars & J. Jankowski. 2006. Occurrence and measurement of salinity stratification in shallow groundwater in the Murrumbidgee Irrigation Area, southeastern Australia. *Agricultural Water Management* **81:** 23–40.

Pandey, C. B. & J. S. Singh. 1992. Influence of rainfall and grazing on belowground biomass dynamics in a dry tropical savanna, India. *Canadian Journal of Botany* **70**: 1885–1890.

Pierce, W. S. & N. Higinbotham. 1970. Compartments and fluxes of K^+, N^+ and Cl^- in *Avena coleoptiles* cells. *Plant Physiology* **46:** 666–673.

Pitman, M. G. & A. Lauchli. 2002. Global impact of salinity and agricultural ecosystems. pp. 3–20. *In*: A. Lauchli & U. Luttge U (eds.) *Salinity: Environment-Plants-Molecules*. Kluwer Academic Publishers, The Netherlands.

Poole, R. J. 1978. Energy coupling for membrane transport. *Annual Review of Plant Physiology* **29**: 437–460.

Rea, P. A. & D. Sanders. 1987. Tonoplast energization: two H+ pumps, one membrane. *Physiologia Plantarum* **71**: 131–141.

Richards, L. A. (ed.). 1954. *Diagnosis and Improvement of Saline and Alkali Soils*. Agricultural Handbook 60, United States Department of Agriculture.

Washington DC.

Robbins, C. W., R. J. Wagenet & J. J. Jurinak. 1980. A combined salt transport-chemical equilibrium model for calcareous and gypsiferous soils. *Soil Science Society America Journal* **44**: 1191–1194.

Sacchi, G. A., A. Abruzzese, G. Lucchini, F. Fiorani & S. Cocucci. 2000. Efflux and active re-adsorption of glucose in roots of cotton plants grown under saline conditions. *Plant and Soil* **220:** 1–11.

Salisbury, F. B. & C. W. Ross. 1986. *Plant Physiology*. CBS Publishers and Distributors, Delhi, India.

Song, J., M. Chen, G. Feng, Y. Jia, B. Wang & F. Zhang. 2009. Effect of salinity on growth, ion accumulation and roles of ions in osmotic adjustment of two populations of *Suaeda salsa*. *Pant and Soil* **314**: 133–141.

Srivastava, S. K., K. P. Singh & R. S. Upadhyay. 1986. Fine root growth dynamics in teak (*Tectona grandis* Linn. F.). *Canadian Journal Forest Research* **16**: 1360–1364.

Szabolcs, I. 1994. Soils and salinization. pp. 3–11. *In:* M. Pessarakli (ed.) *Handbook of Plant and Crop Stresses*. Marcel Dekker.

Tanji, K. K. 2002. Salinity in the soil environment. pp. 21–51. *In:* A. Lauchli & U. Luttge (eds.) *Salinity: Environment-Plants-Molecules*. Kulwer Academic, Dordrecht.

UNEP. 2009. *The Environmental Food Crisis*. United Nations Environment Programme. Nairobi.

Whipps, J. M. & J. M. Lynch. 1985. Energy losses by the plant in rhizodeposition. *Annual Proceedings of Phytochemical Society of Europe* **26**: 59–71.

Wyn Jones, G. 1981. Betains. pp. 171–204. *In*: C. B. Johnson (ed.) *Physiological Processes Limiting Plant Productivity*. Butterworths, London.

Wyn Jones, G. & J. Gorham. 2002. Intra-and inter-cellular compartmentation of ions. pp. 159–180. *In*: A. Lauchli & U. Luttge (eds.) *Salinity: Environment-Plants-Molecules*. Kulwar Academic, Dordrecht.

(Received on 13.07.2016 and accepted after revisions, on 05.02.2018)