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Salinity tolerance of *Aegiceras corniculatum* (L.) Blanco from Gujarat coasts of India

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Resumen

Efectos de la salinidad del suelo en el crecimiento, estado hídrico y acumulación de nutrientes en semillas de Aegiceras corniculatum *(Myrsinaceae).*

Se realizaron experimentos en invernadero para valorar los efectos de la salinidad del suelo en la emergencia, crecimiento, estado hídrico contenido de prolina y acumulación mineral en plántulas de *Aegiceras corniculatum* (L.) Blanco (Myrsinaceae). Se añadió NaCl al suelo y se mantuvo la salinidad a 0,3; 3,9; 7,9; 12,1; 16,1; 19,7; 24,0; 28,0; 32,0; 36,0 y 40,0 dSm^{-1}. Esta especie es muy tolerante a la sal durante la fase de germinación. Las concentraciones bajas de sal estimularon significativamente el crecimiento de las plántulas, siendo su crecimiento óptimo a 24,9 dSm^{-1} aunque salinidades mayores lo inhibieron. Al aumentar la salinidad, se produjeron los siguientes efectos: el potencial hídrico de los tejidos se volvió negativo. La cantidad de prolina aumentó. La concentración de Na en los tejidos aumentó, mientras que disminuyeron el K, Ca, N y P. También se discute sobre los cambios en los patrones de acumulación de otros nutrientes y los posibles mecanismos para evitar la toxicidad del Na, en respuesta a la salinidad.

Palabras clave: *Aegiceras corniculatum*; Acumulación mineral; Contenido de prolina; Germinación de propágulos; Crecimiento de plántulas; Estado hídrico.

Abstract

Greenhouse experiments were conducted to assess the effects of soil salinity on germination, growth, water status, proline content and mineral accumulation of seedlings of *Aegiceras corniculatum* (L.) Blanco (Myrsinaceae). NaCl was added to the soil and salinity was maintained at 0.3, 3.9, 7.9, 12.1, 16.1, 19.7, 24.0, 28.0, 32.0, 36.0 and 40.0 dSm^{-1}. This plant is highly salt tolerant at germination stage. Growth of seedlings was significantly promoted by low salinity and their optimum growth was obtained at 24.0 dSm^{-1}. Moreover, higher salinities inhibited plant growth. Water potential of tissues became significantly more negative with increase in salinity. Proline content in tissues significantly increased as salinity increased. Concentration of Na in tissues significantly increased, whereas K, Ca, N and P content decreased with increase in salinity. Changes in tissues and whole-plant accumulation patterns of other nutrients, as well as possible mechanisms for avoidance of Na toxicity in this plant in response to salinity, are discussed.

Key words: *Aegiceras corniculatum*; Mineral accumulation; Proline content; Propagule germination; Seedling growth; Water status

Introduction

Mangroves inhabit intertidal zones with high salinity (Shan et al. 2008) and are able to tolerate a large range of salinities under natural conditions (Suarez et al. 1998). The growth and physiological mechanisms of mangroves differ in nature due to their complexity of structure and differences in flooding regime, tidal inundation, rapid influx of extra nutrients as well as type of soil (Clough 1984, Naidoo 1987). They possess a variety of adaptations to extreme environmental stresses such as (i) salt exclusion by root ultrafiltration (Scholander 1968), (ii) salt recretion via glands (Roth 1992), (iii) ion accumulation in leaf cells (Popp 1994), (iv) leaf succulence (Roth 1992) and (v) accumulating organic acids as osmotica to counter toxic effects of salinity (Popp 1984). Like other halophytes, mangroves decrease their water and osmotic potentials to maintain turgor at high salinity (Naidoo 1987, Khan et al. 2000a, b). Salinity required for optimal growth varies from 10% to 50% seawater (Downton 1982, Clough 1984, Naidoo 1987, Lin & Sternberg 1992, 1995) and a decline in their optimal growth is obtained with a further increase in salinity. Similarly, lower water potential and accumulation of inorganic ions are the results from extreme saline environments for most of the plants (Ball & Farquhar 1984, Naidoo 1987).

The mangroves are found in sandy and muddy intertidal zones of Arabian Sea along semi-arid region of Saurashtra and contiguous saline desert of Kutch in Gujarat State of India. Overexploitation, pollution and other biotic stresses have drastically reduced and fragmented the mangrove forests. Little information exists on the salt tolerance of mangroves of Saurashtra and Kutch and this information is crucial to the success of restoration effort in the region. *Aegiceras corniculatum* is one of the most common tree species along the coastline in Gujarat. The present study is designed to investigate the salt tolerance of *Aegiceras corniculatum* (L.) Blanco (Myrsinaceae) growing along the coasts of Saurashtra and Kutch in Gujarat.

Material and Methods

Study area

The present study was carried out in a greenhouse of the botanical garden of Saurashtra University at Rajkot (22°18' N Lat, 70°56' E Long) in Gujarat. For propagule germination and growth of seedlings, the top 15 cm black-cotton soil (Vertisol), 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).

Salinisation of soil

Surface soil was collected, air dried and passed through a 2mm mesh screen. Eleven lots of soil, of 100 kg each, were separately spread, about 50 mm thick, over polyethylene sheets. Sodium chloride (NaCl) amounting to 280, 690, 1410, 1900, 2400, 2900, 3300, 3800, 4200 and 4700 g was then thoroughly mixed with soil of ten lots, respectively to give electrical conductivities of 3.9, 7.9, 12.1, 16.1, 19.7, 24.0, 28.0, 32.0, 36.0 and 40.0 dSm^{-1}. There was no addition of NaCl to seventh lot of soil that served as control. Seawater salinity at Jamnagar coast in Saurashtra varies from 45 to 48 dSm^{-1} during the rainy (monsoon) season. Thus, soil salinity in the present investigation was not maintained above 40 dSm^{-1}. The electrical conductivity of control soil was 0.3 dSm^{-1} and this value was approximately equal to 3.0 mM salinity. For the measurement of electrical conductivity a soil suspension was prepared in distilled water at 1:2 soil:water ratio. The suspension was shaken and allowed to stand overnight. Thereafter, electrical conductivity of the supernatant solution was determined with a conductivity meter.

Seedling emergence

Twenty polyethylene bags for each level of soil salinity were each filled with 5 kg of soil. Tap water was added to each bag until water level was 2 cm high above the soil surface. Bags were kept in an uncontrolled greenhouse under natural tem-

perature and light. Propagules of *A. corniculatum* were collected from Jamnagar coast. Ten propagules were sown (propagules were gently pushed to one-third of their length into the soil) in each bag on 27th June 2008. Tap water was added daily to compensate evapotranspiration loss. Emergence of seedlings was recorded daily over a period of 30 days. A linear model was fitted to cumulative proportion of propagule germination and increasing soil salinity using the expression:

$$\mathrm{Sin}^{-1}\sqrt{P} = ß_0 + ß_1X$$

where, $\mathrm{Sin}^{-1}\sqrt{P}$ is the proportion of cumulative seed germination, X is soil salinity and ß0 and ß1 are constants. Salt concentration at which seed germination was reduced to 50% (SG_{50}) was estimated using the model.

Seedling growth

For the growth studies, two seedlings that emerged first were left in each of 20 bags at each level of salinity and others were uprooted. Seedlings grown in soils at 0.3, 3.9, 7.9, 12.1, 16.1, 19.7, 24.0, 28.0, 32.0, 36.0 and 40.0 dSm^{-1} salinities exhibited emergence of the second leaf after 9, 10, 10, 12, 12, 12, 12, 12, 12, 12 and 13 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 eleven grades of soil (0.3, 3.9, 7.9, 12.1, 16.1, 19.7, 24.0, 28.0, 32.0, 36.0 and 40.0 dSm^{-1}) were prepared. This gave a total of 220 bags, which were arranged in twenty randomized blocks. Seedlings were watered daily to maintain water level above the soil surface and experiment was terminated after six months. The mean maximum temperature of the greenhouse during the course of study decreased from 35.6 ± 0.57°C in June to 30.8 ± 0.35°C in August 2008 and further increased to 35.9 ± 0.69°C in October. Following this period, the mean maximum temperature gradually decreased to 27.8 ± 0.32°C in January 2009. Seedlings contained in 20 bags at each salinity level were washed with tap water to remove salt on leaves and soil particles adhered to roots. Roots of *A. corniculatum* are adventitious and arise from the root stock. Morphological characteristics of each propagule were recorded. Shoot height and length of adventitious roots of the propagule were measured. Leaf area was marked out on graph paper. Fresh and dry weights of tissues (leaves, stems and roots) were determined. Water content (gg^{-1} dry weight) in plant tissues was calculated using fresh and dry weight values. Data recorded for morphological characteristics, dry weight and water content of different components were analyzed by one-way ANOVA to assess the effect of salinity on plant growth. In addition, data for growth parameters and water content in tissues were fitted to second order polynomial equation by computer curvilinear method and correlations between examined parameters and soil salinity were computed.

Determination of water potential and proline content

Ten additional plants grown in soil at each level of salinity were used for measurement of water potential and proline determination in plant tissues. Water potential of leaves, stems and roots was measured by Dewpoint Potential Meter WP4 following Patel et al. (2009). All the measurements were taken between 8 to 10.30 A.M. Concentration of proline in plant tissues was estimated following Bates et al. (1973). Extract of 0.5 g fresh plant material with aqueous sulphosalicylic acid was prepared. The extracted proline was made to react with ninhydrin to form chromophore and read at 520 nm. Data were analyzed by one-way ANOVA. Correlations and linear regression equations for water potential and proline content of tissues with salinity were determined.

Mineral analyses of plant materials

Mineral analyses were performed on leaves, stems and root tissues. Plant parts of the seedlings grown in soil at same level of salinity were pooled separately. Plant samples were ground using mortar and pestle. Three subsamples of plant tissues were analyzed. 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 Ca, Mg, Na, K, Zn, Fe, Mn and Cu were determined by Shimadzu double beam atomic absorption spectrophotometer AA-6800 after triacid (HNO_3:H_2SO_4: $HClO_4$ in the ratio of 10:1:4) digestion. Mineral data were analysed by

one-way ANOVA. Correlations and linear regression equations between mineral content and salt concentrations were determined.

Results

Effect of salinity on propagule germination

Propagules began to germinate 3 days after sowing and 100% propagules germinated over a period of 18 days under control (0.3 dSm^{-1} salinity) conditions. (Fig. 1). Propagule germination in saline soils was recorded 4-7 days after sowing. Germination lasted for 19, 19, 20, 20, 20, 20, 20, 20, 20 and 20 days in soils with 3.9, 7.9, 12.1, 16.1, 19.7, 24.0, 28.0, 32.0, 36.0 and 40.0 dSm^{-1} salinities, respectively and corresponding germination was 99.6%, 98.8%, 98.4%, 97.6%, 97.2%, 96.8%, 96.4%, 96.0%, 94.0% and 90.4%. There was a significant reduction in germination of propagules ($p<0.01$) with increasing salt stress. A negative relationship between proportion of cumulative propagule germination and concentration of salt was obtained according to the following expression:

$$Y = 95.700-0.500X \ (R^2_{Adj}=0.969, p<0.01)$$

where, Y is arcsine (degrees) of proportion of cumulative seed germination and X is salt concentration.

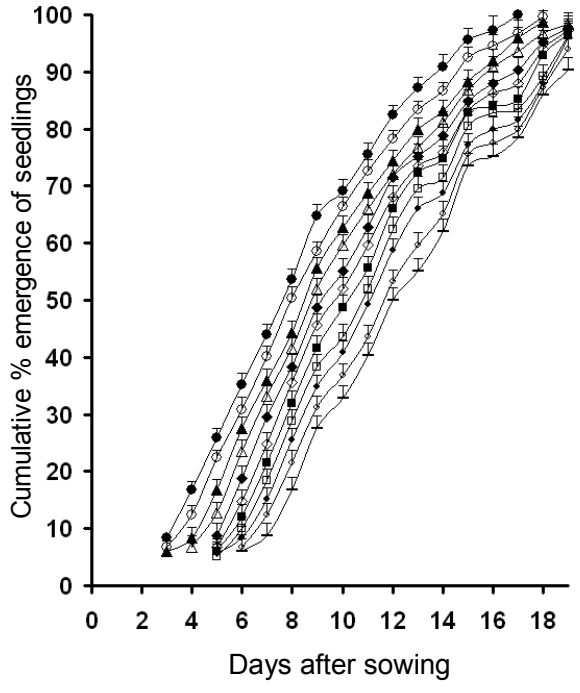

Figura 1. Emergencia acumulada de semillas de *Aegiceras corniculatum* en respuesta a la salinidad del suelo. 0.3 dS m^{-1} (●), 3.9 dSm^{-1} (○), 7.9 dSm^{-1} (▲), 12.1 dSm^{-1} (Δ), 16.1 dSm^{-1} (♦), 19.7 dSm^{-1} (◊), 24.0 dSm^{-1}(■), 28.0 dSm^{-1} (□), 32.0 dSm^{-1} (•), 36.0 dSm^{-1} (○) y 40.0 dSm^{-1} (—). Las barras de error representan ES.

Figure 1. Cumulative emergence of seedlings of *Aegiceras corniculatum* in response to soil salinity. 0.3 dS m^{-1} (●), 3.9 dSm^{-1} (○), 7.9 dSm^{-1} (▲), 12.1 dSm^{-1} (Δ), 16.1 dSm^{-1} (♦), 19.7 dSm^{-1} (◊), 24.0 dSm^{-1}(■), 28.0 dSm^{-1} (□), 32.0 dSm^{-1} (•), 36.0 dSm^{-1} (○) and 40.0 dSm^{-1} (—). Error bars represent SE.

Effect of salinity on stem and root elongation and leaf expansion

Salinity significantly stimulated ($p<0.01$) stem and root elongation until 24.0 dSm^{-1}, but extension growth declined with further increases in salinity (Table 1). In general, stem height was manifold greater than root length under the control and saline conditions. There was a quadratic relationship for shoot height and root length with salt concentration ($p<0.01$). Leaf area significantly increased ($p<0.01$) until 24.0 dSm^{-1} salinity, but decreased at higher salinities (Table 1). A quadratic relationship was obtained between leaf area and salt concentration in soil ($p<0.01$).

Effect of salinity on dry weight

Dry weight of leaves, stems, shoots (leaves + stems) and roots was significantly promoted ($p<0.01$) by salinity until 24.0 dSm^{-1}, but it declined with further increases in salinity (Table 1). There was a quadratic relationship between salt concentration in soil and dry weight of tissues ($p<0.01$). Root/shoot dry weight ratio was 0.10 for plants grown in control soil and it did not change with increasing soil salinity.

Effect of salinity on water content and water potential of tissues

Water content (gg^{-1} dry weight) significantly increased ($p<0.01$) in leaves, stems and roots until 24.0 dSm^{-1} salinity, but declined with further increases in salinity (Fig. 2A). A quadratic relationship was obtained between soil salinity and water content of leaves ($r=0.465$, $p<0.01$), stems ($r=0.565$, $p<0.01$) and roots ($r=0.382$, $p<0.01$). Tissues significantly differed ($p<0.01$) in their water content. Moreover, maximum water content was in leaves and roots, and minimum in stems. Tissues according to their water content can be arranged into the following decreasing order: leaves = roots > stems. Water potential significantly became more negative in tissues ($p<0.01$) as soil sa-

Salinity (dSm^{-1})	Stem 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 $plant^{-1}$)	Root weight (mg $plant^{-1}$)	Root/Shoot dry weight ratio
0.3	21.0 ± 0.6	4.5 ± 0.2	25.7 ± 2.0	424.5 ± 22.4	1826.5 ± 94.8	2251.0 ± 102.3	232.5 ± 14.3	0.1 ± 0.0
3.9	22.9 ± 0.5	5.6 ± 0.2	27.9 ± 1.2	503.0 ± 24.8	2101.0 ± 74.5	2604.0 ± 84.2	271.0 ± 16.1	0.1 ± 0.0
7.9	23.1 ± 0.5	6.0 ± 0.1	28.9 ± 1.1	529.5 ± 27.2	2151.0 ± 80.6	2680.5 ± 97.1	289.0 ± 16.1	0.1 ± 0.0
12.1	24.1 ± 0.5	6.5 ± 0.2	35.5 ± 1.3	617.5 ± 33.3	2328.5 ± 101.8	2946.0 ± 119.8	299.5 ± 19.6	0.1 ± 0.0
16.1	25.5 ± 0.4	7.8 ± 0.2	41.1 ± 1.4	665.5 ± 25.9	2486.5 ± 85.7	3152.0 ± 98.4	336.0 ± 21.6	0.1 ± 0.0
19.7	27.4 ± 0.4	11.0 ± 0.4	47.8 ± 1.4	795.0 ± 27.6	2645.5 ± 82.6	3440.5 ± 97.9	361.5 ± 15.8	0.1 ± 0.0
24.0	29.0 ± 0.2	11.8 ± 0.2	54.1 ± 1.2	1002.0 ± 37.4	2779.5 ± 58.9	3781.5 ± 87.3	394.5 ± 15.4	0.1 ± 0.0
28.0	23.9 ± 0.3	10.1 ± 0.3	45.5 ± 1.2	771.5 ± 22.9	2558.5 ± 71.2	3330.0 ± 85.2	347.0 ± 16.2	0.1 ± 0.0
32.0	23.1 ± 0.3	6.1 ± 0.2	39.4 ± 1.2	736.5 ± 36.9	2341.0 ± 60.4	3077.5 ± 82.3	324.0 ± 12.5	0.1 ± 0.0
36.0	21.9 ± 0.4	5.8 ± 0.2	37.4 ± 0.6	675.5 ± 37.7	2175.5 ± 70.9	2851.0 ± 87.2	294.0 ± 19.7	0.1 ± 0.0
40.0	21.1 ± 0.4	5.1 ± 0.2	31.8 ± 1.1	621.5 ± 27.7	1939.0 ± 72.2	2560.5 ± 87.5	266.5 ± 11.3	0.1 ± 0.0
α	20.350	3.310	20.260	356.900	1746.000	2103.000	218.500	NS
β	-0.014	-0.013	-0.047	-0.726	-1.883	-2.610	-0.281	NS
γ	0.588	0.579	2.189	35.840	80.490	116.300	12.450	NS
r	0.671	0.747	0.742	0.659	0.607	0.666	0.494	NS
$LSD_{0.05}$	1.4	0.8	4.2	97.8	256.7	307.5	53.9	NS

Relationship is significant at $p < 0.01$; NS = Non significant.

Tabla 1. Efecto de la salinidad del suelo en las características de la hoja, tallo y raíz de *Aegiceras corniculatum* indicado por la media ± SEM y las constantes de la ecuación de regresión.

Table 1.Effect of soil salinity on leaf, stem, shoot and root characteristics of *Aegiceras corniculatum* as indicated by mean ± SEM and regression equation constants.

linity increased (Fig. 2B). There was a negative relationship between soil salinity and water potential of leaves ($r=-0.953$, $p<0.01$), stems ($r=-0.926$, $p<0.01$), and roots ($r=-0.912$, $p<0.01$). Tissues significantly differed ($p<0.01$) in their water potential. Tissues according to their negative water potential values (low to high negative values) can be arranged into the following decreasing order: roots > stems > leaves.

Effect of salinity on proline content of tissues

Proline content (μmol/g FW material) significantly increased ($p<0.01$) in leaves, stems, and root tissues with increase in soil salinity (Fig. 2C). Tissues according to their proline content can be arranged into the following decreasing order: stems>leaves > roots. There was a positive relationship between salt concentration and proline content of leaves ($r=0.953$, $p<0.01$), stems ($r=0.952$, $p<0.01$) and roots ($r=0.959$, $p<0.01$). A significant inverse relationship was obtained between water potential (more negative values) and proline content of leaves ($r=-0.911$, $p<0.01$), stems ($r=-0.851$, $p<0.01$) and roots ($r=-0.852$, $p<0.01$).

Effect of salinity on mineral accumulation

Sodium content significantly increased ($p<0.01$) in leaves, stems and roots with increase in salinity (Table 2). A positive relationship was obtained between Na content of tissues and salt stress ($p<0.01$). K content significantly decreased ($p<0.01$) in leaves, stems and root tissues, in response to increase in salinity. There was a negative relationship between K content of tissues and salt concentration in soil ($p<0.01$). The Na/K ratio significantly increased ($p<0.01$) in leaves, stems and root tissues in response to increasing soil salinity. There was positive relationship ($p<0.01$) between Na/K ratio in tissues and salt stress.

Concentration of N, P and Ca significantly de-

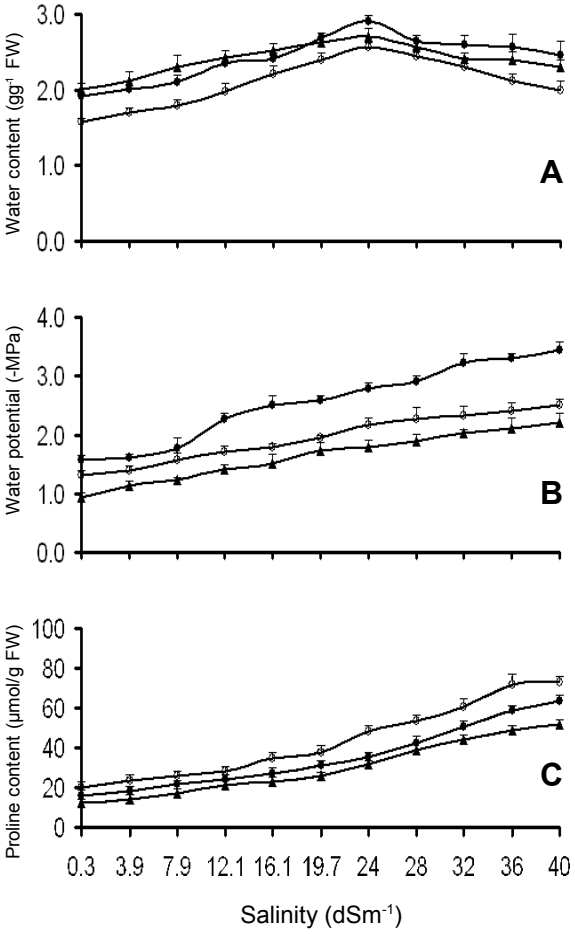

Figura 2. Efecto de la salinidad del suelo en: **A.**. contenido de agua; **B**. potencial hídrico; **C.** contendo de prolina en hojas (●), tallos (○) y raíces (▲) de *Aegiceras corniculatum*. Las barras de error representan SE.

Figure 2. Effect of salinisation of soil on: **A.**. water content; **B**. water potential; **C.** proline content of leaves (●), stems (○) and roots (▲) of *Aegiceras corniculatum*. Error bars represent SE.

creased ($p<0.01$) in leaves, stems and roots in response to increasing salt concentration in soil. A negative relationship was obtained between N, P and Ca content in tissues and salt concentration ($p<0.01$). Mg content in tissues did not change with increase in salt concentration in soil. The concentration of Zn, Mn and Fe significantly increased ($p<0.01$) in leaves, stems and roots in response to increase in salt-stress (Table 2). A positive relationship was obtained between soil salinity and Zn, Mn and Fe content in tissues ($p<0.01$). There was a significant decrease ($p<0.01$) in the concentration of Cu in leaves, stems and roots in response to increase in salinity. A negative relationship was obtained between salt concentration and Cu content in tissues ($p<0.01$).

Discussion

Optimum germination (100%) was obtained in non–saline control soil and increasing salinity delayed and reduced germination of *A. corniculatum*. Similar results have been reported by others for seed germination of halophytes (Khan & Weber 1986, Ungar 1996, Katembe et al. 1998, Gulzar & Khan 2001, Khan 2002, Li et al. 2002). Salt can affect seed germination either by osmotic effect, restricting the supply of water to embryo, (Agboola 1998, Pujol et al. 2000) or by ionic effect, causing specific injury through ions to the metabolic machinery, (Pollack & Waisel 1972, Mohammad & Sen 1990). Propagule germination of *A. corniculatum* could be reduced to 50% (SG_{50}) at salinity of 91.4 dSm^{-1}, whereas SG_{50} for *Cassia montana*, a halophyte tree in coastal region of Saurashtra, was obtained at 6.0 dSm^{-1} (Patel & Pandey 2007). That would suggest that this plant species is highly salt tolerant at germination stage. *A. corniculatum* is characterized by viviparous germination. Adaptation of viviparous propagules to saline environments actually starts when they are still attached to the mother tree by continuously absorbing salt from the tree or by a desalinating process (Joshi et al. 1972, Zheng et al. 1999). Under natural conditions, germination of propagules of *A. corniculatum* occurs during the season with high precipitation when salinity level of seawater is usually reduced. It appears that *A. corniculatum* invades coastline along the Arabian Sea because of its high salt tolerance at seed germination stage.

Growth of *A. corniculatum* seedlings was stimulated by low salinity and their optimum growth was at 24.0 dSm^{-1}. Similar results have been reported for halophytes that have optimal growth in the presence of salt (Naidoo & Raghunanan 1990, Ayala & O'Leary 1995, Khan et al. 2000a, Patel & Pandey 2007). Soil salinity at 24.0 dSm^{-1} was equal to 50% seawater treatment because salinity of seawater during the rainy season at Jamnagar coast is about 48.0 dSm^{-1}. Result does not agree with some other studies in which mangrove species showed their best growth at 25% seawater concentration (Downton 1982, Clough 1984, Naidoo 1987). However, Karim & Karim (1993) reported that the growth for *Avicennia marina* from Bangladesh coast was obtained at 50% seawater. High media salinity affects plant

Tissue	Salinity (dSm^{-1})	N ($mg\ g^{-1}$)	P ($mg\ g^{-1}$)	K ($mg\ g^{-1}$)	Na ($mg\ g^{-1}$)	Ca ($mg\ g^{-1}$)	Mg ($mg\ g^{-1}$)	Na/K ratio	Zn ($\mu g\ g^{-1}$)	Cu ($\mu g\ g^{-1}$)	Mn ($\mu g\ g^{-1}$)	Fe ($\mu g\ g^{-1}$)
Leaf	0.3	24.0 ± 1.4	2.2 ± 0.3	11.4 ± 0.6	7.1 ± 0.8	12.6 ± 0.2	1.4 ± 0.0	0.6 ± 0.1	29.6 ± 2.8	16.3 ± 0.7	85.7 ± 5.2	267.0 ± 27.2
	3.9	24.0 ± 1.5	2.2 ± 0.1	11.0 ± 0.8	7.6 ± 1.0	12.2 ± 0.7	1.4 ± 0.1	0.7 ± 0.1	33.1 ± 2.6	15.4 ± 1.1	91.3 ± 5.4	331.2 ± 16.9
	7.9	22.0 ± 1.7	2.2 ± 0.1	10.3 ± 0.9	9.2 ± 1.5	11.7 ± 0.7	1.3 ± 0.1	0.9 ± 0.1	38.4 ± 2.8	14.4 ± 0.6	97.0 ± 8.4	347.3 ± 15.8
	12.1	21.0 ± 1.3	2.1 ± 0.1	10.0 ± 0.9	10.7 ± 0.6	11.1 ± 0.5	1.3 ± 0.1	1.1 ± 0.1	39.3 ± 2.0	14.0 ± 0.6	103.2 ± 7.3	365.7 ± 19.1
	16.1	20.0 ± 1.3	2.0 ± 0.2	9.8 ± 0.4	10.9 ± 1.1	10.8 ± 0.4	1.3 ± 0.1	1.1 ± 0.1	42.2 ± 1.6	13.0 ± 0.5	109.2 ± 7.1	392.3 ± 20.7
	19.7	19.0 ± 1.5	1.9 ± 0.3	9.0 ± 0.7	11.4 ± 1.0	10.2 ± 0.6	1.2 ± 0.1	1.3 ± 0.1	46.3 ± 2.4	13.0 ± 0.6	114.1 ± 6.8	441.1 ± 14.6
	24.0	19.0 ± 1.0	1.8 ± 0.1	8.5 ± 1.0	11.7 ± 0.8	9.9 ± 0.9	1.2 ± 0.0	1.4 ± 0.3	49.1 ± 2.1	12.3 ± 0.9	116.4 ± 6.5	422.9 ± 13.2
	28.0	19.0 ± 1.2	1.7 ± 0.2	8.3 ± 0.8	11.7 ± 0.8	9.9 ± 0.6	1.2 ± 0.1	1.4 ± 0.2	51.2 ± 2.7	11.4 ± 0.7	122.3 ± 5.8	460.3 ± 18.8
	32.0	18.0 ± 1.0	1.5 ± 0.2	7.8 ± 1.1	12.2 ± 0.9	9.3 ± 0.9	1.2 ± 0.1	1.6 ± 0.3	55.4 ± 2.2	11.3 ± 1.3	123.0 ± 7.1	523.1 ± 19.3
	36.0	17.0 ± 1.0	1.3 ± 0.1	7.2 ± 0.8	12.6 ± 0.7	8.9 ± 0.6	1.1 ± 0.0	1.8 ± 0.3	57.1 ± 2.5	10.4 ± 1.2	127.0 ± 7.6	587.7 ± 21.8
	40.0	17.0 ± 1.3	1.2 ± 0.2	7.1 ± 0.9	12.7 ± 1.0	8.7 ± 1.0	1.1 ± 0.1	1.9 ± 0.4	59.3 ± 2.8	10.0 ± 1.4	129.7 ± 5.9	683.3 ± 14.8
	α	23.656	2.384	11.360	7.994	12.454	NS	0.624	30.725	15.916	88.677	259.941
	β	-0.183	-0.027	-0.112	0.135	-0.098	NS	0.032	0.742	-0.152	1.107	8.784
	r	-0.764	-0.788	-0.769	0.747	-0.783	NS	0.813	0.934	-0.822	0.819	0.933
	$LSD_{0.05}$	3.970	0.550	2.490	2.930	2.070	NS	0.610	7.430	2.800	20.370	56.940
Stem	0.3	22.0 ± 1.0	2.0 ± 0.1	9.1 ± 0.5	10.5 ± 0.5	11.9 ± 0.5	1.3 ± 0.0	1.2 ± 0.1	35.4 ± 4.3	13.3 ± 0.9	59.0 ± 4.9	410.0 ± 20.5
	3.9	21.0 ± 0.7	1.9 ± 0.2	9.0 ± 0.5	10.9 ± 0.3	11.8 ± 0.6	1.3 ± 0.0	1.2 ± 0.1	37.1 ± 3.3	12.7 ± 0.5	65.1 ± 5.8	460.1 ± 21.1
	7.9	21.0 ± 1.0	1.9 ± 0.2	8.7 ± 0.2	11.2 ± 0.7	11.0 ± 0.7	1.3 ± 0.0	1.3 ± 0.1	43.1 ± 2.2	12.4 ± 0.5	69.2 ± 4.5	513.1 ± 15.5
	12.1	20.0 ± 1.2	1.8 ± 0.1	8.3 ± 1.0	11.3 ± 0.4	10.9 ± 0.7	1.2 ± 0.1	1.4 ± 0.2	48.3 ± 2.3	11.3 ± 0.6	77.0 ± 4.7	563.7 ± 17.7
	16.1	19.0 ± 1.0	1.8 ± 0.1	7.9 ± 0.3	11.7 ± 0.4	10.5 ± 0.6	1.2 ± 0.1	1.5 ± 0.1	50.2 ± 2.7	11.0 ± 0.3	79.6 ± 6.5	661.5 ± 16.4
	19.7	18.0 ± 1.1	1.7 ± 0.2	7.7 ± 0.5	11.9 ± 0.2	9.7 ± 0.7	1.2 ± 0.1	1.6 ± 0.1	53.1 ± 2.3	10.8 ± 0.6	83.7 ± 6.5	747.7 ± 16.2
	24.0	18.0 ± 1.0	1.6 ± 0.1	7.3 ± 0.3	12.2 ± 0.2	9.5 ± 0.9	1.1 ± 0.0	1.7 ± 0.1	55.1 ± 3.8	10.3 ± 0.5	95.6 ± 4.9	763.3 ± 19.4
	28.0	18.0 ± 1.1	1.5 ± 0.3	6.8 ± 0.6	12.6 ± 0.3	9.5 ± 0.5	1.1 ± 0.1	1.9 ± 0.1	57.2 ± 3.0	10.0 ± 0.4	102.6 ± 7.1	787.1 ± 20.1
	32.0	17.0 ± 1.0	1.4 ± 0.1	6.6 ± 0.5	12.7 ± 0.5	8.9 ± 0.6	1.1 ± 0.1	1.9 ± 0.2	59.4 ± 2.0	10.0 ± 0.7	106.3 ± 4.3	801.0 ± 15.3
	36.0	16.0 ± 0.6	1.3 ± 0.2	6.4 ± 0.4	12.9 ± 0.5	8.4 ± 0.9	1.1 ± 0.1	2.0 ± 0.1	64.6 ± 1.9	9.8 ± 0.6	111.5 ± 10.2	821.3 ± 17.0
	40.0	16.0 ± 1.0	1.2 ± 0.1	6.4 ± 0.7	13.1 ± 0.7	8.3 ± 0.6	1.0 ± 0.1	2.1 ± 0.2	66.3 ± 1.5	9.3 ± 0.6	116.3 ± 5.7	866.0 ± 15.4
	α	21.785	2.073	9.166	10.615	11.938	NS	1.124	36.471	12.917	58.117	438.467
	β	-0.152	-0.021	-0.076	0.064	-0.094	NS	0.024	0.767	-0.096	1.484	11.690
	r	-0.802	-0.761	-0.770	0.781	-0.770	NS	0.852	0.918	-0.813	0.904	0.957
	$LSD_{0.05}$	2.970	0.470	1.680	1.380	2.080	NS	0.400	8.440	1.750	18.610	54.060

Relationship is significant at $p < 0.01$, NS = non significant.

Tabla 2. Efecto de la salinidad del suelo en el contenido de nutrientes de los tejidos (hoja, tallo y raíz) de *Aegiceras* corniculatum indicado como media ± SEM and constantes de la ecuación de regresión.

Table 2. Effect of soil salinity on nutrient content of tissues (leaf, stem and root) of *Aegiceras* corniculatum as indicated by mean ± SEM and regression equation constants.

Tissue	Salinity (dSm^{-1})	N ($mg\ g^{-1}$)	P ($mg\ g^{-1}$)	K ($mg\ g^{-1}$)	Na ($mg\ g^{-1}$)	Ca ($mg\ g^{-1}$)	Mg ($mg\ g^{-1}$)	Na/K ratio	Zn ($\mu g\ g^{-1}$)	Cu ($\mu g\ g^{-1}$)	Mn ($\mu g\ g^{-1}$)	Fe ($\mu g\ g^{-1}$)
Root	0.3	21.0 ± 1.2	1.4 ± 0.1	6.8 ± 0.2	10.6 ± 0.6	10.7 ± 0.7	1.2 ± 0.1	1.6 ± 0.1	50.3 ± 2.1	11.4 ± 0.2	41.9 ± 2.9	991.7 ± 29.4
	3.9	20.0 ± 0.6	1.3 ± 0.1	6.5 ± 0.3	10.9 ± 0.6	10.6 ± 0.3	1.2 ± 0.1	1.7 ± 0.1	51.7 ± 3.5	11.1 ± 0.1	43.1 ± 3.0	1012.3 ± 20.3
	7.9	20.0 ± 1.2	1.3 ± 0.1	6.5 ± 0.2	11.2 ± 0.5	10.4 ± 0.2	1.2 ± 0.1	1.7 ± 0.1	54.9 ± 2.9	10.8 ± 0.1	46.5 ± 3.0	1101.3 ± 22.7
	12.1	19.0 ± 1.0	1.2 ± 0.2	6.1 ± 0.1	11.3 ± 0.4	10.1 ± 0.5	1.1 ± 0.1	1.8 ± 0.1	57.3 ± 2.5	10.7 ± 0.2	48.7 ± 3.7	1237.6 ± 21.5
	16.1	18.0 ± 1.4	1.0 ± 0.1	6.0 ± 0.3	11.7 ± 1.0	9.9 ± 0.6	1.1 ± 0.1	2.0 ± 0.1	61.7 ± 3.0	10.5 ± 0.2	56.4 ± 2.6	1504.8 ± 16.9
	19.7	17.0 ± 1.0	1.0 ± 0.1	5.8 ± 0.2	11.7 ± 0.5	9.1 ± 0.5	1.1 ± 0.0	2.0 ± 0.1	63.4 ± 2.6	10.5 ± 0.2	59.9 ± 3.8	1696.5 ± 25.8
	24.0	17.0 ± 0.8	0.9 ± 0.1	5.8 ± 0.1	12.1 ± 0.4	9.1 ± 0.7	1.1 ± 0.1	2.1 ± 0.1	67.8 ± 2.8	10.3 ± 0.2	64.5 ± 2.8	1882.0 ± 20.7
	28.0	16.0 ± 1.1	0.9 ± 0.0	5.7 ± 0.2	12.5 ± 0.7	8.7 ± 0.4	1.0 ± 0.0	2.2 ± 0.2	69.1 ± 2.1	10.2 ± 0.2	66.1 ± 2.3	2046.3 ± 27.1
	32.0	16.0 ± 0.7	0.8 ± 0.1	5.6 ± 0.3	13.1 ± 0.4	8.6 ± 0.7	1.0 ± 0.1	2.3 ± 0.1	72.7 ± 2.0	10.1 ± 0.3	68.2 ± 3.2	2156.5 ± 28.7
	36.0	15.0 ± 1.0	0.8 ± 0.1	5.5 ± 0.3	13.6 ± 0.3	8.1 ± 0.3	1.0 ± 0.1	2.5 ± 0.2	75.7 ± 2.6	10.0 ± 0.4	69.1 ± 2.9	2380.0 ± 23.1
	40.0	15.0 ± 1.0	0.8 ± 0.1	5.5 ± 0.2	13.8 ± 0.6	7.9 ± 0.6	1.0 ± 0.0	2.5 ± 0.1	76.1 ± 1.9	9.8 ± 0.3	72.1 ± 2.8	2454.3 ± 32.8
	α	20.787	1.339	6.634	10.440	10.870	NS	1.551	49.656	11.195	41.340	860.545
	β	-0.158	-0.015	-0.032	0.080	-0.075	NS	0.024	0.702	-0.036	0.826	40.897
	r	-0.802	-0.775	-0.751	0.770	0.774	NS	0.857	0.921	-0.776	0.911	0.990
	$LSD_{0.05}$	3.100	0.330	0.730	1.760	1.620	NS	0.390	7.850	0.760	9.190	75.450

Relationship is significant at $p < 0.01$, NS = non significant.

Tabla 2 *(continúa)*. Efecto de la salinidad del suelo en el contenido de nutrientes de los tejidos (hoja, tallo y raíz) de *Aegiceras* corniculatum indicado como media ± SEM and constantes de la ecuación de regresión.

Table 2 *(continues)*. Effect of soil salinity on nutrient content of tissues (leaf, stem and root) of *Aegiceras* corniculatum as indicated by mean ± SEM and regression equation constants.

growth due to low water potential, ion toxicities, nutrient deficiencies or a combination of all these factors (Khan et al. 2000 a). Patel and Pandey (2007) reported that seedlings of *Cassia montana*, a halophyte tree in the coastal area of Saurashtra, exhibited optimum growth at 7.9 dSm^{-1} salinity. Evidently, A. corniculatum can be grouped among highly salt tolerant plants. Root/shoot dry weight ratio did not change with increases in salinity suggesting that there was resemblance in shoot and root growth of *A. corniculatum*.

Water content of tissues increased until 24.0 dSm^{-1} and then declined with increased salinity. Similar result has been reported for *Suadea fruticosa* (Khan et al. 2000a). Halophytes are characterized by their capacity to adjust tissue water potential to a level that is more negative than that of the soil water potential of the habitat in which they are growing (Ungar 1991). Mangroves lower tissue osmotic potential through the net accumulation of solutes in response to salinity and water deficits (Turner & Jones 1993, Suarez et al. 1998). *A. corniculatum* showed a progressive decrease in water potential of leaves and stems with an increase in salinity, indicating that it follows an osmoconformer strategy to maintain its osmotic balance.

The salt secreting *A. corniculatum* had high concentration of Na in tissues when grown in soils with increasing salinity. There are evidences that halophytes and glycophytes accumulate NaCl in vacuoles (Flowers et al. 1977). High internal salt concentrations provide potential benefits to mangrove plants growing under conditions where soil osmotic potential is more negative than that of seawater because of high soil salinity (Ungar 1991). Increased salt content lowers the internal water potential which is required to permit water uptake. Na^+ and Cl^- accumulated in leaf tissues provide osmotic adjustment and turgor to maintain growth (Yeo 1983). The cation K^+ is essential for cell expansion, osmo-regulation and cellular and whole-plant homeostasis (Schachtman et al. 1997). High stomatal K^+ requirement is reported for photosynthesis (Chow et al. 1990). The role of K^+ in response to salt stress is also well documented, where Na^+ depresses K^+ uptake (Fox & Guerinot 1998). In the present study, significant decrease of K^+ content in all the tissues of seedlings with increasing soil salinity suggests that Na^+ inhibited K^+ uptake. The Na/K ratio increased in leaves and stems with increase in salinity suggesting an increase in transportation of Na^+ from root to shoot. Tattini et al. (1995) reported that Na/K ratio increases in salt tolerant species with increasing salinity in the external medium because mass transport of sodium takes place from root to shoot via the transpiration stream.

The accumulation of compatible solutes is a common response to salinity in higher plants (Stewart & Lee 1974, Storey et al. 1977). These compounds are not toxic to cytoplasmic enzymes functions at high concentrations (Storey et al. 1977), thus help in osmotic adjustment. The increase of proline content in tissues with increase in Na content indicates that higher proline accumulation may contribute to the alleviation of NaCl stress in *A. corniculatum*. Shan et al. (2008) reported that proline is the specific osmolyte for this species. The proline accumulation was greater in stems and leaves (shoot tissues) than that in roots. Munns (2002) concluded that organic solutes are often lower in roots than shoots.

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). 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 (Champognol 1979, Grattan & Grieve 1992). However, it is known that P concentration is related to the rate of photosynthesis, since it decreases conversion of fixed carbon into starch (Overlach et al. 1993) and therefore decrease of P in leaves will reduce shoot growth. Calcium is important during salt stress, e.g., in preserving membrane integrity (Rengel 1992), signaling in osmoregulation (Mansfield et al. 1990) and influencing K^+/Na^+ selectivity (Cramer et al. 1987). In the present study, there was a significant decrease of Ca^{2+} content in all the tissues with salinisation of soil. As a result, Na^+ induced Ca^{2+} deficiency in tissues. It is reported that uptake of Ca^{2+} from the soil solution may decrease because of ion interactions, precipitation and increase in ionic strength that reduce the activity of Ca^{2+} (Janzen & Chang 1987). Besides the role of Mg^{2+} in chlorophyll structure and as an enzyme cofactor, another important role of Mg^{2+} in plants is in the export of

photosynthates (Marschner & Cakmak 1989). Results suggested that in extreme saline habitats N, P, K and Ca were limiting factors for the growth of *A. corniculatum* whereas, Mg did not exhibit a similar trend.

It is difficult to suggest mechanistic explanations of salinity influence on micro-elements concentration due to relatively smaller differences between control and salinised tissues (Tozlu et al. 2000). In the present study, accumulation of Zn, Mn and Fe increased, while it decreased for Cu at the whole plant level. Besides, cofactors for enzymes, Fe and Cu are essential for biological redox system, Mn for photolysis of water in photosynthesis and Zn for DNA replication, regulation of gene expression and integrity of biomembranes (Marschner 1995). In addition, high concentration of iron is required for structural and functional integrity of the thylakoid membranes and synthesis of ferredoxin and chlorophyll (Marschner 1995). Decrease of Cu at the whole plant level might limit the growth of plants. Salinity generates an increase in reactive oxygen species (ROS) which have deleterious effects on all metabolisms (Borsani et al. 2001). Superoxide dismutases (SODs) detoxify ROS and may contain Zn, Cu, Mn or Fe as metal component (Slater et al. 2003). Increase of Zn, Mn and Fe content at the whole-plant level might be the requirement of this plant for survival in extreme saline habitats.

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