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ORIGINAL PAPER

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Mycorrhizal inoculant alleviates salt stress in *Sesbania aegyptiaca* and *Sesbania grandiflora* under field conditions: evidence for reduced sodium and improved magnesium uptake

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Abstract A field experiment was conducted to examine the effect of the arbuscular mycorrhizal fungus *Glomus macrocarpum* and salinity on growth of *Sesbania aegyptiaca* and *S. grandiflora*. In the salt-stressed soil, mycorrhizal root colonisation and sporulation was significantly higher in AM-inoculated than in uninoculated plants. Mycorrhizal seedlings had significantly higher root and shoot dry biomass production than non-mycorrhizal seedlings grown in saline soil. The content of chlorophyll was greater in the leaves of mycorrhiza-inoculated as compared to uninoculated seedlings. The number of nodules was significantly higher in mycorrhizal than non-mycorrhizal plants. Mycorrhizal seedling tissue had significantly increased concentrations of P, N and Mg but lower Na concentration than non-mycorrhizal seedlings. Under salinity stress conditions both *Sesbania* sp. showed a high degree of dependence on mycorrhizae, increasing with the age of the plants. The reduction in Na uptake together with a concomitant increase in P, N and Mg absorption and high chlorophyll content in mycorrhizal plants may be important salt-alleviating mechanisms for plants growing in saline soil.

Keywords Arbuscular mycorrhiza · Soil salinity · Mycorrhizal dependency · *Glomus macrocarpum* · Plant establishment

Introduction

Soil salinity is a widespread problem, restricting plant growth and biomass production especially in arid, semi-arid and tropical areas (Apse et al. 1999). The development of salt-tolerant crops or desalination of soil by leaching excessive salts, though successful, is not economical for sustainable agriculture (Hamdy 1990; Cantrell and Linderman 2001). In this respect, biological processes such as mycorrhizal application to alleviate salt stress and use of moderately salt-tolerant tree species are better options (Hartmond et al. 1987; Dixon et al. 1993).

The reclamation of saline soil with multipurpose, fast-growing tree species (MPTS) such as *Sesbania* and *Acacia* sp., which are moderately salt-tolerant legume trees, are commonly used for overcoming salt stress problems (Sharma et al. 2001; Giri et al. 2002). However, these trees usually exhibit a considerable dependence on mycorrhizae, especially arbuscular mycorrhizae (AM) for an adequate supply of phosphorus enabling them to thrive under salt stress conditions (Plenchette et al. 1983; Barea et al. 1992). Many workers have reported the presence of the AM association in salt stress environments (Pond et al. 1984; Ruiz-Lozano and Azcon 2000; Aliasgharzadeh et al. 2001). AM fungi enhance the ability of plants to cope with environmental stresses generally prevalent in the degraded ecosystem.

Most studies concerned with AM-saline soil interactions do not simulate field conditions (Al-Karaki et al. 2001). There have been few attempts to study the role of AM fungi in establishment and growth of MPTS seedlings in saline soil. The present study evaluates the effect of the AM fungus *Glomus macrocarpum* on growth and establishment of *Sesbania aegyptiaca* and *S. grandiflora* seedlings in saline soils.

Materials and methods

The experimental site is located in the Botanical garden, Department of Botany, University of Delhi, India, where high salt concentration has rendered it unproductive, saline fallow. The soil is a sandy loam (clay 35%, silt 33%, sand 32%). Soil extract using the method of Adams et al (1980) had the followings chemical properties: pH 8.9, EC (electrical conductivity) 1.58 S m^{-1} at 32°C, organic C 1.12%, total N 0.85%, and available P, K, Na, Zn, and Mg 8, 12, 122, 20 and 30 mg/kg, respectively. Soil pH and EC were determined with a digital pH and EC meter (Toshniwal Pvt, Dehli, India), organic C by the Walkley and Black method (Singh et al. 2001), total N according to Jackson (Singh et al. 2001), P by the method of Olsen et al. (1954), and K and Na by the ammonium

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acetate method (Hanway and Heidel 1952). The Zn concentration was determined by the DTPA-$CaCl_2$-TEA method (Singh et al. 2001).

Raising mycorrhizal and non-mycorrhizal inoculum

G. macrocarpum Tul. & Tul. is dominant in the experimental site soil, hence it was chosen for the present study. Spores of *G. macrocarpum* were isolated from the soil by the wet sieving and decanting method (Gerdemann and Nicolson 1963). Pot cultures were maintained on *Sorgham halepense* (Sudangrass) plants grown in a poly-house (temperature 32°C/20°C; RH 70%) for 6 months in sterilised soil (autoclaved at 121°C; 20 min; 15 psi) from the same site. Soil inoculum contained about 50–55 infectious AM propagules/10 g. Propagule infectivity was tested according to the method of Sharma et al. (1996). In addition, some of the pots were uninoculated and served as non-mycorrhizal controls.

Seed treatment

S. aegyptiaca (Pers.) and *S. grandiflora* (Pers.) seeds were procured from the Central Arid Zone Research Institute (CAZRI), Jodhpur, India and scarified with dilute sulphuric acid for 10 min. Seeds were washed thoroughly with sterile distilled water and then soaked in sterile water for 12 h. Thereafter the seeds were placed on sterilised moist filter paper to allow germination in a poly-house (temperature 32°C/20°C; RH 70%).

Experimental design

Topsoil to a depth of 30 cm was fumigated twice with 0.1% formaldehyde at 7-day intervals. The soil was then dried and the fumigant allowed to dissipate for a week. The experimental land was divided into four equal plots of 10 m^{-2}, two plots for each plant species. Two treatments were applied to each plant species: (1) control without mycorrhiza, (2) inoculated with *G. macrocarpum* (Gm). Soil inoculum (500 g with 50–55 AM propagules/10 g soil) along with 200 mg chopped AM-colonised sorghum roots with an infection level of 80% were placed in furrows in each plot before sowing of seed (Kapoor et al. 2002).

Measurements and analysis

Five seedlings per treatment were harvested 30 and 60 days after germination. Root and shoot biomass were determined after oven-drying at 70°C for 72 h. Oven-dried plant matter was ground and sieved through a 0.5 mm sieve. The ground material (0.2 g) was digested in a Kjeldahl flask in a triple acid mixture (HNO_3:H_2SO_4:60% $HClO_4$, 10:1:4) for analysis of P, N, Mg and Na according to the methods of Allen (1989). The chlorophyll concentration in the leaves was determined by extracting with dimethyl sulphoxide according to the chlorophyll extraction method of Hiscox and Isrealstan (1979) using the equation of Arnon (1949).

Roots were assessed for AM colonisation 30 and 60 days after seed germination. Randomly sampled roots were clarified and stained with Trypan Blue (Koske and Gemma 1989) and cut into 1 cm pieces. Stained root pieces were examined under a compound microscope (Nikon, Japan) at 40× magnification. All AM fungal structures (hyphae, arbuscules and vesicles) formed in the roots were counted, and the extent of AM colonisation was estimated by the grid line intercept method (Giovennetti and Mosse 1980). Mycorrhizal dependency was calculated as percent increase in dry weight of mycorrhizal plants over dry weight of non-mycorrhizal plants (Plenchette et al. 1983)

Statistical analysis

Data were statistically analysed using one-way analysis of variance and the means were separated by Duncan's multiple range test ($P<0.05$) using Costat software (Cohort; Berkeley, Calif.).

Results and discussion

In saline soil, *G. macrocarpum* successfully colonised the roots of *S. aegyptiaca* and *S. grandiflora* (Fig. 1) although the level of colonisation varied in each plant species. AM colonisation did not occur in control plants 30 days after germination, but very low colonisation was observed in control plants 60 days after germination, which may be due to contamination as the experiment was carried out in open field nursery conditions. In the inoculated plots, percent AM colonisation and spore numbers increased significantly even though there was not much increase in percent colonisation in 30-day-old seedlings. Increased AM fungal sporulation and colonisation under salt-stress conditions has also been reported by Aliasgharzadeh et al. (2001).

In most 30- and 60-day-old seedlings there was a significant increase in root and shoot dry biomass in mycorrhizal compared to non-mycorrhizal plants (Fig. 2). This supports the previous finding that AM-inoculated plants grow better than non-inoculated plants under salt-stress conditions (Al-Karaki 2000; Cantrell and Linderman 2001). Similar increased biomass production has been observed previously (Ojala et. al. 1983; Pond et al.

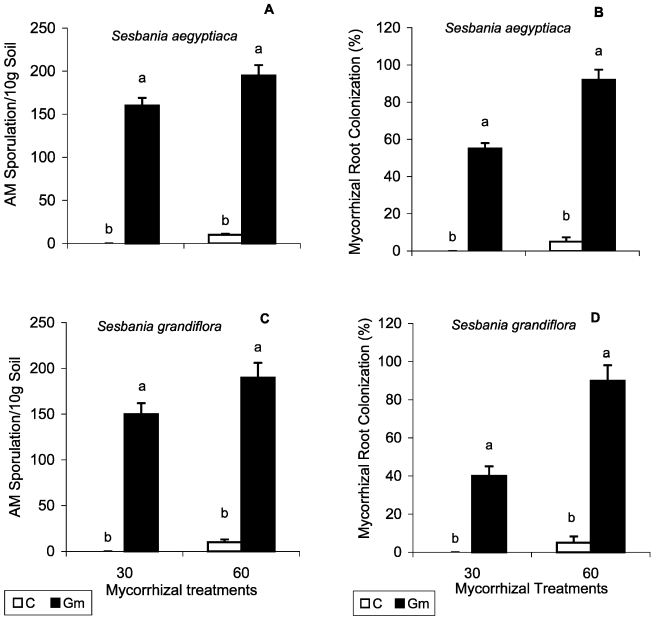

Fig. 1 Effect of salinity and *Glomus macrocarpum* on arbuscular mycorrhiza (AM) sporulation and colonisation of *Sesbania aegyptiaca* (**A**, **B**) and *S. grandiflora* (**C**, **D**) 30 and 60 days after germination. Histograms indicated with the same letter are not significantly different ($P>0.05$) by Duncan's multiple range test; $n=5$. C Control, Gm *G. macrocarpum*

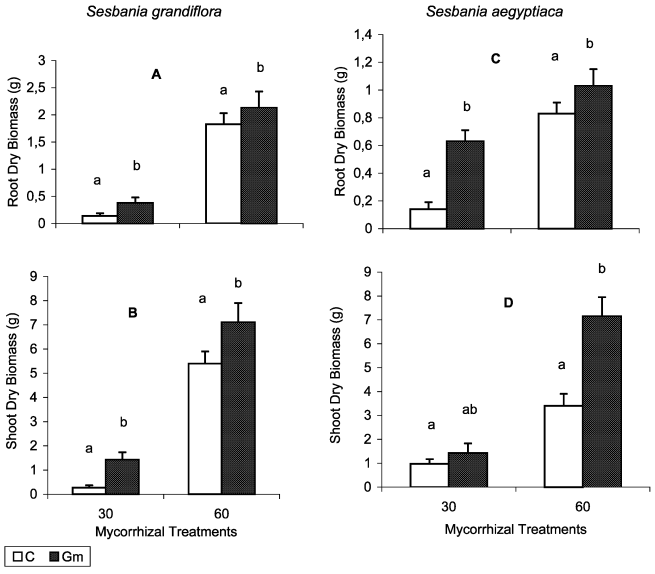

Fig. 2 Influence of salinity and *G. macrocarpum* on biomass production of *S. grandiflora* (**A**, **B**) and *S. aegyptiaca* (**C**, **D**) 30 and 60 days after germination. Within a column, values indicated with the same letter are not significantly different (P>0.05) by Duncan's multiple range test; n=5. C Control, Gm *G. macrocarpum*

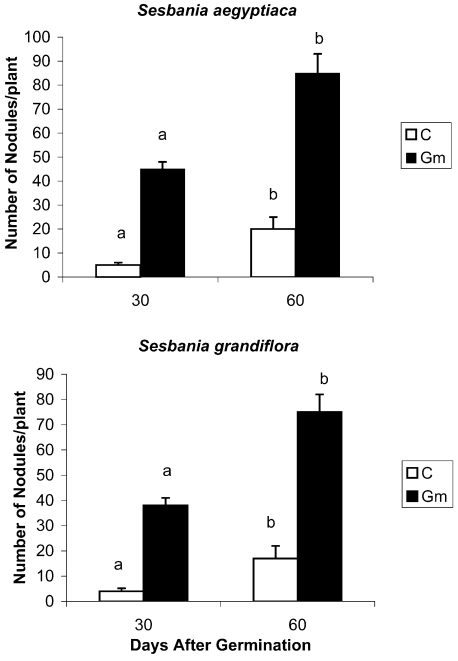

Fig. 3 Influence of salinity and *G. macrocarpum* on nodules formation in *S. grandiflora* and *S. aegyptiaca* 30 and 60 days after germination. Histograms indicated with the same letter are not significantly different (P>0.05) by Duncan's multiple range test; n=5. C Control, Gm *G. macrocarpum*

1984; Juniper and Abbott 1993; Copeman et al. 1996; Al-Karaki et al. 2001; Cantrell and Linderman 2001). *G. macrocarpum* significantly stimulated growth but the magnitude of growth response varied among plant species. Similar results have also been reported by Cantrell and Linderman (2001). The improved growth of AM-inoculated plants may be primarily regulated by supply of nutrients to the root system.

Soil salinity significantly reduces absorption of mineral nutrients, especially P because phosphate ions precipitate with Ca^{2+} ions in salt-stressed soil and become unavailable to plants (Poss et al. 1985; Munns 1993; Grattan and Grieve 1999). Therefore, P improver/fertilisation is necessary for plant growth, which may be helpful in mitigating salt stress by overcoming the P binding capacity of the soil. AM fungi have been shown to have a positive influence on the composition of mineral nutrients (especially poor mobility nutrients such as P) of plants grown in salt-stress conditions (Al-Karaki and Clark 1998). In the present study, mycorrhizal *S. aegyptiaca* and *S. grandiflora* had higher concentrations of P compared to non-mycorrhizal plants (Table 1). In saline soil, higher absorption of P in AM-inoculated plants may improve their growth rate and salt-tolerance and suppress the adverse effect of salinity stress. Poss et al. (1985) also suggested that the salt-tolerance mechanism in onion is primarily related to P nutrition. Similarly, Pfeiffer and Bloss (1988) stated that mycorrhizal fungi have the major effect on salt stress through mediation of P accumulation. Duke et al. (1986) concluded that, besides enhanced P uptake, there are some other mechanisms such as induction of osmotica that lead to osmotic adjustment and improved salt-tolerance in mycorrhizal plants. However, Marschner (1995) demonstrated that balanced nutrition increased the salt-tolerance capacity of plants.

AM-inoculated plants had significantly greater concentration of N than non-mycorrhizal plants (Table 1). Increased N concentration under saline conditions may help to decrease Na uptake, which may be indirectly related to maintaining the chlorophyll content of the plant. Mycorrhizal inoculation had a strong effect on nodule formation. The number of nodules was higher in mycorrhizal than in non-mycorrhizal plants (Fig. 3). Improved

Table 1 Influence of salinity and *Glomus macrocarpum* on nutrient concentration in *Sesbania grandiflora* and *Sesbania aegyptiaca* 60 days after germination. Within a column, values indicated with the same letter are not significantly different (P>0.05) by Duncan's multiple range test; n=5. C Control, Gm *G. macrocarpum*

Plant species	Treat-ment	P (%) root	Shoot	N (%) root	Shoot	Mg (%) root	Shoot	Na (%) root	Shoot
Sesbania grandiflora	C	0.50 a	0.36 a	0.74 a	0.72 a	0.111 a	0.149 a	1.091a	0.921 a
	Gm	0.78 b	0.49 b	1.69 b	1.73 b	0.287 b	0.331 b	0.702 b	0.203 b
Sesbania aegyptiaca	C	0.52 a	0.40 a	0.89 a	0.96 a	0.165 a	0.202 a	1.25 a	1.020 a
	Gm	0.75 b	0.65 b	1.98 b	2.52 b	0.328 b	0.365 b	0.981b	0.431 b

nodulation and N-fixation in mycorrhizal plants may be due to relief from P stress and possibly to uptake of some essential micro-nutrients, which results both in improved growth of plants and has an indirect effect on the N-fixing system (Bethlenfalway 1992; Barea et al. 1992; Founoune et al. 2002).

It was noteworthy that AM plants exhibited reduced Na uptake in root and shoot tissues as compared to uninoculated controls (Table 1). Mycorrhizal *S. grandiflora* and *S. aegyptiaca* had 0.702% and 0.981%, whereas non-mycorrhizal plants showed 1.091% and 1.25% Na concentration in the root tissues, respectively (Table 1). Mycorrhizal inoculation of both plant species prevented Na translocation to shoot tissues. It appears that the role of *G. macrocarpum* in alleviating salt stress is partly to prevent Na absorption to root and translocation to shoot tissues. The accumulation of Na is strongly influenced by the form of N available (NO_3^- or NH_4^+) and it may also be influenced by the synthesis and storage of polyphosphate (Orlovich and Ashford 1993) as well as by other cations, particularly K (Giri et al. 2003). Hence, mycorrhizal plants had less Na intake compared to non-mycorrhizal plants. Plaut and Grieve (1988) found that increased P results in decreased Na, which is indirectly related to Ca and Mg uptake. Moreover, Ojala et al. (1983) found that AM-inoculated onion had higher concentrations of K in shoots and bulbs under salt stress conditions, which could be beneficial by maintaining a high K/Na ratio and by influencing the ionic balance of the cytoplasm (Founoune et al. 2002) or Na efflux from the plant (Allen and Cunningham 1983). Cantrell and Linderman (2001) suggested that AM fungi improve P nutrition of plants under salinity stress and reduce the negative effects of Na^+ and Cl^- by maintaining vacuolar membrane integrity, which prevented these ions from interfering in growth metabolic pathways. Maintained membrane integrity facilitates compartmentalisation within vacuoles and selective ion intake (Rinaldelli and Mancuso 1996).

Further, the chlorophyll content in leaves of mycorrhizal *S. aegyptiaca* and *S. grandiflora* was significantly higher than in non-mycorrhizal plants (Fig. 4). The leaves of non-mycorrhizal plants were more chlorotic than those of mycorrhizal plants. This suggests that salt interferes with chlorophyll synthesis more in non-mycorrhizal than in mycorrhizal plants. Under salinity stress there may be several reasons for low chlorophyll content in plant tissues. One explanation might be that Na has an antagonistic effect on Mg absorption (Alam 1994). In the present investigation, a higher concentration of Mg was observed for both plant species as a result of AM colonisation, which suggests that mycorrhizal fungi reduce the antagonistic effect of Na (Table 1). We have already reported that mycorrhizal fungi are effective in the absorption of Mg and suppression of Na under salt stress conditions (Giri et al. 2002).

The mycorrhizal dependency (MD) of both the Sesbanias was calculated based on the plant dry matter yield, and revealed that *S. aegyptiaca* depended on *G. macrocarpum* to the extent of 69% and 79.2%, and *S. grandiflora* to 55.1% and 68.2% 30 and 60 days after germination, respectively. MD in saline soil was higher in *S. aegyptiaca* than in *S. grandiflora*. However, both *Sesbania* sp. had a considerable degree of dependence on *G. macrocarpum* under salt stress conditions. A similar effectiveness of AM fungi for different plant species was reported by Dixon et al. (1997). In saline soil, the MD of *S. aegyptiaca* and *S. grandiflora* increased with the age of the plants. Our results show that, under salt stress conditions, plants need mycorrhiza not only for acclimatisation but also for continued nutrient uptake during progressive growth stages.

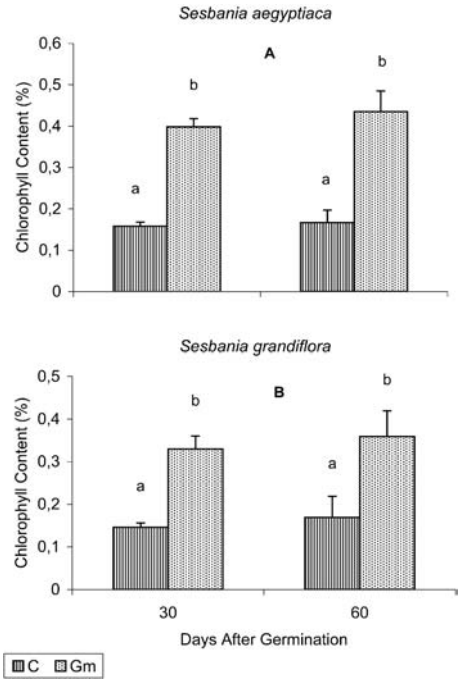

Fig. 4 Influence of *G. macrocarpum* on chlorophyll content of *S. aegyptiaca* (**A**) and *S. grandiflora* (**B**) 30 and 60 days after germination under saline conditions. Histograms indicated with the same letter are not significantly different ($P>0.05$) by Duncan's multiple range test; $n=5$. C Control, Gm *G. macrocarpum*

The present investigation demonstrates that, in saline soil, inoculation with *G. macrocarpum* can promote plant growth and establishment. Nevertheless, absorption of P is the major contribution of the mycorrhizal fungi to plant growth under salt stress. It appears that there are several possible metabolic processes that could be mediated by P nutrition or other elements such as N. The improved Mg and reduced Na concentrations of mycorrhizal plants may help to increase chlorophyll concentration. Moreover, the concentration of Na in *S. grandiflora* decreased to a higher extent (55%) than in *S. aegyptiaca* (38%). However, *S. aegyptiaca* showed a higher degree of dependence on AM fungi than *S. grandiflora*, which revealed that there may be some involvement of non-mediated nutritive effects that could play a more major

role than nutritional effects. Further research must be undertaken to evaluate such non-nutritional effects.

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