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Response of two tomato cultivars differing in salt tolerance to inoculation with mycorrhizal fungi under salt stress

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Abstract Effects of arbuscular mycorrhizal fungi (AMF) and salt stress on nutrient acquisition and growth of two tomato cultivars exhibiting differences in salt tolerance were investigated. Plants were grown in a sterilized, low-P (silty clay) soil-sand mix. Salt was applied at saturation extract (EC_e) values of 1.4 (control), 4.9 (medium) and 7.1 dS m⁻¹ (high salt stress). Mycorrhizal colonization occurred irrespective of salt stress in both cultivars, but AMF colonization was higher under control than under saline soil conditions. The salt-tolerant cultivar Pello showed higher mycorrhizal colonization than the salt-sensitive cultivar Marriha. Shoot dry matter (DM) yield and leaf area were higher in mycorrhizal than nonmycorrhizal plants of both cultivars. Shoot DM and leaf area but not root DM were higher in Pello than Marriha. The enhancement in shoot DM due to AMF inoculation was 22% and 21% under control, 31% and 58% under medium, and 18% and 59% under high salinity for Pello and Marriha, respectively. For both cultivars, the contents of P, K, Zn, Cu, and Fe were higher in mycorrhizal than nonmycorrhizal plants under control and medium saline soil conditions. The enhancement in P, K, Zn, Cu, and Fe acquisition due to AMF inoculation was more pronounced in Marriha than in the Pello cultivar under saline conditions. The results suggest that Marriha benefited more from AMF colonization than Pello under saline soil conditions, despite the fact that Pello roots were highly infected with the AMF. Thus, it appears that Marriha is more dependent on AMF symbiosis than Pello.

Keywords Arbuscular mycorrhizal fungi · Cultivar · Growth · *Lycopersicon esculentum* · Salinity

Introduction

One of the most serious agricultural problems in arid and semiarid regions is the accumulation of salt on the soil surface, which renders fields unproductive. In general, salinity inhibits plant growth and productivity. Detrimental effects of salinity on plant growth result from direct effects of ion toxicity (Al-Karaki 2000a; Ayers and Westcot 1985; Hasegawa et al. 1986) and/or indirect effects of saline ions that cause soil/plant osmotic imbalance (Wyn Jones and Gorham 1983). Incorporating or applying factors that enable plants to better withstand salt stress could help improve crop production under saline conditions.

The introduction of arbuscular mycorrhizal fungi (AMF) to sites with saline soil may improve plant tolerance and growth (Al-Karaki 2000b; Jain et al. 1989). The improved productivity of AMF plants has been attributed especially to enhanced acquisition of low mobility nutrients such as P, Zn, and Cu (Al-Karaki and Al-Raddad 1997; Al-Karaki and Clark 1998; George et al. 1994; Marschner and Dell 1994) and improved water relations (Al-Karaki 1998; Bethlenfalvay et al. 1988; Sylvia et al. 1993). Mycorrhizal association with plant roots not only enhances growth and mineral element uptake, but mycorrhizal plants may have a greater tolerance of salt stress (Al-Karaki 2000b; Ruiz-Lozano et al. 1996). Improved salt tolerance following mycorrhizal colonization may be caused by more efficient P uptake by mycorrhizal plants in P-deficient soils (Poss et al. 1985), leading to increased growth and subsequent dilution of toxic ion effects (Juniper and Abbott 1993). In some cases, however, salt tolerance of AMF plants appears to be independent of plant P concentration (Danneberg et al. 1992; Ruiz-Lozano et al. 1996).

Salinity tolerance in tomato (*Lycopersicon esculentum* Mill) plants is of major importance in Mediterranean regions, where plants are often subjected to high levels of salinity in the soil from soluble salts in irrigation water and fertilizers; there is a negative correlation between excess salinity and yield (Al-Karaki 2000a; Feigin et al.

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1987; Shalhevet and Hsiao 1986). Wide variation in plant responses to AMF inoculation has been reported for different plant species under environmental stresses (Al-Karaki and Al-Raddad 1997; Hirrel and Gerdemann 1980; Poss et al. 1985). It has been suggested that mycorrhizal colonization is a host-dependent and heritable trait (Lackie et al. 1988; Mercy et al. 1990).

Symbiotic interactions (especially in terms of growth and mineral nutrient acquisition) between AMF and host plants (e.g. differing in salt tolerance) need to be studied under salt-stress conditions in order to optimize the beneficial effects of AMF. The objectives of this present study were to determine the effects of salt stress and AMF inoculation on growth and mineral nutrient acquisition by two tomato cultivars differing in salt tolerance.

Materials and methods

A greenhouse experiment was conducted at 25±5°C under natural illumination during the spring of 1999. Tomato plants were grown in a silty clay soil (fine, mixed, thermic, Typic Xerochrept) mixed with sand [soil:sand, 2:1 (v/v)]. Soil properties before mixture with sand were 6.5% sand, 45% silt, 48.5% clay, 1.2% organic matter, pH 8.1(soil:water, 1:1), electrical conductivity (ECe) 1.4 dS m⁻¹; 0.26 P (NaHCO₃-extractable), 23.1 K, 6.2 Na, 0.2 Fe, 0.02 Zn, and 0.03 Cu (5 mM DTPA-extractable) in mmol per kg soil. The soil mix was fumigated with methyl bromide under airtight plastic sheets for 3 days and the fumigant allowed to dissipate for 10 days. The soil mix was dispensed into plastic pots (4.5 kg soil per pot) for plant growth. No P was added to the soil.

Half of the pots received the AMF *Glomus mosseae* (Nicol. And Gerd.) Gerd. And Trappe by placing 50 g (moist weight) of inoculum in the soil directly adjacent to the roots of tomato seedlings. The AMF inoculum consisted of soil and root fragments and ~1,350 chlamyospores per kg air-dried soil. The inoculum was isolated initially from a wheat (*Triticum durum* desf.) field in northern Jordan (Al-Raddad 1993) and multiplied in pot cultures using chickpea (*Cicer arifinum* L.) as host (Al-Karaki and Al-Raddad 1997). Control treatments received no AMF inoculum. Seeds of tomato cultivars Pello (salt tolerant) and Marriha (salt sensitive) (Al-Karaki 2000c) were germinated in a moist mix of peat and sand in polystyrene trays. Three 20-day-old seedlings, uniform in size, were transplanted into each pot. Nitrogen as NH₄NO₃ was added at a rate of 30 mg N per kg soil 7 days after transplantation.

Plants were established for 3 weeks before being subjected to three salt levels by addition of a solution of NaCl and CaCl₂

(1 M NaCl, 1 M CaCl₂) to soil with the irrigation water. This gave saturation extract (ECe) values of 1.4 (control), 4.9 (medium), and 7.1 (high salt stress) dS m⁻¹. Electrical conductivity's in soil were measured with a Model LF539 Conductivity Meter (WTW, Weilheim, Germany). The soil was salinized step-wise to avoid subjecting plants to an osmotic shock. Plants were watered with tap water (EC= 0.4 dS m⁻¹) until harvest. When leaching occurred, the leachate was collected and added back to soil to maintain salinity treatments near target levels.

The experiment was terminated by severing shoots from roots after 8 weeks growth under salt-stress conditions. Leaf area was determined using an LI-3000 leaf-area meter. Shoots were then oven-dried at 70°C for 48 h, weighed and saved for mineral analysis. Roots were rinsed free from soil and cut into 1-cm fragments. The fragments were thoroughly mixed and representative fresh samples (1 g) were removed for determination of root AMF colonization. The remaining roots were dried and weighed. Root samples for determination of root colonization with AMF were cleared with 10% KOH and stained with 0.05% trypan blue in lactophenol as described by Phillips and Hayman (1970). AMF colonization in terms of percentage root segments containing arbuscules and vesicles was determined using a gridline intercept method (Bierman and Linderman 1981).

Dried shoots were ground to pass through a 0.5-mm sieve in a cyclone laboratory mill and saved for determination of mineral nutrients. Shoot P was determined colorimetrically (Watanabe and Olsen 1965) and Zn, Fe and Cu were determined by atomic absorption spectroscopy. Potassium and Na in plant shoots were determined using flame photometry (Ryan et al. 1996).

The experiment was randomized in complete blocks with three salt stress levels, two AMF inoculum treatments and two tomato cultivars to give a 3×2×2 factorial with four replications. Data were analyzed statistically using analyses of variance with MSTATC (Michigan State University, East Lansing, Mich.). Probabilities of significance among treatments and interactions and LSDs (*P*<0.05) were used to compare means within and among treatments. Mean percentages of AMF colonization were calculated from arcsine transformed data.

Results

Nearly all salinity and AMF treatments produced significant effects on growth and nutrient acquisition traits (Table 1). Salt × AMF interactions were significant for shoot and root dry matter (DM) yields, leaf area, AMF colonization, and P and Fe contents. Cultivars showed significant differences only for shoot DM, leaf area, AMF colonization, and P, K and Fe contents. AMF ×

Table 1 Significance levels for plant dry matter (DM) and leaf area, root colonization by arbuscular mycorrhizal fungi (AMF) and shoot mineral (P, Na, K, Fe, Cu, Zn) contents in two tomato cul-

vars (C) grown at different salinity levels (salt) and inoculated or not with AMF. NS Not significant

Trait	Salt level	AMF status	Cultivar (C)	Salt×AMF	Salt×C	AMF×C	Salt×AMF×C
Shoot DM	**	**	**	**	NS	NS	NS
Root DM	**	**	NS	**	NS	NS	NS
Leaf area	**	**	**	**	NS	NS	NS
AMF colonization	**	**	**	**	NS	**	NS
P content	**	**	**	**	NS	NS	NS
K content	**	**	**	NS	NS	NS	NS
Na content	**	NS	NS	NS	NS	NS	NS
Cu content	**	**	NS	NS	NS	NS	NS
Fe content	**	**	*	*	NS	NS	NS
Zn content	**	**	NS	NS	NS	NS	NS

* Significant at *P*≤0.05

** Significant at *P*≤0.01

Table 2 Root AMF colonization (%), shoot and root dry matter yields (g per plant) and leaf area (cm² per plant) of nonmycorrhizal (*NonAMF*) and mycorrhizal (*AMF*) tomato cultivars grown at different salinity levels. Different letters in each column indicate significant differences at $P < 0.05$ according to LSD

Salt level dS m ⁻¹	AMF status	Cultivar	AMF colonization	Dry matter		Leaf area
				Shoot	Root	
1.4	NonAMF	Pello	0.0 f	4.62 b	0.45 b	317 b
		Marriha	0.0 f	4.30 b	0.42 b	286 c
	AMF	Pello	51.6 a	5.61 a	0.86 a	479 a
		Marriha	47.3 b	5.20 a	0.87 a	469 a
4.9	NonAMF	Pello	0.0 f	3.19 d	0.31 bc	171 f
		Marriha	0.0 f	2.43 e	0.31 bc	139 g
	AMF	Pello	38.9 c	4.19 bc	0.42 b	250 d
		Marriha	36.9 cd	3.83 c	0.34 b	218 e
7.1	NonAMF	Pello	0.0 f	1.63 f	0.09 c	78 hi
		Marriha	0.0 f	1.14 g	0.06 c	58 i
	AMF	Pello	33.4 d	1.92 f	0.28 bc	101 h
		Marriha	27.0 e	1.81 f	0.14 c	81 hi

Table 3 Shoot contents (mg per plant) of P, K, and Na in nonmycorrhizal (*NonAMF*) and mycorrhizal (*AMF*) tomato cultivars grown at different salinity levels. Different letters in each column indicate significant differences at $P < 0.05$ according to LSD

Salt level dS m ⁻¹	AMF status	Cultivar	Shoot content		
			P	K	Na
1.4	NonAMF	Pello	4.42 d	175 bc	17.3 c
		Marriha	3.85 d	158 cd	17.3 c
	AMF	Pello	8.86 a	233 a	17.4 c
		Marriha	7.71 b	197 b	17.5 c
4.9	NonAMF	Pello	2.27 e	103 e	76.2 a
		Marriha	1.43 f	66 f	72.8 ab
	AMF	Pello	5.95 c	144 cd	67.1 ab
		Marriha	5.24 c	129 de	60.7 b
7.1	NonAMF	Pello	0.94 fg	38 fg	68.7 ab
		Marriha	0.51 g	23 g	67.1 ab
	AMF	Pello	1.66 ef	49 fg	62.5 ab
		Marriha	1.35 f	43 fg	61.1 b

Table 4 Shoot contents (µg per plant) of Cu, Fe, and Zn in nonmycorrhizal (*NonAMF*) and mycorrhizal (*AMF*) tomato cultivars grown at different salinity levels. Different letters in each column indicate significant differences at $P < 0.05$ according to LSD

Salt level dS m ⁻¹	AMF status	Cultivar	Shoot content		
			Cu	Fe	Zn
1.4	NonAMF	Pello	55.0 bc	634 b	205 b
		Marriha	49.9 c	571 bc	188 bc
	AMF	Pello	87.5 a	1041 a	307 a
		Marriha	72.9 ab	932 a	268 a
4.9	NonAMF	Pello	21.6 d	420 cd	92 de
		Marriha	12.0 d	315 d	67 ef
	AMF	Pello	51.2 c	637 b	142 cd
		Marriha	46.3 c	569 bc	126 d
7.1	NonAMF	Pello	7.8 d	181 de	40 ef
		Marriha	4.0 d	126 e	26 f
	AMF	Pello	19.9 d	281 de	61 ef
		Marriha	14.4 d	259 de	57 ef

cultivar interaction was significant only for AMF colonization (Table 1).

No AMF colonization was noted in roots of control plants. Tomato plants grown in nonsaline soil had relatively high AMF root colonization, which decreased as soil salinity increased (Table 2). Under the conditions nonsaline (1.4 dS m⁻¹) and high salt (7.1 dS m⁻¹) but not moderate salt (4.9 dS m⁻¹), the roots of the salt-tolerant cultivar Pello showed a significantly higher AMF colonization than the roots of the salt-sensitive cultivar Marriha (Table 2).

Tomato shoot and root DM and leaf area were generally higher for mycorrhizal than for nonmycorrhizal plants (Table 2). However, AMF inoculation had no significant effects on either shoot DM for Pello or leaf area for both cultivars at the high salinity treatment. Moreover, similar root DM values were noted at medium and high salinity for both mycorrhizal and nonmycorrhizal plants of both cultivars (Table 2). Shoot and root DM and leaf area declined in both mycorrhizal and nonmycorrhizal plants as soil salinity increased (Table 2). Pello had significantly higher shoot DM than Mar-

riha only in nonmycorrhizal plants at the medium and high salinity levels. Leaf area of Pello was higher than Marriha for nonmycorrhizal plants in the nonsaline treatment and for both mycorrhizal and nonmycorrhizal plants in the medium salinity treatment (Table 2). There were no significant differences between cultivars in root DM due to AMF inoculation at any salinity level (Table 2).

Shoot P contents were generally higher in mycorrhizal than nonmycorrhizal tomato plants of both cultivars regardless of salinity level (Table 3). However, no significant differences were noted in shoot P content between mycorrhizal and nonmycorrhizal plants of Pello at the high salinity level. Shoot P content decreased with increasing soil salinity in both mycorrhizal and nonmycorrhizal plants (Table 3). Differences in P content between cultivars due to AMF inoculation were noted only under nonsaline conditions, when Pello had higher shoot P contents than Marriha. However, Pello shoot P contents were also higher than Marriha in nonmycorrhizal plants at the moderate salinity level, suggesting a genotypic difference between the cultivars.

Table 5 Percent change in shoot dry matter (DM) yield and nutrient contents due to of mycorrhizal colonization of two tomato cultivars grown at different salinity levels. Shoot DM = $DM_{AMF} - DM_{nonAMF} \times 100 / DM_{nonAMF}$. Nutrient content (NC) increase/decrease = $NC_{AMF} - NC_{nonAMF} \times 100 / NC_{nonAMF}$

Salt level dS m ⁻¹	Cultivar	Shoot DM	Nutrient content					
			P	K	Na	Cu	Fe	Zn
1.4	Pello	22	100	33	1	59	64	50
	Marriha	21	100	25	1	46	63	43
4.9	Pello	31	162	40	-12	137	52	54
	Marriha	58	266	95	-17	286	81	88
7.1	Pello	18	77	29	-9	155	55	53
	Marriha	59	165	87	-9	260	106	119

Shoot K contents were higher in mycorrhizal than nonmycorrhizal plants for both cultivars in the nonsaline and medium salinity treatments (Table 3). Shoot K content decreased as soil salinity increased. Pello had higher shoot K contents than Marriha in mycorrhizal plants in the nonsaline treatment and in nonmycorrhizal plants at the medium salinity level (Table 3).

Shoot Na contents of both mycorrhizal and nonmycorrhizal plants increased significantly as soil salinity increased from the nonsaline to medium salinity levels (Table 3). No significant differences between cultivars due to AMF inoculation were noted for Na content regardless of salinity level. However, Na contents of nonmycorrhizal Marriha and Pello were similar at all salinity levels (Table 3).

Shoot contents of Cu, Fe and Zn were apparently higher for mycorrhizal than nonmycorrhizal plants, but the differences were not significant for Cu and Fe at the high salinity level or for Zn in Pello at medium salinity and both cultivars at the high salinity level (Table 4). Shoot contents of Cu, Fe and Zn decreased as soil salinity increased. No significant differences between cultivars were noted for shoot contents of Cu, Fe and Zn in either mycorrhizal or nonmycorrhizal plants.

The overall effects of AMF colonization on shoot DM yield and mineral nutrient acquisition of saline and nonsaline plants are summarized in Table 5. The enhancement in shoot DM due to AMF inoculation was 22 and 21% under control, 31 and 58% under medium, and 18 and 59% under high salinity level for Pello and Marriha, respectively. The enhancement in P, K, Zn, Cu, and Fe acquisition due to AMF inoculation was more pronounced in Marriha than in Pello at the medium and high salinity levels (Table 5).

Discussion

Plants inoculated with *Glomus mosseae* had significantly higher shoot and root DM yields and leaf area than nonmycorrhizal plants under medium salinity (4.9 dS m⁻¹). This was also true for shoot DM and leaf area and for root DM under nonsaline conditions. Enhanced growth of mycorrhizal plants grown in saline environments has been related partly to mycorrhizal-mediated enhancement of host plant P nutrition (Al-Karaki 2000b; Hirrel and Gerdemann 1980; Pond et al. 1984; Poss et al. 1985). In this present study, mycorrhizal plants had high-

er P contents than nonmycorrhizal plants at all salinity levels, except for Pello plants at the high salinity level. This may have occurred because of reduced P transport and uptake under these conditions. Plants grown under high salinity may have lower H₂PO₄⁻ activity (preferred phosphate ion for plant uptake) than under low salinity conditions (Al-Karaki 1997; Sentenac and Grignon 1985). Reduced uptake of P by mycorrhizal plants grown at high salinity levels has been reported by other workers (Al-Karaki 2000b; Hirrel and Gerdemann 1980; Pond et al. 1984; Poss et al. 1985).

Many studies have indicated that AMF contributes to plant growth via enhancement of mineral nutrient uptake, especially of immobile soil nutrients (P, Cu, Zn) (Al-Karaki and Al-Raddad 1997; Al-Karaki and Clark 1998; Bethlenfalvay et al. 1988; Marshner and Dell 1994). In this present study, mycorrhizal tomato plants had higher shoot P contents than nonmycorrhizal plants regardless of salinity level. Higher Fe and Cu contents in mycorrhizal than nonmycorrhizal plants were also noted. The higher mineral nutrient acquisition by mycorrhizal than by nonmycorrhizal plants likely occurred because of increased availability or increased transport (absorption and/or translocation) by AMF hyphae. Enhanced acquisition of P, Cu, and Fe by mycorrhizal plants has been reported (Al-Karaki and Al-Raddad 1997; Al-Karaki and Clark 1998; Marshner and Dell 1994; Trimble and Knowles 1995). However, AMF root colonization had little effect on shoot K content in plants grown at the medium and high salinity levels. Poss et al. (1985) reported that K uptake was little affected by AMF root colonization in tomatoes grown under saline conditions.

The lack of change in Na content with AMF treatment may be explained by the dilution effects of plant growth enhancement caused by AMF colonization. Similar results were reported by other researchers (Al-Karaki 2000b; Bernstein et al. 1974; Jarrell and Beverly 1981).

Plant growth response to AMF inoculation was higher in Marriha than in Pello under saline but not under nonsaline conditions, even though AMF colonization was higher in Pello than in Marriha. However, enhanced growth may not be related to degree of AMF root colonization in some plants (Al-Karaki and Clark 1998).

The host plant species, cultivar and growing conditions can influence the effects of AMF symbiosis on nutrient acquisition (Al-Karaki 2000b; Al-Karaki and Al-Raddad 1997; Al-Karaki and Clark 1998; Mercy et al. 1990). From the results of this present study, it ap-

pears that AMF colonization was more effective in increasing P, Cu, Fe and Zn acquisition under saline conditions for the salt-sensitive cultivar Marriha than the salt-tolerant cultivar Pello. Higher nutrient acquisition in response to AMF colonization was suggested to be a plant strategy for salt-stress tolerance (Hirrel and Gerdemann 1980; Pond et al. 1984; Poss et al. 1985).

Despite the paucity of significant differences between mycorrhizal Pello and Marriha plants in the different parameters measured, it is clear that Marriha plants benefited more from mycorrhizal symbiosis than Pello plants under increased salinity. This is further confirmation that mycorrhizal symbiosis is especially beneficial for plant growth under adverse conditions such as soil salinity.

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