Anales de Biología 33: 23-34, 2011 ARTICLE

Implications of calcium nutrition on the response of *Acacia senegal* (Mimosaceae) to soil salinity

Neha Tusharbhai Patel[1], Nilesh Sundarjibhai Panchal[1], Indu Bhushan Pandey[2] & Amar Nath Pandey[1]

1 Department of Biosciences, Saurashtra University, Rajkot-360005, India

2 Department of Agronomy, Rajendra Agriculture University, Samastipur-848125, India

Correspondence
A.N. Pandey
E-mail: anpandey2001@gmail.com
Tel (O): +91–281–2586419
Tel (M): +919427495989
Fax (O): +91–281–2577633
Received: 10 September 2010
Accepted: 18 February 2011
Published on-line: 24 **March 2011**

Resumen

Implicaciones de la nutrición del calcio en la respuesta de Acacia senegal *(Mimosaceae) a la salinidad del suelo*

Se investigaron los efectos del nivel del Ca^{2+} sobre la respuesta de germinación y crecimiento de las plántulas de *Acacia senegal* (L.) Willd. (Mimosaceae) a la salinidad (NaCl) del suelo. La salinidad retrasó significativamente la germinación y el crecimiento de las plántulas pero, al añadir un suplemento de calcio, con un nivel crítico de (1:0,75 Na/Ca), se paliaron los efectos nocivos del NaCl sobre la geminación y se restauró el crecimiento de las plántulas. Añadir más calcio sobre el nivel crítico aumentó el retraso de la germinación y el crecimiento plantular, ya que aumentaba la salinidad del suelo. El estrés salino redujo el contenido de N, P, K, Ca y Mg que se recuperaron al añadir calcio hasta el nivel crítico. El efecto contrario se observó al añadir Na^+. Se discuten estos resultados en relación a los beneficios del suplemento cálcico en la germinación y crecimiento plantular de esta especie, bajo condiciones de salinidad.

Palabras clave: Nutrición del calcio, Recuperación, Estrés salino, Tolerancia a la sal, Crecimiento de plántulas, Estado hídrico.

Abstract

Effects of Ca^{2+} level on the response of germination and seedling growth of *Acacia senegal* (L.) Willd. (Mimosaceae) to NaCl salinity in soil were investigated. Salinity significantly retarded the seed germination and seedling growth, but the injurious effects of NaCl on seed germination were ameliorated and seedling growth was restored with calcium supply at the critical level (1:0.75 Na/Ca ratio) to salinised soil. Calcium supply above the critical level further retarded the seed germination and seedling growth due to the increased soil salinity. Salt stress reduced N, P, K, Ca and Mg content in plant tissues, but these nutrients were restored by addition of calcium at the critical level to saline soil. The opposite was true for Na^+. The results are discussed in terms of the beneficial effects of calcium supply on the seedling growth of this species under saline conditions.

Key words: Calcium nutrition, Recovery, Salt stress, Salt tolerance, Seedling growth, Water status.

Introduction

Salinisation of soil is more common in arid and semi-arid regions than in humid ones. The high salt content lowers osmotic potential of soil water and consequently the availability of soil water to plants. The salt-induced water deficit is one of the major constraints for plant growth in saline soils (Ramoliya et al. 2004).

In addition, high concentrations of Na^+ and Cl^- in the soil solution may depress nutrient–ion activities and produce extreme ratios of Na^+/Ca^{2+}, Na^+/K^+, Ca^{2+}/Mg^{2+} and Cl^-/NO_3^- (Grattan & Grieve 1999). As a consequence, ionic injury and nutritional disorders can reduce or damage the plant growth in saline soils (Taiz & Zeiger 2006).

The availability and uptake of nutrients by plants in saline soils are affected by many factors in the soil – plant environment. The solid phase of the soil and the concentration and composition of solutes in the soil solution control the activity of the nutrient ion. Soil solution pH and pE (the negative logarithm of the activity of the electron) will influence the speciation and thus availability of certain nutrients. The concentration and ratios of different ionic species can influence the uptake and transport of a particular nutrient and indirectly may affect uptake and translocation of others (Grattan & Grieve 1999). These nutrient interactions are complicated further by concentration and composition of salts.

The application of gypsum has long been considered a common practice in reclamation of saline-sodic and sodic soils (Marschner 1995). The addition of calcium to the soil (as gypsum or lime) displaces Na^+ from clay particles. This prevents the clay from swelling and dispersing (Sumner 1993) and also makes it possible for Na^+ to be leached deeper into the soil. Thus, exogenously supplied calcium not only improves soil structure, but also alters soil properties in various ways (Shabala et al. 2003) that benefit the plant growth. Moreover, an improved Ca/Na ratio in the soil solution enhances the capacity of roots to restrict Na^+ influx (Marschner 1995). Importance of interaction between Na and Ca was recognized after LaHaye & Epstein (1969) reported that exogenously supplied calcium may significantly alleviate detrimental effects of Na^+ on the physiological performance of hydroponically grown plants. Since that time, many investigators became interested in understanding the effects of divalent cations, specifically the effects of Ca^{2+} on various physiological processes and/or plant growth (Cramer et al. 1985, 1989, Lauchli 1990, Rengel 1992, Shabala et al. 2003, 2006, Chen et al. 2007, Vaghela et al. 2009). The spectrum of Na/Ca interactions in plants seems to be extremely broad, ranging from those at the molecular level, such as reduced binding of Na^+ to cell wall or plasma membrane, to those manifested at the whole-plant level, such as effects on root and shoot elongation growth, increased uptake and transport of K^+ or reduced Na^+ accumulation in plants (Lauchli 1990, Rengel 1992). Though a positive response to Ca^{2+} application on plant growth under saline conditions has been reported (Shabala et al. 2006, Vaghela et al. 2009), it did not increase the germination percentage in cotton (Kent & Lauchli 1985) and seedling growth of rice (Yeo & Flowers 1985).

Acacia senegal (L.) Willd. (Mimosaceae), a small deciduous tree species, grows abundantly in the marginal saline area of Kutch (north–west saline desert) of Gujarat State in India. It also grows successfully in coastal area as well as in non–saline and semi–arid central area of Saurashtra region, south to the Kutch. This tree species yields commercial gum arabic. Wood is a good fuel. Leaves and pods are eaten by herbivores. Earlier study (Hardikar & Pandey 2008) suggested that NaCl reduced the growth of *A. senegal* and this tree species has no effective mechanisms to block the sodium transfer to shoot tissues at high salinity. There is evidence that Na^+ induces calcium deficiencies in plant tissues (Cramer 1997, Patel & Pandey 2008, Patel et al. 2010). Consequently, it is assumed that calcium supply to saline soil may mitigate Na^+ toxicity to plants. An understanding of how and how far Ca^{2+} supply modifies responses of plant species to salinity may be of practical significance. In the present investigation the remedial effects of Ca^{2+} on salt stressed seedlings of *A. senegal* was determined by studying germination, growth, water status and acquisition of macro- nutrients.

Material and methods

Study area

The present study was carried out in a greenhouse of the botanical garden of Saurashtra University at Rajkot (22º18' N, 70º56' E) in Gujarat. For the

emergence and growth of seedlings, the top 15 cm black-cotton soil, which is predominant in Saurashtra region of Gujarat, was collected from an agricultural field. This soil is a clayey loam containing 19.6% sand, 20.3% silt and 60.1% clay. The available soil water between wilting coefficient and field capacity ranged from 18.3% to 35.0%, respectively. The total organic carbon content was 1.3% and pH was 7.2. The electrical conductivity of soil was 0.3 dSm^{-1}. Nitrogen, phosphorus, potassium, calcium and sodium contents were 0.15%, 0.05%, 0.03%, 0.05%, and 0.002%, respectively. This soil is fertile and fit for intensive agriculture. Physical and chemical properties of soil are given earlier (Pandya et al. 2004).

Na/Ca ratios

Surface soil was collected, air dried and passed through a 2mm mesh screen. Eight lots of soil, of 100 Kg each, were separately spread, about 50mm thick, over polyethylene sheets. Sodium chloride (NaCl) amounting to 600 g was thoroughly mixed with soil of 7 lots to give electrical conductivity of 5.7 dSm^{-1}. Soil was salinised to this level because in our earlier study (Hardikar & Pandey 2008) seedlings of *A. senegal* exhibited a considerable reduction in growth at 6.2 dSm^{-1} soil salinity though the seedlings could survive up to 10.0 dSm^{-1} salinity. Further, gypsum ($CaSO_4.2H_2O$) to the quantity of 150, 300, 450, 600, 750 and 900 g was separately mixed with soil of six lots to give 1:0.25, 1:0.50, 1:0.75, 1:1, 1:1.25 and 1:1.50 Na/Ca ratios, respectively, and then soil salinity for corresponding lots was 5.9, 6.2, 6.8, 7.2, 7.6 and 7.9 dSm^{-1}. The soil of seventh lot containing only NaCl was considered as the saline soil and its Na/Ca ratio was 1:0. There was no addition of NaCl and $CaSO_4.2H_2O$ to eighth lot of soil that served as control with 0:0 Na/Ca ratio. The electrical conductivity of control soil was 0.3 dSm^{-1} and this value was approximately equal to 3.0 mM salinity. Total eight grades of soils were used in this study. For the measurement of electrical conductivity a soil suspension was prepared in distilled water at a ratio of 1:2 in terms of weight. The suspension was shaken and allowed to stand overnight. Thereafter, electrical conductivity was determined with a conductivity meter.

Available calcium, potassium, sodium and magnesium in soil

For all grades of soil, calcium, potassium, sodium and magnesium were extracted with 1N CH_3COONH_4 adjusted to pH 7.0 and measured using flame atomic absorption spectrophotometer.

Seedling emergence

Twenty polyethylene bags for each grade of soil were each filled with 5 kg of soil. Tap water was added to each bag to bring the soils to field capacity and soils were allowed to dry for 7 days. Soils were then raked using fingers and seeds were sown on 3 January 2007. Seeds of *A. senegal* were collected from the saline desert of Kutch. Bags were kept in an uncontrolled greenhouse under natural temperature and light. Ten seeds were sown in each bag at a depth of 8–12 mm. Immediately after sowing soils were watered (300 mL water was added to raise the soil moisture to field capacity) and thereafter about 100-150 mL water was added to the soils (just to wet the surface soil) on alternate days. Irrigation of soil with required amount of water was taken as a measure to control the Na/Ca ratio. Emergence of seedlings was recorded daily over a period of 30 days and data of cumulative emergence of seedlings were analyzed by t-test (compared 0:0 and 1:0 Na/Ca treatments) and one-way ANOVA (compared treatments ranging from 1:0 to 1:1.50 Na/Ca).

Seedling growth

For the growth studies, two seedlings that emerged first were left in each of 20 bags for each grade of soil and others were uprooted. Seedlings grown in soils at 0:0 (control), 1:0 (saline), 1:0.25, 1:0.50, 1:0.75, 1:1, 1:1.25 and 1:1.50 Na/Ca ratios exhibited emergence of the second leaf after 31, 35, 32, 34, 34, 35, 35 and 37 days, respectively. Emergence of the second leaf confirmed the establishment of seedlings. Following emergence of the second leaf, one seedling having better vigor was allowed to grow in each bag and another seedling was further uprooted. Thus twenty replicates factorialzed with eight grades of soil (0:0, 1:0, 1:0.25, 1:0.50, 1:0.75, 1:1, 1:1.25 and 1:1.50 Na/Ca ratios) were prepared. This gave a total of 160 bags, which were arranged in twenty randomized blocks. Seedlings were watered (to raise the soil moisture to field capacity) at alternate days and allowed to grow for 6 months. Experiment was terminated on 4 July 2007. The mean maximum temperature of the greenhouse during the course of study increased from 28.1±0.22ºC in

January to 41.3±0.41ºC in May and declined thereafter to 33.0±0.21ºC in July 2007. Five seedlings at 1:1.50 Na/Ca ratio died during the course of experiments. Therefore, seedlings contained in 15 bags at each grade of soil were washed to remove soil particles adhered to roots. Morphological characteristics of each seedling were recorded. Shoot height and root length (tap root) were measured. Leaf area was marked out on graph paper. Fresh and dry weights of leaves, stems, tap roots and lateral roots were determined. Water content (gg^{-1} dry weight) in plant tissues (leaves, stems, tap roots and lateral roots) was calculated using fresh and dry weight values. Data recorded for morphological characteristics, dry weight and water content of tissues were analyzed by t-test to assess the effect of salinity on plant growth and by one-way ANOVA to assess the effect of gypsum treatment on the growth of salinised plants.

Determination of water potential and proline content

Ten additional plants grown in soil at each grade of soil were used for measurement of water potential and proline determination in plant tissues. Water potential of leaves, stems, tap roots and lateral root tissues was measured by Dewpoint Potential Meter WP4 (Decagon Devices, Inc., USA) following Patel et al. (2010). All the measurements were taken between 7.30 to 10.30 A.M. Concentration of proline in plant tissues was determined following Bates et al. (1973). Extract of 0.5g fresh plant material with aqueous sulphosalicylic acid was prepared. The extracted proline was made to react with ninhydrin to form chromophore and quantified spectrophotometrically at 520 nm. Data were analyzed by t-test and one-way ANOVA.

Mineral analyses of plant materials

Mineral analyses were performed on leaves, stems, tap roots and lateral root tissues. Plant parts of the seedlings grown in soil at same level of Na/Ca ratio were pooled separately and ground using mortar and pestle. Plant tissues were analyzed in triplicate. Total nitrogen was determined by Kjeldahl method and phosphorus content estimated by the chlorostannous molybdophosphoric blue colour method in sulphuric acid (Piper 1944). Concentrations of calcium, magnesium, sodium and potassium were determined by Shimadzu double beam atomic absorption spectrophotometer AA-6800 (Shimadzu corporation, Kyoto, Japan) after triacid (HNO_3: H_2SO_4: $HClO_4$ in the ratio of 10: 1: 4) digestion. Data were analyzed by t-test and one-way ANOVA.

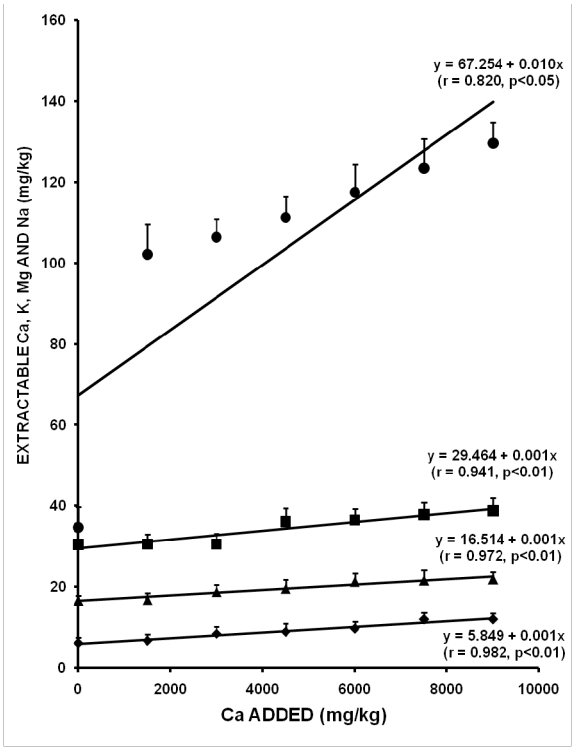

Figura 1. Concentraciones extraíbles de CH_3COONH_4 (mg/kg) de Ca (●), K (■), Mg (▲) y Na (♦) en suelo salinizado, en relación a la adicción creciente de $CaSO_4.2H_2O$. Los puntos corresponden a radios de Na/Ca 1:0; 1:0,25; 1:0,50; 1:0,75; 1:1; 1:1,25 y 1:1,50 respectivamente. Las barras de error corresponden al ES.

Figure 1. CH_3COONH_4 extractable concentrations (mg/kg) of Ca (●), K (■), Mg (▲) and Na (♦) in salinised soil in relation to increasing supply of $CaSO_4.2H_2O$. The data points shown correspond to 1:0, 1:0.25, 1:0.50, 1:0.75, 1:1, 1:1.25 and 1:1.50 Na/Ca ratios respectively, on the X axis. Bars on data points represent SE.

Results

The concentration of available calcium, potassium, magnesium and sodium in salinised soil increased linearly with increasing gypsum ($CaSO_4$ $2H_2O$) treatment (Fig. 1). Salt stress significantly ($p<0.01$) reduced the total emergence of seedlings (Table 1). Calcium supply to the salinity treatment significantly enhanced the germination percentage ($p<0.01$) and the process was stimulated. These effects were evident until Na/Ca ratio in soil increased to 1:0.50. Seed germination again decreased with further supply of calcium to salinised soil.

Salinity significantly retarded ($p<0.05$) elongation

Na/Ca ratio	Total seedling emergence (%)	Shoot height (cm)	Root length (cm)	Leaf area ($cm^2 plant^{-1}$)	Leaf weight (mg $plant^{-1}$)	Stem weight (mg $plant^{-1}$)	Shoot weight (leaf+stem) (mg $plant^{-1}$)	Tap root weight (mg $plant^{-1}$)	Lateral root weight (mg $plant^{-1}$)	Total root weight (mg $plant^{-1}$)
0:0	92.8 ± 2.20	49.0 ± 1.2	36.9 ±1.2	90.9 ± 3.4	744.7 ± 61.0	814.7 ± 42.0	1559.3 ± 62.6	638.0± 35.3	97.3 ± 4.8	735.3± 35.6
1:0	73.0 ± 1.83	38.5 ± 1.8	29.5 ± 0.9	63.0 ± 1.7	434.0 ± 18.0	568.7 ± 67.4	1002.7 ± 77.0	389.3 ± 67.6	73.3 ± 3.2	462.7 ± 67.7
1:0.25	82.0 ± 1.88	45.9 ± 1.4	34.3 ± 0.7	77.7 ± 4.2	492.0 ± 24.0	648.7 ± 55.3	1140.7 ± 65.6	449.3± 55.8	77.3 ± 2.8	526.7 ±56.0
1:0.50	88.8 ± 2.60	51.1 ± 1.3	38.9 ± 0.8	85.4 ± 3.1	635.3 ± 14.4	723.3 ± 39.1	1358.7 ± 48.3	556.7 ± 66.0	85.3 ± 4.0	642.0 ± 69.0
1:0.75	74.0 ± 2.80	54.7 ± 1.9	42.4 ± 1.6	99.8 ± 2.0	755.3 ± 18.1	836.7 ± 22.6	1592.0 ± 29.2	655.3 ± 45.9	104.7 ± 9.1	760.0 ± 46.4
1:1	64.0 ± 1.88	48.5 ± 1.7	36.3 ± 0.4	78.1 ± 0.9	607.3 ± 20.1	681.3 ± 43.8	1288.7 ± 58.8	478.7 ± 44.4	91.3 ± 4.9	570.0 ± 44.0
1:1.25	60.0 ± 1.33	40.1 ± 1.5	34.4 ± 0.6	65.7 ± 0.9	472.0 ± 20.1	654.0 ± 43.8	1126.0 ± 58.8	427.3 ± 44.4	68.0 ± 4.9	495.3 ± 44.0
1:1.50	52.0 ± 2.60	37.9 ± 1.4	30.4 ± 0.5	51.9 ± 2.0	408.0 ± 53.9	594.7 ± 35.0	1002.7 ± 66.3	343.3 ± 64.7	58.7 ± 3.5	402.0 ± 65.8
t - values	4.985**	4.134*	9.002*	6.637*	5.088*	2.805*	5.182*	3.782*	3.674*	4.120*
F-values	15.163**	19.257**	30.340**	37.991**	16.799**	3.296**	12.178**	3.539**	10.154**	4.437**
$LSD_{0.05}$	8,123	4.102	2.257	7.032	84.295	134.003	167.030	153.545	13.202	155.670

Results of 1:0 and 0:0 Na/Ca treatments were compared by t-test.
Results of treatments ranging from 1:0 to 1:1.50 were compared by F- test.
** Values are significant at p< 0.01; * values are significant at p< 0.05; NS = Non significant.

Tabla 1. Efecto de la salinidad y la nutrición del calcio sobre las características de las hojas, tallos, brotes y raíces de *Acacia senegal*, indicado como media ± ESM.
Table 1. Effect of salinity and calcium nutrition on leaf, stem, shoot and root characteristics of *Acacia senegal* as indicated by mean ± SEM.

of stems and roots (Table 1). Increasing supply of calcium to salinity treatment reversed the negative effect of NaCl. For example, stem height and root length of seedlings grown in soil at 1:0.50 Na/Ca ratio were almost equal to those of seedlings grown under control conditions. Extension growth of seedlings continued up to 1:0.75 Na/Ca ratio. Further increase in calcium to salinised soil where Na/Ca exceeded the 1:0.75 ratio caused reduction in stem height and root length. In addition, salinity significantly reduced ($p<0.05$) the expansion of leaves. There was recovery in leaf expansion with increasing calcium supply to salinised soil until 1:0.75 Na/Ca ratio in soil. Following this Na/Ca ratio in soil, leaf expansion exhibited a decreasing trend.

Dry weight significantly decreased for leaves, stems, shoots (leaves+stems), tap roots, lateral roots and total roots (tap roots+lateral roots) ($p<0.05$) in response to salinity (Table 1). When compared with control, the reduction of dry matter caused by salinity was 41.7%, 28.0%, 39.0% and 24.6% for leaves, stems, tap roots and lateral roots, respectively. However, dry weight of tissues exhibited either a complete or a significant recovery ($p<0.01$) in the seedlings grown with 1:0.75 Na/Ca ratio. Calcium supplies to the saline soil exceeding 1:0.75 Na/Ca ratio caused significant reduction in dry weight of tissues. Root/shoot dry weight ratio of seedlings did not change with salinity and calcium treatments.

Salt stress significantly reduced ($p<0.05$) the water content in leaves, stems, tap roots and lateral roots (Table 2). Increase in calcium supply to salinity treatment resulted in a significant recovery ($p<0.05$) of water content in tissues. Results suggested that water content in tissues of seedlings increased up to 1:0.75 Na/Ca ratio and was almost equal to that in tissues of control plants. Moreover, water content in tissues exhibited a decreasing trend when Na/Ca exceeded the 1:0.75 ratio. Tissues according to their water content can be arranged in the following decreasing order: lateral roots>tap roots>leaves>stems. Water potential became significantly more negative ($p<0.05$) for leaves, stems, tap roots and lateral roots of seedlings grown in saline soil than that in tissues of control plants (Table 2). A significant recovery ($p<0.01$) in water potential of tissues was obtained with increase in calcium supply to salinity treatment. It is evident that water potential of tissues of seedlings grown in soil at 1:0.75 Na/Ca ratio was almost equal to that in tissues of control plants. Further increase in supply of external calcium to salinity treatment again reduced water potential of tissues. Tissues according to their water potential (less to high negative values) can be arranged in the following decreasing order: lateral roots>tap roots>leaves=stems.

Proline content significantly increased ($p< 0.05$) in leaves, stems, tap roots and lateral root tissues in response to salinity (Table 2). Results suggested that proline content in examined tissues decreased to minimum level with 1:0.75 Na/Ca treatments. Tissues according to their proline content can be arranged in the following decreasing order: leaves>stems>tap roots>lateral roots.

Sodium content in tissues significantly increased ($p<0.05$) in response to salinity (Table 3), but increasing supply of calcium to salinity treatment significantly reduced ($p<0.01$) the Na content in the tissues. Salinity significantly reduced ($p<0.05$) potassium content in tissues, but increasing calcium in saline soil resulted in a significant recovery of K content in leaves, stems, tap roots and lateral roots ($P<0.01$) of seedlings. There was a complete recovery in K content in tissues of seedlings grown in soil at 1:0.75 Na/Ca ratio. The K/Na ratio significantly decreased ($P<0.05$) in response to salinity, but increasing supply of calcium to salinity treatment significantly increased ($p<0.01$) K/Na ratio in tissues. Concentrations of nitrogen, phosphorus, calcium and magnesium significantly decreased ($p<0.05$) in tissues in response to salinity. Moreover, concentration of these nutrients significantly increased ($p<0.01$) in response to calcium supply to salinity treatment. It is evident that concentrations of these nutrients were completely restored in tissues of seedling grown in soil at 1:0.75 Na/Ca ratio. Moreover, high calcium supply to saline soil reduced the concentration of these nutrients in tissues.

Discussion

The injurious effects of NaCl on germination of *A. senegal* were ameliorated by increase of calcium to a critical level (1:0.50 Na/Ca ratio) in the salinised soil. The detrimental effect of NaCl salinity on germination is associated with an accumulation of toxic ions (Mohammad & Sen 1990), a decrease of available water to the seed (Pujol et

Na/Ca	Water Content (gg^{-1} DW)				Water Potential (-MPa)				Proline Content (µ mol / g FW)			
ratio	Leaves	Stems	Tap Roots	Lateral Roots	Leaves	Stems	Tap Roots	Lateral Roots	Leaves	Stems	Tap Roots	Lateral Roots
0:0	2.6 ± 0.1	2.2 ± 0.1	3.4 ± 0.1	3.8 ± 0.1	4.8 ± 0.2	4.9 ± 0.2	3.7 ± 0.2	1.9 ± 0.1	16.2 ± 0.2	15.5± 0.2	13.3 ± 0.1	11.2 ± 0.2
1:0	2.0 ± 0.1	1.8 ± 0.1	2.4± 0.1	2.8 ± 0.1	5.7 ± 0.3	5.5 ± 0.1	4.7 ± 0.3	3.2 ± 0.2	17.8 ± 0.2	16.4 ± 0.2	14.2 ± 0.2	12.6 ± 0.1
1:0.25	2.5± 0.2	2.1± 0.1	2.8 ± 0.1	3.1 ± 0.1	5.4 ± 0.2	5.2 ± 0.2	3.9 ± 0.3	2.5 ± 0.3	17.2 ± 0.3	15.7 ± 0.3	13.4 ± 0.3	12.1 ± 0.4
1:0.50	2.6 ± 0.1	2.2 ± 0.1	3.1 ± 0.2	3.4 ± 0.1	5.2 ± 0.2	5.0 ± 0.2	3.8 ± 0.3	2.1 ± 0.4	16.6± 0.3	14.4 ± 0.3	11.6 ± 0.4	10.9 ± 0.3
1:0.75	3.0 ± 0.2	2.4 ± 0.2	3.3 ± 0.2	3.7 ± 0.3	5.0 ± 0.1	4.9 ± 0.3	3.6 ± 0.2	1.8 ± 0.4	16.3 ± 0.3	13.8 ± 0.4	11.4 ± 0.3	10.5 ± 0.3
1:1	2.4 ± 0.1	2.1 ± 0.2	3.2 ± 0.1	3.5 ± 0.2	5.8 ± 0.2	5.5 ± 0.3	5.3 ± 0.4	3.2 ± 0.3	16.9 ± 0.2	16.2 ± 0.3	14.0 ± 0.5	11.6 ± 0.3
1:1.25	1.7 ± 0.1	1.4 ± 0.1	2.1± 0.1	2.8 ± 0.1	7.0 ± 0.3	6.6 ± 0.3	5.8 ± 0.2	3.4 ± 0.3	17.6 ± 0.4	16.4 ± 0.3	14.3 ± 0.3	12.5 ± 0.3
1:1.50	1.4 ± 0.1	1.1 ± 0.1	1.7 ± 0.1	2.1 ± 0.1	7.2 ± 0.2	7.6 ± 0.3	6.7 ± 0.3	4.0 ± 0.2	18.1 ± 0.3	17.7 ± 0.4	14.6 ± 0.4	13.0 ± 0.5
t - values	2.247*	2.179*	2.173*	2.512*	7.211*	4.750*	6.546*	4.681*	4.532*	9.449*	5.196*	12.124*
F-values	2.202*	2.234*	2.210*	2.220*	15.477**	15.774**	17.870**	6.933**	4.696**	17.156**	13.902**	7.023**
$LSD_{0.05}$	1.036	1.097	1.099	1.433	0.268	0.302	0.337	0.368	0.379	0.356	0.432	0.422

Results of 1:0 and 0:0 Na/Ca treatments were compared by t-test.

Results of treatments ranging from 1:0 to 1:1.50 were compared by F- test.

** Values are significant at p< 0.01; * values are significant at p< 0.05

Tabla 2. Efecto de la salinidad y la nutrición del calcio sobre el contenido hídrico, potencial hídrico y contenido de prolina en tejidos de *Acacia senegal*, indicado como media ± ESM.

Table 2. Effect of salinity and calcium nutrition on water content, water potential and proline content in tissues of *Acacia senegal* as indicated by mean ± SEM.

al. 2000) or both. The beneficial effect of Ca^{2+} did not persist when calcium supply exceeded the critical level. In the present study, concentration of available sodium and soil salinity increased with increase in external supply of calcium to the saline soil. Secondly, the water uptake by the germinated seeds decreased with both salinity (20.2±1.5%) and increased Ca^{2+} levels (12.8± 1.0%). Therefore, the beneficial effect of Ca^{2+} on *A. senegal* seed germination appears due to counteraction of the toxic effect of Na^{+}. The absence of sufficient level of Ca^{2+} in the germination medium could result in a general deterioration and loss of selectivity of the plasma membrane (Whittington & Smith 1992). This aggravates salt effects, probably by increasing membrane permeability and leads to a higher accumulation of toxic ions and/or leakage of solutes (Cramer et al. 1987, Lauchli 1990). A positive response to Ca^{2+} application on germination rate under saline conditions has also been reported in *Phaseolus vulgaris* (Cachorro et al. 1994), in *Wimmera ryegrass* (Marcar 1986), in barley (Bliss et al. 1986), in *Salvadora oleoides* (Vaghela et al. 2009). Detrimental effect of calcium, above the critical 1:0.50 Na/Ca ratio, on seed germination might be due to the decreased osmotic potential of soil solution because soil salinity increased with increase in calcium supply.

A reduction in water content and water potential of leaves, stems, tap roots and lateral roots of seedlings grown in saline soil might have resulted in internal water deficit to plants, which in turn, reduced the elongation of stems and roots and dry matter accumulation in tissues. It is found that plants subjected to water stress show a general reduction in size and dry matter production (Taiz & Zeiger 2006). In general, salinity reduces plant growth or causes damage to the plants through (i) osmotic effect (causing water deficit), (ii) toxic effect of ions and (iii) imbalance of the uptake of essential nutrients. These modes of action may

Tissue	Na/Ca ratio	N (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	Na (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})	K/Na ratio
Leaf	0:0	24.0 ± 1.0	1.8 ± 0.0	7.8 ± 0.2	4.1 ± 0.1	5.9 ± 0.1	2.1 ± 0.0	1.9 ± 0.1
	1:0	20.0 ± 0.2	1.6 ± 0.0	7.1 ± 0.3	4.8 ± 0.1	5.1 ± 0.1	1.6 ± 0.1	1.5 ± 0.1
	1:0.25	21.0 ± 0.5	1.6 ± 0.0	7.4 ± 0.2	4.6 ± 0.1	5.4 ± 0.0	1.7 ± 0.1	1.6 ± 0.0
	1:0.50	23.0 ± 1.1	1.7 ± 0.1	7.6 ± 0.2	4.4 ± 0.0	5.5 ± 0.1	1.8 ± 0.1	1.7 ± 0.1
	1:0.75	24.0 ± 0.7	1.7 ± 0.1	8.0 ± 0.1	4.2 ± 0.1	5.8 ± 0.1	2.0 ± 0.1	1.9 ± 0.0
	1:1	19.0 ± 0.9	1.4 ± 0.1	7.6 ± 0.1	4.1 ± 0.1	5.6 ± 0.1	1.8 ± 0.1	1.9 ± 0.1
	1:1.25	18.0 ± 0.7	1.1 ± 0.1	7.1 ± 0.1	4.0 ± 0.1	5.1 ± 0.1	1.7 ± 0.1	1.8 ± 0.0
	1:1.50	18.0 ± 1.1	1.0 ± 0.1	7.0 ± 0.2	3.9 ± 0.1	5.0 ± 0.1	1.5 ± 0.1	1.8 ± 0.0
	t - values	4.886*	5.765*	4.588*	4.626*	6.266*	6.629*	4.707*
	F-values	8.812**	13.737**	4.677**	11.344**	12.982**	5.358**	8.218**
	$LSD_{0.05}$	2,421	0,235	0,522	0,288	0,248	0,200	0,147
Stem	0:0	22.0± 0.6	1.5 ± 0.0	4.9 ± 0.1	3.1± 0.3	6.7 ± 0.0	1.8 ± 0.1	1.6 ± 0.2
	1:0	18.0 ± 0.4	1.3 ± 0.0	4.3 ± 0.1	3.7± 0.2	6.1 ± 0.1	1.5 ± 0.1	1.2 ± 0.1
	1:0.25	19.0 ± 1.5	1.4 ± 0.1	4.6 ± 0.1	3.4 ± 0.1	6.2 ± 0.1	1.7 ± 0.0	1.3 ± 0.0
	1:0.50	21.0 ± 0.9	1.4 ± 0.0	4.6 ± 0.2	3.2 ± 0.1	6.4 ± 0.1	1.8 ± 0.0	1.4 ± 0.0
	1:0.75	22.0 ± 0.7	1.5 ± 0.1	5.1 ± 0.1	3.0± 0.1	6.6 ± 0.1	1.8 ± 0.1	1.7 ± 0.1
	1:1	18.0 ± 1.0	1.3 ± 0.1	4.7 ± 0.2	3.0 ± 0.1	6.3 ± 0.1	1.5 ± 0.1	1.6 ± 0.1
	1:1.25	17.0 ± 0.6	1.0 ± 0.1	4.4 ± 0.1	2.9 ± 0.1	5.9 ± 0.0	1.4 ± 0.1	1.5 ± 0.1
	1:1.50	17.0 ±0.4	1.0 ± 0.1	4.1 ± 0.1	2.8 ± 0.1	5.7 ± 0.1	1.3 ± 0.1	1.5 ± 0.1
	t - values	6.394*	4.323*	4.715*	4.798*	8.373*	5.615*	4.886*
	F-values	4.912**	4.769**	4.647**	8.568**	17.615**	6.346**	4.780**
	$LSD_{0.05}$	2.653	0.277	0.450	0.332	0.228	0.200	0.228
Tap root	0:0	19.0 ± 0.5	1.4 ± 0.0	3.5 ± 0.1	2.9 ± 0.2	4.3 ± 0.0	1.6 ± 0.0	1.2 ± 0.1
	1:0	16.0 ± 0.4	1.0 ± 0.1	3.0 ± 0.1	3.6 ± 0.0	3.7 ± 0.1	1.3 ± 0.0	0.8 ± 0.0
	1:0.25	17.0 ± 0.8	1.2 ± 0.1	3.3 ± 0.1	3.2 ± 0.1	3.8 ± 0.1	1.5 ± 0.1	1.0 ± 0.0
	1:0.50	19.0 ± 0.9	1.3 ± 0.1	3.4 ± 0.1	3.0 ± 0.1	3.9 ± 0.1	1.6 ± 0.1	1.1 ± 0.1
	1:0.75	20.0 ± 0.6	1.5 ± 0.0	3.6 ± 0.1	2.8 ± 0.1	4.3 ± 0.1	1.7 ± 0.0	1.3 ± 0.1
	1:1	18.0 ± 0.4	1.4 ± 0.1	3.2 ± 0.0	2.8 ± 0.1	3.9 ± 0.1	1.5 ± 0.1	1.1 ± 0.0
	1:1.25	16.0 ± 0.5	1.2 ± 0.1	3.2 ± 0.1	2.7 ± 0.0	3.5 ± 0.1	1.4 ± 0.1	1.1 ± 0.0
	1:1.50	16.0 ± 0.4	0.9 ± 0.1	3.0 ± 0.1	2.7 ± 0.1	3.5± 0.1	1.3± 0.1	1.1 ± 0.1
	t - values	5.275*	6.047*	8.000*	4.939*	6.638*	4.673*	5.372*
	F-values	6.838**	9.287**	5.163**	12.547**	12.058**	5.137**	11.793**
	$LSD_{0.05}$	1.868	0.215	0.282	0.288	0.254	0.200	0.124
Lateral root	0:0	18.0 ± 0.7	1.2 ± 0.1	3.2 ± 0.1	5.2 ± 0.2	4.0 ± 0.2	1.7 ± 0.0	0.6 ± 0.0
	1:0	15.0 ± 0.3	0.8 ± 0.1	2.8 ± 0.1	5.8 ± 0.1	3.4 ± 0.2	1.4 ± 0.0	0.5 ± 0.0
	1:0.25	16.0 ± 0.5	0.9 ± 0.1	3.0 ± 0.1	5.4 ± 0.1	3.6 ± 0.1	1.6 ± 0.1	0.5 ± 0.0
	1:0.50	17.0 ± 0.4	1.0 ± 0.0	3.1 ± 0.1	5.4 ± 0.0	3.7 ± 0.1	1.7 ± 0.1	0.6 ± 0.0
	1:0.75	19.0 ± 0.8	1.2 ± 0.0	3.3 ± 0.2	5.1 ± 0.1	4.2 ± 0.1	1.8 ± 0.1	0.7 ± 0.0
	1:1	15.0 ± 0.5	1.0 ± 0.1	2.8 ± 0.1	4.6 ± 0.1	3.7 ± 0.1	1.6 ± 0.1	0.6 ± 0.0
	1:1.25	13.9 ± 0.4	0.8 ± 0.1	2.6 ± 0.1	4.5 ± 0.1	3.6 ± 0.1	1.6 ± 0.0	0.6 ± 0.0
	1:1.50	14.0 ± 0.5	0.8 ± 0.1	2.5 ± 0.1	4.5 ± 0.1	3.6 ± 0.1	1.5 ± 0.0	0.6 ± 0.0
	t - values	7.000*	8.271*	6.928*	4.862*	4.580*	5.5000*	7.000*
	F-values	13.709**	5.050**	4.676**	39.422**	4.587**	5.767**	4.887**
	$LSD_{0.05}$	1.478	0.200	0.388	0.254	0.323	0.200	0.055

Results of 1:0 and 0:0 Na/Ca treatments were compared by t-test.
Results of treatments ranging from 1:0 to 1:1.50 were compared by F- test.
** Values are significant at p< 0.01; * values are significant at p< 0.05.

Tabla3. Efecto de la salinidad y la nutrición del calcio sobre el contenido de nutrientes de los tejidos de *Acacia senegal*, indicado como media ± ESM.

Table 3. Effect of salinity and calcium nutrition on nutrient content of tissues of *Acacia senegal* as indicated by mean ± SEM.

opterate on the cellular as well as on higher organiza-ional levels and influence all the aspects of plant metabolism (Kramer 1983, Garg & Gupta 1997). *A. senegal* exhibited a reduction in leaf area (photosynthetic area) in response to salinity treatment. Garg & Gupta (1997) reported that salinity causes reduction in leaf area as well as in rate of photosynthesis, which together result in reduced crop growth and yield. Also, high concentration of salt tends to slow down or stop root elongation (Kramer 1983) and causes reduction in root production (Garg & Gupta 1997). Calcium supply to the salinised soil ameliorated the injurious effects of NaCl on *A. senegal* and plant growth was restored at 1:0.75 Na/Ca ratio. It has been reported that supplemental Ca^{2+} in salinised

growth media alleviated inhibition of root growth of barley (Shabala et al. 2003), shoot growth of *P. vulgaris* (Cachorro et al. 1994), shoot and root growth both for Salvadora oleoides (Vaghela et al. 2009). In maize plants grown with a high Na:Ca ratio, the hydraulic conductance was reduced; supplemental Ca (10 mM) improved growth by restoring hydraulic conductance back to that of the control plants (Cramer 1992).

The inhibiting effect of salinity on seedling growth was more striking in the leaves and tap roots than in lateral roots and stems. Consequently, lateral roots and stems were more resistant and leaves and tap roots were sensitive to soil salinity. Likewise, recovery of dry weight at 1:0.75 Na/Ca ratio was 101.4%, 102.7%, 102.7% and 107.5% for leaves, stems, tap roots and lateral roots, respectively. Results suggested that there was resemblance in shoot and root growth of seedlings and their root/shoot dry weight ratio did not change with salinity and calcium treatments.

In some plant species, salt tolerance is associated with accumulation of organic solutes in cytoplasm to balance the osmotic pressure of ions in the vacuoles. The compounds that accumulate most commonly are proline and glycine betaine, although other molecules can accumulate to high concentration in certain species (Hasegawa et al. 2000). Proline accumulates in the cytoplasm without having any detrimental effects on cytosolic enzymes activities (Stewart & Lee 1974). In *A. senegal*, osmotic adjustment was achieved by K^+ and increase in quantity of proline in tissues when water content decreased because of salinity. In addition to its conventional osmoprotective role, proline prevents NaCl–induced K^+ efflux from roots and may operate as ion channel regulators (Cuin & Shabala 2005) or reactive oxygen species (ROS) scavangers (Bohnert et al. 1995). Such regulatory role does not require significant amounts of proline to be accumulated and is, therefore, of low carbon cost to the plant. Results further indicated that increase in water content and water potential of tissues with calcium treatment was related to decrease of proline content.

In the present study, there was a significant decrease of Ca content in all the tissues with salinity treatment. As a result, Na induced Ca deficiency in tissues. It is reported that uptake of Ca^{2+} from the soil solution may decrease because of ion interaction, precipitation and increase in ionic strength that reduce the activity of Ca^{2+} (Janzen & Chang 1987). It is found that salinity can alter Ca^{2+} uptake and transport leading to Ca^{2+} deficiency in plants (Cramer et al. 1987). Consequently, addition of Ca to salinised soil to the critical level resulted in recovery of shoot and root growth. Calcium supply exceeding the critical level again reduced the shoot and root growth. In the present study, the increased sulfate content together with chloride content caused increase in soil salinity with calcium treatment. The increased soil salinity, in other words, decreased osmotic potential might be responsible for retardation of growth at high supply of calcium.

Potassium is a major osmoticum in plant cells (Marschner 1995) and, therefore is essential for all extension growth. It is evidenced that in salt stressed roots of cotton, Na displaced membrane-associated Ca, which was believed to be primarily located at the plasma membrane (Cramer et al. 1985). In addition, NaCl-salinity displaced membrane-associated Ca on protoplasts of corn (Lynch & Lauchli 1988) and barley (Bittisnich et al. 1989), and on plasma membrane vesicles of melon (Yermiyahu et al. 1994). One consequence of the displacement of membrane-associated Ca by Na is the immediate increase of K efflux across the plasma membrane of salt-stressed cotton roots (Cramer et al. 1985). This effect may be related to the rapid depolarization of the membrane potential upon salinisation (Cramer 1997). In the present study, the increased efflux of K^+ might be one of the reasons for the significant decrease of K content in tissues of *A. senegal* in response to NaCl salinity. However, recovery of K content in tissues with external calcium supply at the critical level (1:0.75 Na/Ca ratio) may be the result of repolarization of membrane. There is abundant evidence that salinity alters the ion transport and contents of plants (Cramer 1997). In general, Na uptake and concentrations increase and Ca uptake and concentrations decrease in plant cells and tissues as the external Na concentration increases (Rengel 1992, Cramer 1997). Likewise, as external Ca concentrations increase Na uptake and concentrations decrease and Ca uptake and concentrations increase. One consequence of these Na:Ca interactions is the reduction of K content in salinised plants, which can be prevented with supplemental Ca. Shabala et al. (2006) reported that supplemental Ca may prevent

K^+ efflux from the cell by blocking the depolarization – activated outward – rectifying K^+ channels. In addition, salinity generates reactive oxygen species (Slater et al. 2003) which activates non-selective cation channels (NSCC) inducing further K^+ leak (Demidchik et al. 2002). This leak is additional to one caused by membrane depolarization (Chen et al. 2007). As a result supplemental Ca may prevent such ROS – induced NSCC activation and associated K^+ leak. However, increase in soil salinity with high calcium supply caused a decrease in K content in tissues and it can be accounted for low osmotic potential of soil solution. Isosmotic concentrations of mannitol have similar effects as saline treatments with supplemental Ca (10mM) indicating that K efflux is affected by osmotic factors in these solutions and not associated with Na-specific displacement of membrane-associated Ca (Cramer et al. 1985).

Sodium content significantly increased in tissues of salt-stressed plants, but decreased with increase in calcium supply to saline soil. It is reported that uptake mechanisms of both K and Na are similar (Watad et al. 1991, Schroeder et al. 1994). Na^+ can not move through the plasma membrane lipid bilayer, but the ion is transported through both low- and high- affinity transport systems, which are necessary for K^+ acquisition. As a consequence, Na^+ could enter the cell through high affinity K^+ carriers or through the low affinity channels called nonselective cation channels. These cation channels could allow entry of large amount of Na^+ from a highly saline soil if not adequately regulated (Amtmann & Sanders 1999). Low affinity K uptake is not inhibited by Na but the high affinity process is restricted (Watad et al. 1991, Schroeder et al. 1994). Similarly Na toxicity in plants is correlated with two proposed Na uptake pathways (Niu et al. 1995). The K and Na profiles of *A. senegal* suggest that similar mechanism might operate in this species. It is evidenced that Ca^{2+} is an efficient blocker of nonselective cation channels, a major route for Na uptake into the cell (Demidchik & Tester 2002, Demidchik & Maathuis 2007) and, thus, may directly reduce amount of Na accumulation in plants. For *A. senegal*, external supply of calcium reduced Na content on the whole plant level. Further, high K content and low Na content in leaves, stems and tap roots tissues suggest that this plant has the characteristic for rapid transport of K to shoot tissues. Intracellular K^+/Na^+ homeostasis is a key component of salinity tolerance in plants (Tester & Davenport 2003). Lateral roots being salt tolerant retain a high amount of Na and inhibit its long-distance transport.

In general, salinity reduces N accumulation in plants (Feigin 1985).This is due to the fact that an increase in chloride uptake and accumulation is mostly accompanied by a decrease in shoot nitrate concentration (Torres & Bingham 1973, Garg & Gupta 1997). The interaction between salinity and P is very complex and there is no clear cut mechanistic explanation for decreased, increased or unchanged P uptake in response to salinisation in different species (Grattan & Grieve 1992). However, it is known that P concentration is related to the rate of photosynthesis, but it decreases the conversion of fixed carbon into starch (Overlach et al. 1993) and therefore decrease of P in leaves will reduce shoot growth. Besides the role of Mg in chlorophyll structure and as an enzyme cofactor, another important role of Mg in plants is in the export of photosynthates (Marschner 1995). External calcium supply reversed the effects of Na^+ and concentrations of N, P and Mg were restored in tissues of seedlings grown at 1:0.75 Na/Ca ratio. The high influx or low efflux of nutrients might be responsible for recovery of nutrients. The increased salinity (low osmotic potential) can be accounted for decrease of nutrients when calcium supply exceeded the critical level.

In the present study available Ca^{2+} in salinised soil with supplemental calcium at the critical level (1: 0.50 and 1: 0.75 Na/Ca ratios) was three times higher than that in non-saline control soil. Thus, it can be suggested that available Ca^{2+} in saline soil should be maintained nearly three times higher than that in normal soil in order to ameliorate the injurious effects of NaCl on seed germination and growth of *A. senegal*.

Conclusion

Results of the present investigation show that germination and growth of *A. senegal* seedlings were dependent upon external supply of calcium up to the critical level (1:0.75 Na/Ca ratio) to the salinised soil. The beneficial effects of high Ca^{2+} concentration are reflected in: (a) almost a complete recovery in germination percentage. From an ag-

ronomical point of view this result may be advantageous; (b) the negative effect of soil salinity on elongation of stems and roots, leaf area development and dry matter accumulation in tissues can be reduced by additional supply of calcium; (c) water content and water potential of leaves, stems, tap roots and lateral root tissues increased with increase in calcium to the critical level in salinised soil; (d) it seems that much of growth reduction associated with salinity is due to high Na^+ and low Ca^{2+} levels in tissues, thus increasing Ca^{2+} concentration reduces the uptake of Na^+ and increases Ca^{2+} uptake, consequently decreasing Na^+ toxicity; (e) a partial preservation of membrane integrity from NaCl damage takes place decreasing the efflux of K^+ and probably of other mineral nutrients. Moreover, beneficial effects of calcium did not persist when external supply of this element exceeded the critical level because further calcium supply increased soil salinity.

Acknowledgement

This study was supported with funds from Departmental Special Assistance provided by the University Grants Commission, New Delhi, Government of India.

References

Amtmann A & Sanders D. 1999. Mechanisms of Na^+ uptake by plant cells. Advances in Botanical Research 29:76-112.

Bates LS, Waldren RP & Teare FD 1973. Rapid determination of free proline from water stress studies. Plant and Soil 39: 205-207.

Bittisnich D, Robinson D & Whitecross M. 1989. Plant Membrane Transport: The Current Position. In: Dainty J, Michelis de MJ, Marré E & Rasi-Caldogno F. (Eds.), Membrane-associated and intracellular free calcium levels in root cells under NaCl stress. Proceedings of the Eighth International Workshop on Plant Membrane Transport, Venice, Italy, 25-30 June 1989, Inc., New York: Elesevier Science Publishing Company, pp. 681-682.

Bliss RD, Platt-Aloia KA & Thomson WW. 1986. Osmotic sensitivity in relation to salt sensitivity in germinating barley seeds. Plant Cell and Environment 9: 721-725.

Bohnert HI, Nelson DE & Jensen RG.1995. Adptation to environmental stresses. The Plant Cell 7: 1099-1111

Cachorro P, Ortiz A & Cerda A. 1994. Implications of calcium nutrition on the response of Phaselous vulgaris L. to salinity. Plant and Soil 159: 205-212.

Chen Z, Pottosin II, Cuin TA, Fuglsang AT, Tester M, Jha D, Zepeda-Jazo I, Zhou M, Palmgren MG, Newman IA & Shabala S. 2007. Root plasma membrane transporters controlling K^+/Na^+ homeostasis in salt-stressed barley . Plant Physiology 145 : 1714-1725.

Cramer GR 1992. Kinetics of maize leaf elongation. II. Response of a Na-excluding cultivar and Na-including cultivar to varying Na/Ca salinities. Journal of Experimental Botany 43: 857-864.

Cramer GR, Epstein E & Lauchli A. 1989. Na-Ca interactions in barley seedlings: relationship to ion transport and growth. Plant Cell and Environment 12: 551-558.

Cramer GR, Lauchli A & Polito VS. 1985. Displacement of Ca^{2+} by Na^+ from the plasmalemma of root cells. A primary response to salt stress? Plant Physiology 79: 207-211.

Cramer GR, Lynch J, Lauchli A & Epstein E. 1987. Influx of Na^+, K^+ and Ca^{2+} into roots of salt-stressed cotton seedlings. Effects of supplemental Ca^{2+}. Plant Physiology 83: 510-516.

Cramer GR. 1997. Uptake and role of ions in salt tolerance. In: Jaiwal PK, Singh RP & Gulati A. (Eds.), Strategies for Improving Salt Tolerance in Higher Plants. New Delhi: Oxford & IBH Publishing Co. Pvt. Ltd, pp. 55-86.

Cuin TA & Shabala S.2005.Exogenously supplied compatible solutes rapidly ameliorate NaCl-induced potassium efflux from barley roots. Plant Cell Physiology 46: 1924-1933.

Demidchik V & Maathuis FJM. 2007. Physiological roles of nonselective cation channels in plants : from salt stress to signalling and development. New Phytologist 175: 387-404.

Demidchik V & Tester MA.2002. Sodium fluxes through nonselective cation channels in the plant plasma membrane of protoplasts from Arabidopsis roots. Plant Physiology 128: 379-387.

Demidchik V, Bowen HC, Maathuis FJM, Shabala SN, Tester MA, White PJ & Davies JM. 2002. Arabidopsis thaliana root nonselective cation channels mediate calcium uptake and are involved in growth. Plant Journal 32: 799-808.

Feigin A. 1985. Fertilization management of crops irrigated with saline water. Plant and Soil 89: 285-299.

Garg BK & Gupta IC. 1997. Saline Wastelands Environment and Plant Growth. Jodhpur: Scientific Publishers, pp. 283.

Grattan SR & Grieve CM. 1999. Salinity-mineral nutrient relation in horticultural crops. Scientia Horticulturae 78: 127-157.

Grattan SR & Grieve CM. 1992. Mineral element acquisition and growth response of plants grown in saline environments. Agriculture, Ecosystem and Environment 38: 5-300.

Hardikar SA & Pandey AN 2008. Growth, water status and nutrient accumulation of seedlings of Acacia senegal (L.) Willd. In response to soil salinity. Anales de Biologia 30: 17-28.

Hasegawa PM, Bressan RA, Zhu JK & Bohnert HJ. 2000. Plant cellular and molecular responses to high salinity. Annual Review of Plant Physiology and Plant Molecular Biology 51: 463-499.

Janzen HH & Chang C. 1987. Cation nutrition of barley as influenced by soil solution composition in a saline soil. Canadian Journal of Soil Science 67: 619-629.

Kent LM & Lauchli A.1985. Germination and seedling growth of cotton : salinity-calcium interactions. Plant Cell and Environment 8: 155-159.

Kramer PJ. 1983. Water Relations of Plants. New York: Academic Press, pp. 489.

LaHaye PA & Epstein E. 1969. Salt toleration by plants: enhancement with calcium. Science 166: 395-396.

Lauchli A. 1990. Calcium, salinity and the plasma membrane. In: Leonard, R T & Hepler, P K. (Eds.), Calcium in Plant Growth. Rockville MD, The American Society of Plant Physiologists, pp. 26-35.

Lynch J & Lauchli A. 1988. Salinity affects intracellular calcium in corn root Protoplasts. Plant Physiology 87: 351-356.

Marcar NE. 1986. Effect of the calcium on the salinity tolerance of Wimmera ryegrass (Lolium rigidum Gaud., cv. Wimmera) during germination. Plant and Soil 93: 129-132.

Marschner H. 1995. Mineral Nutrition of Higher Plants. London: Academic Press, pp 889.

Mohmmad S & Sen DN. 1990. Germination behavior of some halophytes in Indian desert. International Experimental Biology 28: 545-549.

Niu X, Bressan RA, Hasegawa PM & Pardo JM. 1995. Ion homeostasis in NaCl stress environments. Plant Physiology 109: 735-742.

Overlach S, Diekmann W & Raschke K. 1993. Phosphate translocator of isolated guard-cell chloroplasts from Pisum sativum L. transport glucose-6-phosphate. Plant Physiology 101: 1201-1207.

Pandya DH, Mer RK, Prajith PK & Pandey AN. 2004. Effect of salt stress and manganese supply on growth of barley seedlings. Journal of Plant Nutrition 27: 1361-1379.

Patel AD & Pandey AN. 2008. Growth, water status and nutrient accumulation of seedlings of Holoptelea integrifolia (Roxb.) Plaunch in response to soil salinity.Plant Soil and Environment 54: 367-373.

Patel AD, Jadeja HR & Pandey AN. 2010. Effect of salinisation of soil on growth, water status and nutrient accumulation in seedlings of Acacia auriculiformis (Fabaceae). Journal of Plant Nutrient 33: 914-932.

Piper CS. 1944. Soil and Plant Analysis. New York: Interscience, pp. 368.

Pujol JA, Calvo JF & Daiz LR. 2000. Recovery of germination from different osmotic conditions by four halophytes from southeastern Spain. Annals of Botany 85: 279-386.

Ramoliya PJ, Patel HM & Pandey AN. 2004. Effect of salinization of soil on growth and macro- and micronutrient accumulation in seedlings of Salvadora persica (Salvadoraceae). Forest Ecology and Management 202: 181-193.

Rengel Z. 1992. The role of calcium in salt toxicity. Plant Cell and Environment 15: 625-632.

Schroeder JI, Ward JM & Gassmann W. 1994. Perspectives on the physiology and structure of inward-rectifying K channels in higher plants, biophysical implications for K uptake. Annual Review Biophysics and Bimolecular Structure 23: 441-471.

Shabala S, Demidchik V, Shabala L, Cuin TA, Smith SJ, Miller AJ, Davies JM & Newman IA.2006. Extracellular Ca^{2+} ameliorates NaCl-induced K^+ loss from Arabidopsis root and leaf cells by controlling plasma membrane K^+-permeable channels. Plant Physiology 141: 1653-1665.

Shabala S, Shabala L & Volkenburgh EV. 2003. Effect of calcium on root development and root ion fluxes in salinised barley seedlings. Functional Plant Biology 30: 507-514.

Slater A, Scott NW & Fowler MR. 2003. Plant Biotechnology. The genetic manipulation of plants. New york : Oxford University Press. Inc. pp. 364.

Stewart GR & Lee JA. 1974. The role of proline accumulation in halophytes. Planta 120: 279-289.

Sumner ME. 1993. Sodic soils: new perspectives. Australian Journal of Plant Physiology 31: 683-750.

Taiz L & Zeiger E. 2006. Plant physiology (Fourth Edition). Sunderland, USA: Sinauer Associates Inc. Publishers, pp. 764.

Tester M & Davenport R. 2003. Na^+ tolerance and Na^+ transport in higher plants. Annals of Botany 91: 503-527.

Torres BC & Bingham FT. 1973. Salt tolerance of Mexican wheat. I. Effect of NO3 and NaCl on mineral nutrition, growth and grain production of four wheats. Soil Science Society of America Proceedings 37: 711-715.

Vaghela PM, Patel NT, Pandey IB & Pandey AN. 2009. Implications of calcium nutrition on the response of Salvadora oleoides (Salvadoraceae) to soil. Arid Land Research and Management 23: 311-326.

Watad AA, Reuveni M, Bressan RA & Hasegawa PM. 1991. Enhanced net K uptake capacity of NaCl-adapted cells. Plant Physiology 95: 1265-1269.

Whittington J & Smith FA. 1992. Calcium-salinity interactions affect ion transport in Chara corallina. Plant Cell and Environment 15: 727-733.

Yeo AR & Flowers TJ.1985. The absence of an effect of the Na/Ca ratio on sodium chloride uptake by rice (Oryza sativa L.) New Phytologist 99: 81-90.

Yermiyahu U, Nir S, Ben-Hayyim G & Kafkafi U. 1994. Quantitative competition of calcium with sodium or magnesium for sorption sites on plasma membrane vesicles of melon (Cucumis melo L.) root cells. Journal of Membrane Biology 138: 55-63.