Microbial Ecology

Improved Tolerance of *Acacia nilotica* to Salt Stress by Arbuscular Mycorrhiza, *Glomus fasciculatum* may be Partly Related to Elevated K/Na Ratios in Root and Shoot Tissues

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Abstract

A pot experiment was conducted to examine the effect of arbuscular mycorrhizal fungus, *Glomus fasciculatum*, and salinity on the growth of *Acacia nilotica*. Plants were grown in soil under different salinity levels (1.2, 4.0, 6.5, and 9.5 dS m^{-1}). In saline soil, mycorrhizal colonization was higher at 1.2, 4.0, and 6.5 dS m^{-1} salinity levels in AM-inoculated plants, which decreased as salinity levels further increased (9.5 dS m^{-1}). Mycorrhizal plants maintained greater root and shoot biomass at all salinity levels compared to nonmycorrhizal plants. AM-inoculated plants had higher P, Zn, and Cu concentrations than uninoculated plants. In mycorrhizal plants, nutrient concentrations decreased with the increasing levels of salinity, but were higher than those of the nonmycorrhizal plants. Mycorrhizal plants had greater Na concentration at low salinity levels (1.2, 4.0 dS m^{-1}), which lowered as salinity levels increased (6.5, 9.5 dS m^{-1}), whereas Na concentration increased in control plants. Mycorrhizal plants accumulated a higher concentration of K at all salinity levels. Unlike Na, the uptake of K increased in shoot tissues of mycorrhizal plants with the increasing levels of salinity. Our results indicate that mycorrhizal fungus alleviates deleterious effects of saline soils on plant growth that could be primarily related to improved P nutrition. The improved K/Na ratios in root and shoot tissues of mycorrhizal plants may help in protecting disruption of K-mediated enzymatic processes under salt stress conditions.

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Introduction

Salinization of soils is a serious land degradation problem in arid and semi-arid areas and is increasing steadily in many parts of the world including India [3]. Globally, almost 1000-million-ha land (7% of all land area) is affected by soil salinity [43]. Out of 1.5 billion ha cultivated land, about 77 million ha (5%) are affected by excess salt content [30]. In India alone, salinity affects 7 million ha of land, which is mainly attributed to irrigation with ground water of high salt content, sodic and alkaline parent material [1, 19].

Among the most common effects of soil salinity is growth inhibition by Na^- and Cl^- [44]. Elevated Na^+ in soil solution inhibits the uptake of other nutrients by disrupting the uptake of nutrients directly by interfering with various transporters in the root plasma membrane, such as K^+-selective ion channels and inhibiting root growth by the osmotic effects of Na^+ on soil structure [46]. Thus, the uptake of water and essential mineral nutrients, such as P, K, Fe, Cu, and Zn, and the growth of soil microorganisms can be reduced. Moreover, high Na^+/K^+ ratio disrupts various metabolic processes such as protein synthesis in the cytoplasm [44].

Arbuscular mycorrhiza (AM) occurs naturally in saline soils [39]. Salinity affects the formation and function of mycorrhizal symbiosis [19, 24, 28]. However, several studies have demonstrated that inoculation with mycorrhizal fungi improves growth and productivity of plants under a variety of salt stress conditions [6, 13, 14, 18]. Owing to the importance of AM fungi under salt stress conditions, they have been considered as bio-ameliorators of saline soils [13, 14]. It is well established that mycorrhizal fungi uptake immobile nutrients, particularly phosphorus (P). The improvement in the plant P status has been suggested as the most important strategy of salinity stress tolerance in AM colonized

plants [4, 19, 22]. However, other studies have shown that salt stress tolerance of AM plants is not always related to improved P status [13, 35, 37], although there are some other physiological processes that help in AM plant growth improvement under such conditions [19].

The purpose of this study was to investigate the effect of mycorrhizal fungi on growth and mineral acquisition by *Acacia nilotica* seedlings over a wide range of soil salinity. We further estimated root and shoot K/Na ratios to understand the mechanisms underlying alleviation of salt stress in mycorrhizal plants.

Materials and Methods

Test Plant. *Acacia nilotica* (Benth.), (subfamily Mimosoidae) was used as test plant. This species has been recognized to be especially suitable for the reclamation and reforestation of semi-arid lands [40], and comes up well even in saline soils [21, 22].

AM Fungal Inoculum and Seed Treatment. Indigenous AM fungal spores were isolated from soil samples collected from Jodhpur (loam soil, pH 8.6, electrical conductivity [EC] 1.9 dS m^{-1}, total dissolved solids (TDS) 0.24 part per trillion (ppt), old Delhi ridge (sandy loam soil, pH 8, EC 1.4 dS m^{-1}, TDS 0.19 ppt), and Asola wildlife sanctuary (loam soil, pH 8.5, EC 1.3 dS m^{-1}, TDS 0.2 ppt) by the wet sieving and decanting method [16]. Electrical conductivity in the soil was measured with a conductivity meter (μ P Based Conductivity Meter, Model 160 E, Scientific Systems, New Delhi). Isolated spores were multiplied in pots on *Trigonella foenum-graecum* roots [25] for 1 year in a polyhouse under high-salt (10 dS m^{-1}) condition to select and maintain salt-tolerant strain of AM fungi. *Glomus fasciculatum* (Thaxter *sensu* Gerd.) Gerd. and Trappe was found to be most salt tolerant, hence it was selected for raising the culture. After 1 year, *Trigonella* was cut at ground level and the roots chopped into small pieces and mixed with the soil mass of the culture pots. This soil-based inoculum was collected and used for inoculation. The inoculum contained about 100 infectious AM propagules 10 g^{-1} of soil. Propagules infectivity was tested according to the method of Sharma *et al.* [40]. Seeds of *Acacia nilotica* were procured from Center Arid Zone Research Institute (CAZRI), Jodhpur, India. Seeds were scarified with 1% dilute sulfuric acid for 10 min and washed thoroughly with sterilized distilled water and then soaked in water for 12 h for imbibitions to remove traces of chemical. Thereafter the seeds were placed on sterilized moist filter paper for germination.

Soil Analysis. Loam soil (sand 41.7%, silt 35.5%, clay 22.8%) collected from the Botanical garden of Delhi University was used as test soil. The soil was collected from 0 to 25 cm depth, air-dried passed through a 2-mm sieve and chemically analyzed. Soil extracts were prepared as reported by Adams *et al.* [2]. Soil had the following properties: loam texture; pH (H_2O) 7.2, EC 1.2 dS m^{-1}, TDS 0.20 ppt, organic C (%) 1.12, total N (%) 0.5, available P, K, Na, Mg, Ca, and Cu 11.1, 55, 61.3, 45, 150, and 22 (mg kg^{-1}), respectively. Organic C was determined by the Walkley & Black method [41], total N by the Jackson method [23], P by the Olsen's method [41], K and Na by an ammonium acetate method [20], Ca and Mg by the Versenate titration method [41], Zn and Cu by the DTPA-$CaCl_2$-TEA method [41]. Soil was fumigated thoroughly with 0.1% formaldehyde under airtight plastic sheets for 5 days and the fumigant allowed to dissipate for 10 days. Then, the soil was dispensed into earthen pots of 28 cm in height × 25 cm in diameter.

Experimental Design and Treatment The experiment consisted of a randomized block design with two factors: (1) mycorrhizal inoculation with *G. fasciculatum* plus a nonmycorrhizal treatment, and (2) four salinity levels (EC 1.2 [TDS 0.22 ppt], 4.0 [TDS 0.32 ppt], 6.5 [TDS 0.41 ppt], and 9.5 [TDS 0.61 ppt] dS m^{-1}). To raise salinity in soil, three different solutions (25, 50, and 100 mM) of NaCl was added to earthen pots containing 2 kg soil per pot, which confers electrical conductivity of 4.0, 6.5, and 9.5 dS m^{-1}, respectively. These solutions were applied only once at the beginning of the experiment for each salt treatment. Soil-based inoculum, containing about 100 infectious AM fungal spores 10/g soil, along with chopped AM-colonized *Trigonella foenum-graecum* roots with infection level 85–90%, was used. Plants without mycorrhizal treatment served as control. *Acacia nilotica* seeds were germinated on sterilized blotting paper in plastic trays and the 10 g of AM inoculum was placed below the germinated seeds at the time of transplantation to pots. There were eight treatments (without mycorrhiza and with mycorrhiza for each salinity level) with 12 replicate plants per treatment. Ten randomly chosen replicates were harvested and two replicates were used for the assessment of AM colonization in root at the end of the experiment. During the first weeks, *Acacia nilotica* plants were grown without addition of NaCl to avoid salt effects on AM establishment. The experiment was conducted in a poly house (Semax Pvt Ltd., India) at 30°C day and 20°C night and around 70% relative humidity. After 2 weeks, seedlings were thinned to one per pot.

Measurements. The plants were harvested 45 days after transplantation. Percentage of root colonization by AM fungus and dry weight of root and shoot were recorded. Roots and shoots were dried for 72 h in a hot air oven at 80°C. Assessment of roots for AM colonization was made at the end of the experiment on a random sampling of the root system. All AM fungal structures including hyphae, arbuscules, and vesicles found in the

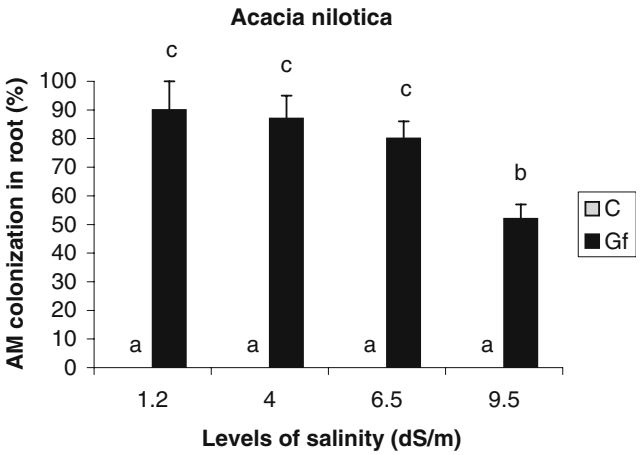

Figure 1. AM colonization in the roots of *Acacia nilotica*. Histograms followed by different letters are significantly different ($P < 0.05$). C = Control, Gf = *Glomus fasciculatum*

roots were recorded. Roots were cleared in 10% KOH and stained with 0.05% trypan blue in lactophenol (*v*/*v*) (Koske & Gemma, 1989). Mycorrhizal percentage was determined by the gridline-intersection method of Giovannetti and Mosse [17].

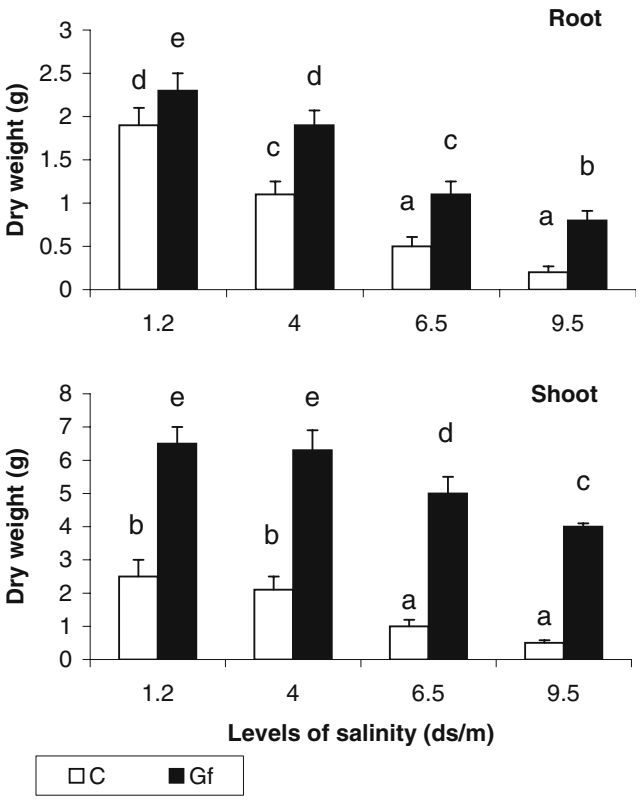

Figure 2. Influence of *Glomus fasciculatum* on plant growth at different levels of salinity. Histograms followed by different letters are significantly different ($P < 0.05$). C = Control, Gf = *Glomus fasciculatum*

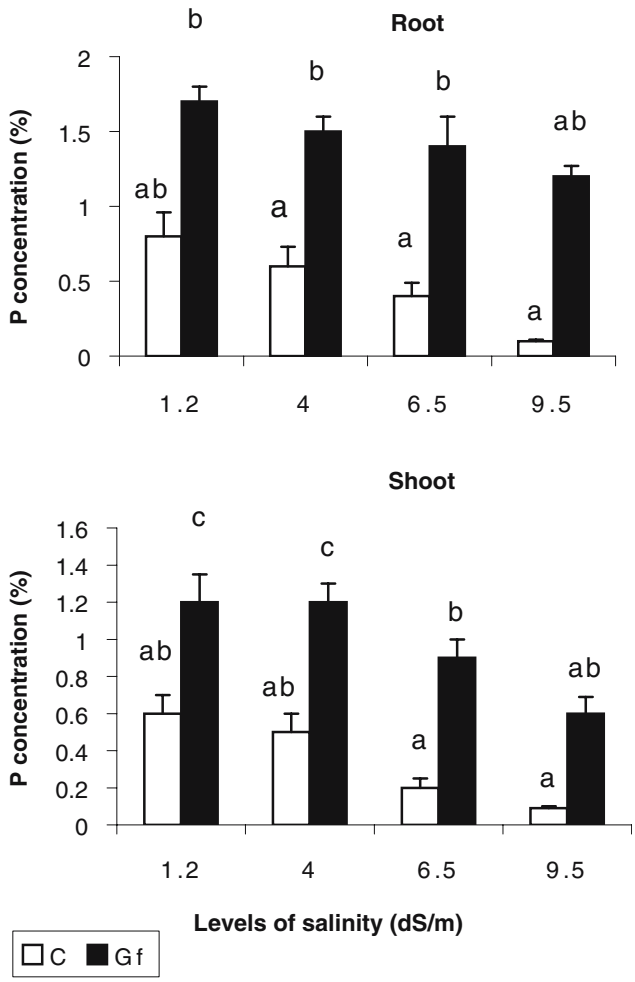

Figure 3. Influence of mycorrhiza and soil salinity on P concentration grown at different levels of salinity. Histograms followed by different letters are significantly different ($P < 0.05$). C = Control, Gf = *Glomus fasciculatum*

Root and shoot tissues were analyzed for their nutrient content. Dried shoot tissues were digested in a Kjeldahl flask with 1 mL (9.2 M) $HClO_4$, 5 mL (14.3 M) HNO_3 and 0.5 mL (17.8 M) H_2SO_4. Phosphorus concentrations of the root and shoot tissues were determined by an ammonium molybdate blue method, Cu and Zn by the atomic absorption spectrophotometer [7], and those of K and Na by flame photometry [39].

The data were subjected to factorial analysis of variance using Statistical Package for Social Sciences (SPSS version 10) and means were separated by Tukey's Post Hoc Tests at the 5% level ($P < 0.05$).

Results

The present study showed a positive influence of *G. fasciculatum* on root colonization under salt stress conditions. The amount of root length colonized by mycorrhizal fungi was higher in case of inoculated plants

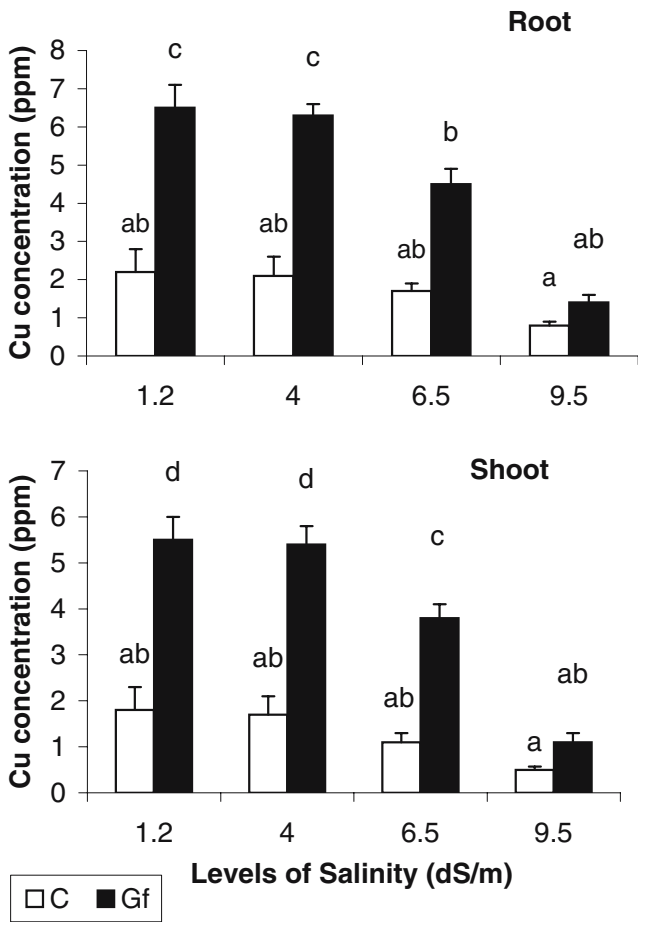

Figure 4. Effect of AM fungus, *G. fasciculatum*, on Cu concentration at different levels of salinity. Histograms followed by different letters are significantly different ($P<0.05$). C = Control, Gf = *Glomus fasciculatum*

grown in soils at 1.2 (90%) and 4.0 dS m^{-1} (87%) salinity levels (Fig. 1). The extent of AM colonization decreased with increase in soil salinity (6.5, 9.5 dS m^{-1}). At 6.5 dS m^{-1} (80%) and 9.5 dS m^{-1} soil salinity levels, only 49% AM colonization was recorded. None of the *A. nilotica* control (without mycorrhiza) plants were colonized by AM fungus.

There was a significant ($P<0.05$) influence of mycorrhizal inoculation on plant growth regardless of salinity levels (Fig. 2). In saline soil, mycorrhizal seedlings had significantly higher root and shoot dry weights than the nonmycorrhizal seedlings. High salinity levels (6.5 and 9.5 dS m^{-1}) reduced root and shoot biomass production in both AM-inoculated and uninoculated plants. But, compared to uninoculated plants, the biomass production was higher in case of AM-inoculated plants, even under high salinity levels.

The concentrations of P, Zn, and Cu were higher in the root and shoot tissues of AM than non-AM plants at all salinity levels (Figs. 3, 4, 5). In fact, the concentrations of P, Zn, and Cu were higher for mycorrhizal plants, but the magnitude decreased with increasing levels of salinity. High level of salinity (9.5 dS m^{-1}) drastically reduced uptake of P in control plants.

Na concentration of roots and shoot tissues of AM-inoculated plants increased significantly ($p<0.05$) as soil salinity increased from 1.2 to 4.0 dS m^{-1} salinity levels but decreased at 9.5 dS m^{-1} salinity level. However, control plants showed a consistent increase in Na concentration at all salinity levels in both roots and shoot tissues. Comparatively, Na concentration was higher in roots (2%) than in shoot tissues (1.5%) of AM plants at a high salinity level (9.5 dS m^{-1}) (Fig. 6).

In this study, AM inoculation had a profound effect on the uptake of potassium under salt stress conditions. AM-inoculated plants accumulated more K in both root and shoot tissues than uninoculated plants at all salinity levels (Fig. 7). The accumulation of K decreased as soil salinity increased. But, unlike Na, the uptake of K increased in shoot tissues of mycorrhizal plants at high salinity level (9.5 dS m^{-1}). Root and shoot tissues of AM-inoculated plants had higher K/Na ratio at all salinity levels. However, the magnitude of K/Na ratio decreased as levels of soil salinity increased (Fig. 8). Moreover, *P* values from univariate analyses of K and Na concen-

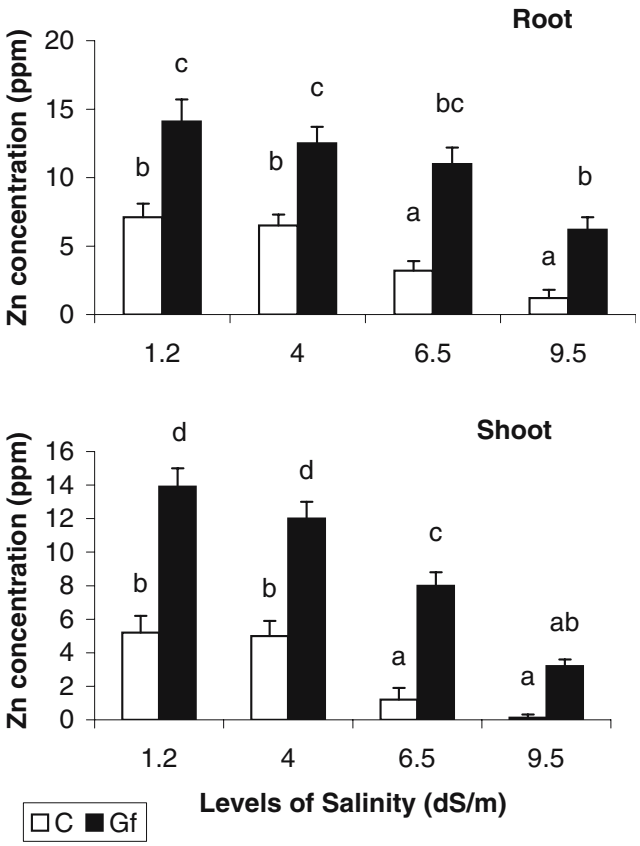

Figure 5. Effect of AM inoculation and soil salinity on Zn concentration. Histograms followed by different letters are significantly different ($P<0.05$). C = Control, Gf = *Glomus fasciculatum*

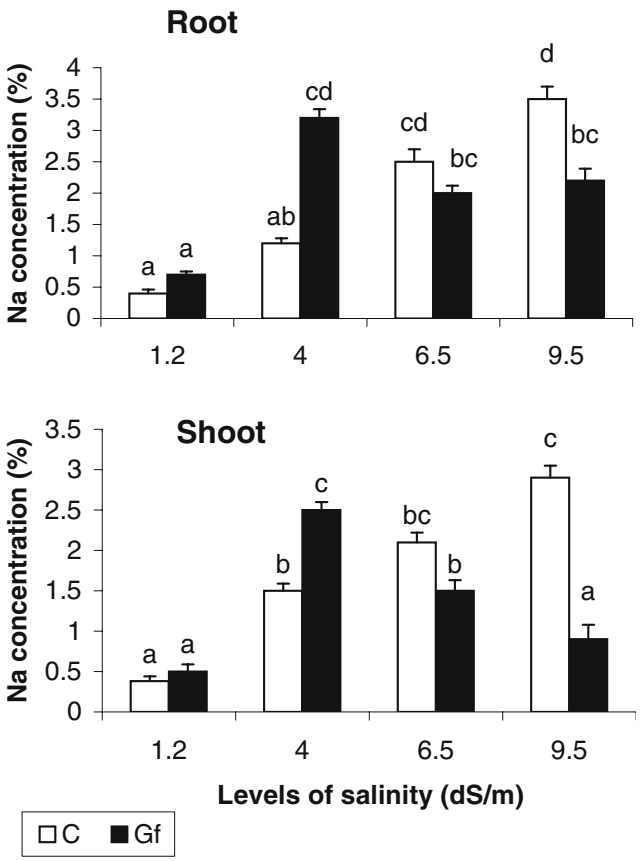

Figure 6. Sodium concentration in root and shoot tissues of AM-inoculated and uninoculated plants grown in saline soil. Histograms followed by different letters are significantly different ($P < 0.05$). C = Control, Gf = *Glomus fasciculatum*

trations in root and shoot showed significant interaction between salinity levels and AM treatments (Table 1).

Discussion

Mycorrhizal symbiosis is a key component in helping plants cope with adverse environmental conditions [19]. In this study, plants inoculated with *G. fasciculatum* had higher root colonization, root and shoot dry biomass production and greater nutrient acquisition than that of the uninoculated plants at all salinity levels. However, more apparent responses were reported only on 1.2, 4.0, and 6.5 dS m^{-1} levels of salinity. The positive influence of AM inoculation on plant growth exhibits that root colonization by *G. fasciculatum* can alleviate the adverse effects of salt stress. Our findings are consistent with previous reports for AM response in saline conditions [13, 14, 22, 32]. It is pertinent to point out that the beneficial effects of AM fungi on the plant growth occurred not only during salt stress but also in other conditions like drought and water stresses [8, 36], heavy metal stress [45], and even in nonstress conditions, which implies that the improved plant growth by AM fungi was not a specific process induced by salinity stress.

Optimum level of phosphorus relieves salt stress in plants [9]. It is well known that AM fungi improve plant P status while growing under nutrient-deficient conditions. The improved growth of mycorrhizal plants in saline conditions is primarily related to mycorrhiza-mediated enhancement of host plant P nutrition [4, 20, 22, 32, 34, 35]. Improved P uptake by mycorrhizal plants does not totally account for the improved salt tolerance, whereas other mechanisms may be involved in improvement of salt tolerance in mycorrhizal plants [12]. Pfeiffer and Bloss [33] stated that major effect of the mycorrhiza on sodium uptake is through mediation of P accumulation. In this study, root and shoot tissues of mycorrhizal plants had apparently higher concentrations of P than nonmycorrhizal plants at all salinity levels. The higher P accumulation by mycorrhizal plants further substantiates the fact that improved plant P uptake under saline condition is a primary strategy of mycorrhizal fungi to protect the plant from deleterious effect of excess salts. In

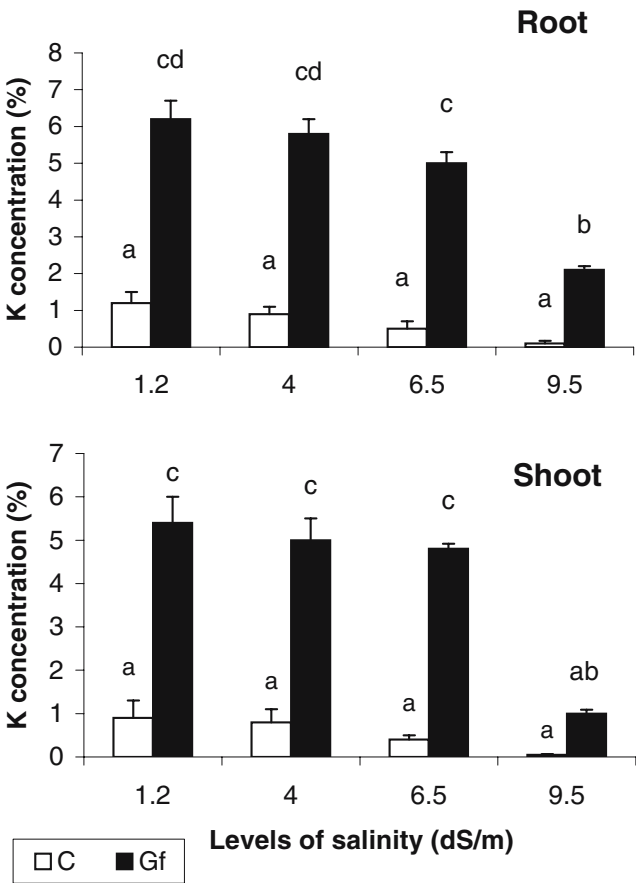

Figure 7. Potassium concentration in root and shoot tissues of mycorrhizal and non-mycorrhizal plants grown in saline soil. Histograms followed by different letters are significantly different ($P < 0.05$). C = Control, Gf = *Glomus fasciculatum*

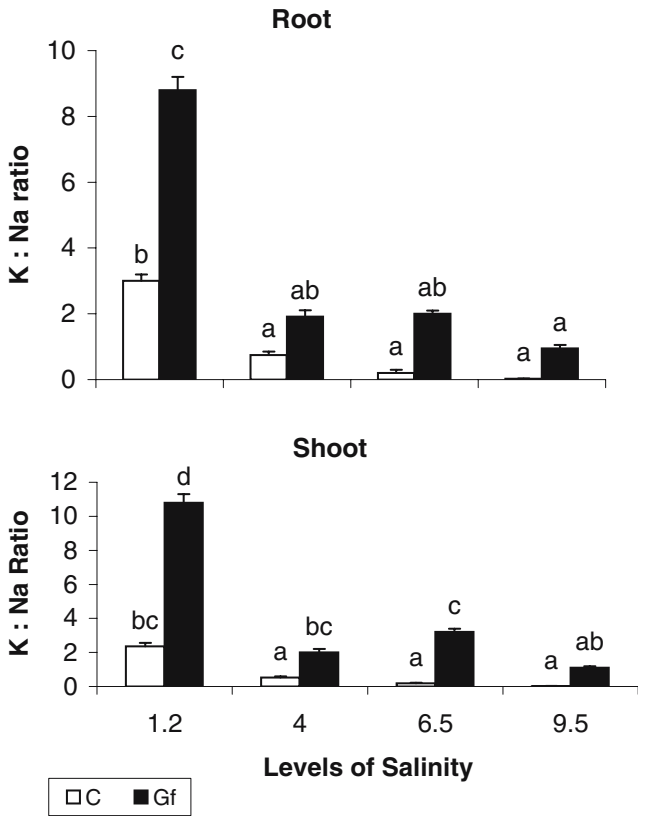

Figure 8. K/Na ratio of root and shoot tissues of AM inoculated and uninoculated *Acacia nilotica* grown under increasing levels of soil salinity. Histograms followed by different letters are significantly different ($P<0.05$). C = Control, Gf = *Glomus fasciculatum*

the present study, P concentration decreased at high salinity level, which may be caused by the toxic effect of Na ions on AM fungal development. A similar decrease in P concentration has been reported earlier [4]. It has also been reported that high salt content inhibits the growth of the AM fungal hyphae [28], which in turn reduced transport of P into roots and its uptake, by the plant.

In addition to improved P uptake, our results showed greater concentrations of zinc and copper in root and shoot tissues of mycorrhizal *A. nilotica* plants. This may be the result of increased absorption and translocation by AM fungal hyphae. Enhanced acquisition of Zn, Cu, and Fe by mycorrhizal plants has been reported [4, 5, 27]. It seems that improved plant nutrition by AM allows cells to more effectively regulate and separate flowing ions.

High concentration of Na creates various osmotic and metabolic problems (e.g., reduced photosynthesis, protein synthesis) for plants [45]. Sodium transport is largely suggested as a unidirectional flow and thus results in progressive accumulation of Na in the shoot and leaf tissues with age of the plant. In this study, mycorrhiza-inoculated plants had lower concentration of Na in shoot tissue seven at a high salinity level (9.5 dS m^{-1}), which increased drastically in uninoculated plants at same salinity level. This suggests that AM fungus in *A. nilotica* roots accumulated more salt and thus prevented transport of Na to shoot tissues and this may be another strategy whereby AM fungi alleviate the detrimental effect of salinity. Although we have not determined where Na was retained in the roots, we agree with Cantrell and Lindermann [11], who suggested that it might have been retained in intraradical AM fungal hyphae. Further investigations are required to find out this mechanism.

Moreover, the detrimental effect of Na is largely a result of its ability to compete with K for binding sites essential for various cellular functions. Potassium has many roles in plant metabolism. It activates a range of enzymes, and Na cannot substitute in this role [10]. Thus, high levels of Na, or high Na/K ratios can disrupt various enzymatic processes in the cytoplasm. Mycorrhizal *A. nilotica* plants had a higher concentration of K in root and shoot tissues at all salinity levels. Similar increase in the concentration of K has also been reported previously [20, 29, 32]. It seems that higher K accumulation by mycorrhizal plants under salt stress conditions may help in maintaining a high K/Na ratio, thus preventing the disruption of various enzymatic process and inhibition of protein synthesis.

In conclusion, the study indicates that plant tolerance to salt stress is improved by mycorrhizal colonization, although greater nutrient acquisition seems the most likely mechanism by which plant growth has improved. The improved K/Na ratios in roots and shoot tissues of mycorrhizal plants may help in protecting disruption of K-mediated enzymatic processes under salt stress conditions. Moreover, high K/Na ratios in mycorrhizal plants could be beneficial in influencing the ionic balance of the cytoplasm.

Table 1. *P* **values from univariate analyses of K and Na concentrations in root and shoot of *Acacia nilotica***

Parameter	*Salinity*	*AM treatment*	*Salinity × AM treatment*
K Root	***0.021***	***0.000***	***0.023***
K Shoot	***0.000***	***0.000***	***0.001***
Na Root	***0.000***	***0.017***	***0.007***
Na shoot	***0.000***	***0.019***	***0.001***

Significant *P* values are in bold ($P<0.05$)

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