Soil & Tillage Research 103 (2009) 282–290

Contents lists available at ScienceDirect

Soil & Tillage Research

journal homepage: www.elsevier.com/locate/still

Effects of soil compaction and arbuscular mycorrhiza on corn (*Zea mays* L.) nutrient uptake

M. Miransari [a,*], H.A. Bahrami [b], F. Rejali [c], M.J. Malakouti [b]

[a] Department of Soil Science, College of Agricultural Sciences, Shahed University, P.O. Box: 18151/159, Tehran, Iran
[b] Department of Soil Science, College of Agriculture, Tarbiat Modares University, Tehran, Iran
[c] Department of Soil Science, Soil and Water Research Institute, Tehran, Iran

ARTICLE INFO

Article history:
Received 7 July 2008
Received in revised form 10 October 2008
Accepted 19 October 2008

Keywords:
Arbuscular mycorrhiza
Corn (*Zea mays* L.) growth
Nutrient uptake
Soil compaction
Soil sterilization

ABSTRACT

Soil compaction is of great importance, due to its adverse effects on plant growth and the environment. Mechanical methods to control soil compaction may not be economically and environmentally friendly. Hence, we designed experiments to test the hypothesis that use of plant symbiotic fungi, arbuscular mycorrhiza (AM) may alleviate the stressful effects of soil compaction on corn (*Zea mays* L.) growth through enhancing nutrient uptake. AM continuously interact with other soil microorganisms and its original diversity may also be important in determining the ability of the fungi to cope with the stresses. Hence, the objectives were: (1) to determine the effects of soil compaction on corn nutrient uptake in unsterilized (S1) and sterilized (S2) soils, and (2) to determine if inoculation of corn with different species of AM with different origins can enhance corn nutrient uptake in a compacted soil. Using 2 kg weights, soils (from the field topsoil) of 10 kg pots were compacted at three and four levels (C1, C2, C3 and C4) (C1 = non-compacted control) in the first and second experiment, respectively. Corn (cv. 704) seeds were planted in each pot and were inoculated with different AM treatments including control (M1), Iranian *Glomus mosseae* (M2), Iranian *G. etunicatum* (M3), and Canadian *G. mosseae*, received from GINCO (Glomales *In Vitro* Collection), Canada (M4). Corn leaf nutrient uptake of N, P, K, Fe, Mn, Zn and Cu were determined. Higher levels of compaction reduced corn nutrient uptake, however different species of AM and soil sterilization significantly increased it. The highest increase in nutrient uptake was related to P (60%) and Fe (58%) due to treatment M4S2C3. Although it seems that M3 and M4 may be the most effective species on corn nutrient uptake in a compacted soil, M2 increased nutrient uptake under conditions (C3 and C4 in unsterilized soil) where the other species did not. Through increasing nutrient uptake AM can alleviate the stressful effects of soil compaction on corn growth.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Arbuscular mycorrhiza (AM) are able to be in beneficial symbiosis with plants and their genetic diversity and geographical distribution do not adversely affect this symbiosis (Burleigh et al., 2002). This indicates that different species of AM have the ability for adaptation to different conditions and being synergistic with indigenous soil microorganisms. In this symbiosis the fungi and the host plant provide each other with nutrients and necessary C, respectively (Hodge et al., 2001). The species and even the isolates of the same species may determine the formation and function of mycorrhiza (Smith and Smith, 1997; Smith et al., 2000).

The functional diversity of AM may be an important factor, determining the ability of the fungi to help the host plant tolerate the stressful conditions (Smith and Read, 1997). In addition, AM–plant combination and environmental conditions may determine the tendency of plant growth including enhanced growth, neutral and even parasitic relationship (Johnson et al., 1997).

Soil stresses such as compaction (a result of using agricultural machinery in the field) may adversely affect plant growth, through limiting root growth, resulting in decreased water and nutrient uptake. Although there is some data related to the effects of soil compaction on the growth of *Trifolium subterraneum* treated with AM (Nadian et al., 1996, 1997, 1998), however there is only one paper (Miransari et al., 2007) related to the effects of soil compaction on the growth of corn treated with AM.

* Corresponding author. Tel.: +98 21 51212469; fax: +98 21 5277512.
E-mail addresses: Miransari1@Gmail.Com, Miransari@Shahed.Ac.Ir (M. Miransari).

Abbreviations: S, soil; AM, arbuscular mycorrhiza; S1and S2, unsterilized and sterilized soils, respectively; C1, C2, C3 and C4, non-compacted control, first, second and third level of compaction, respectively; M1, M2, M3, and M4, control, Iranian *Glomus mosseae*, Iranian *G. etunicatum*, and Canadian *G. mosseae*, respectively.

0167-1987/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.still.2008.10.015

Both soil conditions and the interaction between roots and shoots, regarding functional and signal aspects, determine the growth of root tip. Parameters such as turgor pressure, yield threshold and the extend to which the cell wall grow determine root elongation (Munns and Cramer, 1996).

Due to the adverse effects of soil compaction on soil properties, and hence root growth, plant water and nutrients uptake is very much affected in a compacted soil. For example, in a compacted soil N uptake efficiency decreases due to increased N emission (Ruser et al., 2006). Soil macropores are subjected to reduction, compared with micropores, which increase in a compacted soil (Arvidsson, 1999). Compacting soil increases bulk density and soil resistance to penetrometer (Pereira et al., 2007).

AM enable the host plant to grow more efficiently under biotic and abiotic stressful conditions including drought (Subramanian and Charest, 1997; Porcel et al., 2003), salinity, heavy metal contamination (Rivera-Becerril et al., 2002), suboptimal root zone temperature (Liu et al., 2004) and soil compaction (Miransari et al., 2007, 2008), through a series of complex communications between the two partners (Harrier, 2001).

Since AM are able to grow beyond the depletion zones around the plant roots, they are able to increase the uptake of immobile nutrients such as P and also micronutrients, resulting in the enhanced growth of plants (Hodge et al., 2001). The extended network of AM enable the fungi to directly (Harrier, 2001) or indirectly, increase nutrient uptake in plants through improving soil structure (Rillig and Mummey, 2006). This is because soil structure affects many biological, physical and chemical properties of soil (Díaz-Zorita et al., 2002; Six et al., 2004).

AM isolates may differ in their ability to influence the stability of soil aggregates (Piotrowski et al., 2004; Enkhtuya and Vosatka, 2005). AM produces a glycoprotein called glomalin, attaching the soil particle together and forming the stable structures of aggregates (Wright and Upadhyaya, 1996; Rillig, 2004).

Under stress free conditions AM and bacteria are able to synergistically act and enhance plant growth through a series of mechanisms such as increased fungal germination and growth (Carpenter-Boggs et al., 1995) and enhanced permeability of root cells resulting in increased water and nutrient uptake (Artursson et al., 2006). But under stressful conditions the fungi and the bacteria may behave differently. To address this question we used both unsterilized and sterilized compacted soils.

Since there is not any data on the effects of AM on corn nutrient uptake in a compacted soil, we hypothesized that use of plant symbiotic fungi; AM may alleviate the stressful effects of soil compaction on corn (*Zea mays* L.) growth through enhancing nutrient uptake. AM interaction with the other soil microorganisms may also influence plant nutrients uptake under such conditions. The objectives were to: (1) determine the effect of soil compaction on corn nutrient uptake under both sterilized and unsterilized conditions, and (2) determine if inoculation of corn with different species of AM with different origins can enhance corn nutrient uptake in a compacted soil.

2. Materials and methods

2.1. Soil characteristics and measurements

Top soil layer (0–30 cm), a Xeric Haplocalcids (Banaei, 2000), of the Research field of Soil and Water Research Institute at Meshkin-Dasht, Karaj, Iran was air dried, sieved and transferred to 10 kg pots, measuring 20 cm × 20 cm. Using 20 kg cotton bags, half of it was sterilized at 121 °C and high vapor pressure for an hour using an autoclave (Toshihiro et al., 2004). Soil physical and chemical properties were determined before autoclaving. Nitrogen was measured using Kjeldahl method (Nelson and Sommers, 1973). Phosphorous was determined by sodium bicarbonate extraction (Olsen, 1954). Potassium was measured using flame photometer (emission spectrophotometry) (Knudsen et al., 1982). Iron, manganese, zinc and copper were determined by diethyenetriaminepentaacetic acid (DTPA) method (Baker and Amachar, 1982) using atomic absorption spectrometer (Model PerkinElmer 3110).

Acidity of a saturated paste and electrical conductivity of a saturated extract (Rhoades, 1982) were also measured. Organic carbon was measured using wet oxidation (Nelson and Sommers, 1982). The soil texture was determined by the hydrometric method (Gee and Bauder, 1986). Soil moisture at field capacity (−0.033 atm) and permanent wilting point (−15 atm) (Rhoades, 1982) were determined using pressure plates apparatus. Soil data analyses are presented by Miransari et al. (2007).

In the second experiment we used a soil with a higher rate of clay, and hence, higher saturation percentage, to compact the soil at a higher level (Miransari et al., 2007, 2008). Although, according to literature, it may be a good idea to divide the soil into layers and then compact them, since the field soils is usually compacted non-homogenously, we compacted the complete pot soil at once (Miransari et al., 2007, 2008), producing a slight compaction gradient in the soil profile.

Although, the role of soil water is of significance, compacting wet soils may create very compacted soils, which are very much suppressing to the growth of root, and hence, plant growth. The compaction levels were selected according to Barzegar et al. (2000) and also according to our own testing, meaning that the 20-time compaction was the highest level we could create in the pots (Miransari et al., 2007, 2008).

Soil moistures at field capacity and permanent wilting point were 19.4 and 11%, respectively, and soil textures were loam and clay loam for the first and second experiment, respectively. Compaction levels were imposed using 2 kg weights, with a little less diameter than the pots diameter, covering the soil surface in the pots. The weights were released from a 20-cm height, 4 (C2) and 12 times (C3) in the first experiment and in the second experiment a 20 times compaction (C4) level was also included. Both experiments included a non-compacted soil as a control (C1).

In the standard Proctor procedure a 2.5-kg rammer is released from a 30.5-cm height producing 7.5 J energy and 7.3 kJ/m^3 compactive efforts each time (American Society for Testing Materials, 2000; Barzegar et al., 2000). In our experiments using a 2-kg weight, released from a 20-cm height, produced 3.92 J energy each time according to the "$e = mgh$" formula. The bulk density of pot soils was also measured (Miransari et al., 2007).

2.2. Experimental method

Experimental designs were 2 × 3 × 4 and 2 × 4 × 4 factorials on the basis of completely randomized block in the first and second experiment, respectively. The duration of both experiments lasted for 4 months. The first experiment was conducted in a growth chamber in which plants received 14 h of florescent light, with an average temperature of 24 °C, and since more space was required for the second experiment the second experiment was conducted in a greenhouse, with the average temperature of 27 °C, in which plants received natural light. Treatments included unsterilized (S1) and sterilized (S2) soils, three levels of soil compaction with bulk densities of 1.18, 1.29 and 1.40 g cm^{-3} in the first experiment and four levels of soil compaction with bulk densities of 1.2, 1.27, 1.34 and 1.51 g cm^{-3} in the second experiment, treated with three mycorrhizal species and a non-mycorrhizal control. Therefore, there were 24 and 32 treatments in four replicates in the first and second experiment, respectively.

Four seeds of corn (cv. 704, a very common cultivar in Iran) were planted in each pot and were thinned to one plant after germination. At seeding mycorrhizal species that had already been produced (Feldmann and Idczak, 1992) on sorghum roots in sterilized sand in a 4-month period were added underneath the seeds as much as 1.6 g including 80 ± 10 active organs (Sood, 2003; Toshihiro et al., 2004). Mycorrhizal treatments included control (without mycorrhiza) (M1), *Glomus mosseae* (M2) and *G. etunicatum* (M3) both isolated from the Iranian soils, and *G. mosseae* (M4), received from GINCO (Glomales *In Vitro* Collection), Canada. These species were selected based on their high inoculating potential (Miransari et al., 2007, 2008).

Before conducting the experiments the total active organs of mycorrhizal fungi in inoculums were determined using the Most Probable Number (MPN) method (Feldmann and Idczak, 1992). For this purpose AM dilutions of 0, 0.1, 0.01 and 0.001 were used in 70 cm^3 tubes containing sterilized sand. Sorghum seeds were planted in the tubes and harvested after 1 month. Roots were stained to observe AM inoculation at the different dilutions and using statistical tables the fungi active organs were determined (Mahaveer et al., 2000).

Pots were watered with sufficient water to fill the soil to its maximum water holding capacity and the excess was allowed to drain out. During the growing period and according to soil testing 1.48 g of urea, 0.46 g of triple super phosphate and 1.32 g of potassium sulfate were added twice to each pot.

2.3. Measurements of nutrient uptake

At tasseling corn leaf was harvested and analyzed for nutrient uptake of N, P, K, Fe, Mn, Zn, and Cu. Nitrogen was measured using Kjeldahl method (Nelson and Sommers, 1973). Phosphorous was determined, spectrophotometrically, by acetic acid extraction (Prokopy, 1995). Potassium was measured using acetic acid extraction and flame photometer (emission spectrophotometery) (Johnson and Ulrich, 1959; Knudsen et al., 1982). Iron, manganese, zinc and copper were determined by diethylenetriaminepentaacetic acid (DTPA) method (Lindsay and Norvell, 1978; Baker and Amachar, 1982) using atomic absorption spectrometer (Model PerkinElmer 3110).

Nutrient uptake of N, P and K was calculated using the formula: $(A \times B)/100$ in which A is the leaf N, P, or K percentage and B is the leaf dry weight. For Fe, Mn, Zn and Cu their leaf uptake was calculated using the formula: $(A_1 \times B_1)/1000$ in which A_1 is mg/kg of leaf Fe, Mn, Zn and Cu and B_1 is the leaf dry weight.

2.4. Statistical analysis

Using SAS (Sas Institute Inc, 1988) data were analyzed and the significant differences between different treatments were determined. Using GLM method and the least significant difference (LSD) test the means were compared (Steel and Torrie, 1980). Contrast comparisons were made to compare the effects of different species of AM on nutrient uptake with control.

3. Results

Soil sterilization significantly enhanced nutrient uptake of mycorrhizal corn in both experiments (Tables 1, 3, 4, 5 and 6). AM increased N uptake at both experiments, and significantly for M4 in the second experiment (Tables 1, 3 and 5). The soil resistance values were also determined (Miransari et al., 2007), indicating that with increased compaction soil resistance also increased. AM was also effective to increase P uptake at different levels of compaction in both experiments in both soils. However, interestingly at the highest level of compaction (C4) in S1 in the second experiment AM did not increase N and P uptake compared with control, while in S2 they still effectively resulted in higher N and P uptake at C4. This is also confirmed by the statistically significant effect of soil on N and P uptake and also the tendency of the interaction effects of S × C in both experiments (Tables 3 and 5).

The highest increase in N uptake was related to treatment S2C2M4 in the second experiment in which N uptake was increased by 25% in comparison with control (Table 5). The effect of M3 on P uptake was significant in S1 in the first experiment (Table 2). Treatment S2C3M4 in the second experiment resulted in the highest P uptake (60%) in comparison with control (Table 5).

M3 significantly affected K uptake (Tables 3 and 5). The highest increase in K uptake was related to treatment S2C3M3 (41%), compared with control (Table 5). K uptake increased due to AM at different levels of compaction. At S1C4 in the second experiment only M2 was able to enhance K uptake while at S2C4 all species of AM resulted in higher K uptake, as it is also clear from the significant effect of soil on K uptake (Table 5). The increased leaf dry weight in mycorrhizal plants also verifies the alleviating effects of AM on corn growth, in a compacted soil, through enhancing nutrient uptake (Tables 3 and 5).

In both experiments AM resulted in greater Fe uptake at different levels of soil compaction. Although at S1C4 in the second experiment AM species did not increase Fe uptake, at S2C4 they were able to increase Fe uptake, which is also evident from the statistically significant effects of soil ($P = 0.001$) and the tendency of the interaction of S × C ($P = 0.1$) (Table 6). The effect of M3 on Fe uptake at S1 soil in the first experiment was significant (Table 1) and the highest increase in Fe uptake was related to treatment S2C3M4 (58%) (Table 6).

Higher Mn and Zn uptake was resulted due to AM at different levels of soil compaction in both experiments. AM behaved differently in S1 and S2 soils, and only M2 was able to increase Mn uptake at S1C4. Soil sterilization resulted in enhanced Mn uptake by M3 and M4 in comparison with control at C4. The statistical analysis also approved this different behavior by indicating the significant effect of soil and the tendency of the interaction effect of S × C ($P = 0.16$) (Table 6). M3 significantly increased Mn uptake in the first experiment (Table 1). The highest increase in Mn uptake was related to treatment S2C3M4 (35%) in comparison with control (Table 6).

Although AM resulted in higher Zn uptake at different levels of compaction, corn Zn uptake was very sensitive to higher rates of compaction (C3 and C4) in unsterilized soil. Soil sterilization could compensate for the decreased uptake as all species of AM increased corn Zn uptake in comparison with control (Tables 4 and 6). The significant effect of soil on Zn uptake also verifies this case (Table 6). M4 resulted in the highest Zn uptake in S2 in the second experiment (Table 1). A maximum increase of 48% in Zn uptake was resulted due to treatment S2C1M3 in the second experiment, followed by S2C4M2 (Table 6).

AM increased Cu uptake at different levels of compaction. Unsterilized soil decreased Cu uptake at C4 in comparison with control, while in the sterilized soil AM species adsorbed higher rates of Cu at C4 (Table 6). Statistical analysis also indicated the significant effect of soil and also the tendency of the two and three way interaction effects of S × C ($P = 0.16$) and S × C × M ($P = 0.12$) on Cu uptake, respectively (Tables 4 and 6). M3 indicated a tendency enhancing Cu uptake in the first experiment (Table 1). The highest increase in Cu uptake was related to treatment S1C2M3 (54%) in the second experiment in comparison with control (Table 6).

Table 1
Mean comparisons of nutrient uptake by different species of arbuscular mycorrhiza in unsterilized and sterilized soils and at all levels of compaction in the first (n = 10–12) and second experiment (n = 14–16).

AM	N (mg/plant)	P (mg/plant)	K (mg/plant)	Fe (mg/plant)	Mn (mg/plant)	Zn (mg/plant)	Cu (mg/plant)
First experiment (S1)							
M1	92a	8.1b	96a	0.294b	0.252bc	0.207a	0.029a
M2	88a	8.5ab	105a	0.306ab	0.293ab	0.216a	0.032a
M3	87a	9.2a	107a	0.345a	0.300a	0.232a	0.033a
M4	88a	8.4ab	98a	0.291b	0.238c	0.183a	0.030a
Mean	89	8.6	102	0.309	0.271	0.210	0.031
LSD (α = 0.05)	11	1.1	12.0	0.049	0.049	0.057	0.006
First experiment (S2)							
M1	93a	9.4a	100a	0.318a	0.353a	0.186a	0.031a
M2	90a	8.7a	99a	0.309a	0.349a	0.175a	0.031a
M3	100a	9.9a	112a	0.335a	0.348a	0.190a	0.033a
M4	101a	10.2a	112a	0.336a	0.371a	0.185a	0.035a
Mean	96	9.6	106	0.325	0.355	0.159	0.033
LSD (α = 0.05)	15.5	1.5	15.9	0.072	0.079	0.051	0.006
Second experiment (S1)							
M1	164a	11.4a	167a	0.708a	0.533a	0.199a	0.066a
M2	163a	12.4a	168a	0.640a	0.504a	0.186a	0.061a
M3	165a	13.1a	174a	0.669a	0.496a	0.197a	0.073a
M4	170a	12.3a	167a	0.731a	0.490a	0.183a	0.067a
Mean	166	12.3	169	0.687	0.506	0.191	0.067
LSD (α = 0.05)	29	2.7	35	0.161	0.113	0.44	0.014
Second experiment (S2)							
M1	188a	12.8a	190a	0.740a	0.708a	0.217a	0.075a
M2	218a	13.7a	209a	0.849a	0.835a	0.264a	0.085a
M3	210a	13.3a	199a	0.848a	0.752a	0.257a	0.080a
M4	228a	14.3a	222a	0.892a	0.850a	0.278a	0.085a
Mean	211	13.5	205	832	786	254	0.081
LSD (α = 0.05)	45	3.4	41	0.203	0.192	0.067	0.018

S1: unsterilized soil, S2: sterilized soil. Values within the same column followed by different letter(s) are statistically different using protected least significant difference (LSD) test. M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum* (Iranian), M4: *G. mosseae* (Canadian).

4. Discussion

4.1. AM, soil sterilization and nutrient uptake

Soil sterilization significantly enhanced corn nutrient uptake indicating that corn response is different to AM symbiosis in S1 and S2 soils under compacted conditions (Miransari et al., 2007, 2008), which is also verified by the tendency of interaction between S × C. This may be attributed to the existing competition between AM and other soil microorganisms, which is intensified with increased compaction.

At the highest levels of compaction in the S1 soil the competition between AM and other soil microorganisms for soil resources especially oxygen increases. This may result in changing the nature of the relationship between AM and the host plant from symbiotic to parasitic (Standish et al., 2007), as it is clear from the data at the highest level of compaction AM inoculation reduced nutrient uptake in the S1 soil (Johnson et al., 1997). This may even more clarify the role of AM in decreasing the stressful effect of compaction stress on nutrient uptake, because AM were able to alleviate the reduced nutrient uptake in the S2 soil, especially at the highest levels of compaction.

Table 2
Mean comparisons of nutrient uptake by different species of arbuscular mycorrhiza at all levels of compaction in the first (n = 20–22) and second experiment (n = 27–30).

AM	N (mg/plant)	P (mg/plant)	K (mg/plant)	Fe (mg/plant)	Mn (mg/plant)	Zn (mg/plant)	Cu (mg/plant)
First experiment							
M1	92a	8.8ab	98b	0.307a	0.304a	0.196a	0.030a
M2	89a	8.6b	102ab	0.308a	0.324a	0.193a	0.031a
M3	94a	9.6a	110a	0.339a	0.327a	0.209a	0.033a
M4	94a	9.3ab	105ab	0.312a	0.301a	0.184a	0.032a
LSD (α = 0.05)	9	0.9	10	0.044	0.045	0.041	0.004
Second experiment							
M1	176a	12.1a	178a	0.723a	0.617a	0.207a	0.070a
M2	191a	13.1a	189a	0.748a	0.675a	0.227a	0.074a
M3	187a	13.2a	186a	0.759a	0.624a	0.227a	0.076a
M4	198a	13.3a	193a	0.809a	0.664a	0.229a	0.076a
LSD (α = 0.05)	25	2.0	26	0.122	0.113	0.037	0.011

M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum* (Iranian), M4: *G. mosseae* (Canadian). Values within the same column followed by different letter(s) are statistically different using protected least significant difference (LSD) test.

Table 3
The effects of arbuscular mycorrhiza in unsterilized and sterilized compacted soils on N, P, and K uptake in corn (*Zea mays* L.), in the first experiment; means (S.E., $n = 3–4$).

Level of compaction	AM	Leaf dry weight (g)	N (mg/plant)	P (mg/plant)	K (mg/plant)
Unsterilized soil					
C1	M1	3.0 (0.9)	85.0 (22)	7.4 (1.6)bc	91.0 (20)
	M2	3.0 (0.5)	81.0 (15)	7.9 (1.3)abc	101.0 (18)
	M3	3.2 (0.4)	88.0 (11)	8.8 (1)abc	106.0 (13)
	M4	2.8 (0.5)	77.0 (7)	7 (0.8)c	92.0 (16)
C2	M1	3.4 (0.6)	103.0 (23)	8.5 (1)abc	102.0 (7)
	M2	3.1 (0.5)	90.0 (8)	8.7 (1.2)abc	105.0 (22)
	M3	2.9 (1.1)	78.0 (25)	9.5 (0.9)a	108.0 (10)
	M4	3.1 (0.4)	88.0 (5)	9 (1)ab	99.0 (10)
C3	M1	3.0 (0.2)	89.0 (4)	8.7 (0.7)abc	97.0 (11)
	M2	3.2 (0.3)	95.0 (7)	9 (1.6)ab	111.0 (13)
	M3	3.5 (0.5)	100.0 (15)	9.3 (1.5)ab	106.0 (21)
	M4	3.4 (0.3)	99.0 (6)	9.4 (1.1)a	104.0 (12)
Sterilized soil					
C1	M1	3.2 (0.6)	92.0 (15)	9.3 (2)	96 (21)ab
	M2	3.0 (1.2)	82.0 (29)	7.9 (2.4)	89 (31)b
	M3	3.6 (0.6)	104.0 (23)	10.2 (1.5)	110 (15)ab
	M4	3.7 (0.2)	106.0 (5)	10.4 (0.6)	116 (6)ab
C2	M1	3.1 (0.7)	95.0 (24)	9.8 (2.4)	100 (30)ab
	M2	3.4 (0.1)	97.0 (7)	9.7 (1.6)	111 (18)ab
	M3	3.5 (0.7)	96.0 (15)	10.1 (1.7)	123 (25)a
	M4	3.5 (0.1)	98.0 (3)	9.8 (0.6)	112 (14)ab
C3	M1	3.2 (0.8)	93.0 (23)	9.3 (2.9)	104 (30)ab
	M2	3.2 (1.0)	92.0 (24)	8.7 (2.3)	97 (27)ab
	M3	3.5 (0.3)	99.0 (11)	9.2 (1)	101 (13)ab
	M4	3.6 (0.4)	100.0 (10)	10.3 (1.4)	110 (15)ab
Model		n.s.	n.s.	$P = 0.08$	**
S		$P = 0.065$	**	**	n.s.
C		n.s.	n.s.	$P = 0.10$	n.s.
M		n.s.	n.s.	n.s.	n.s.
C × M		n.s.	n.s.	n.s.	n.s.
S × M		n.s.	n.s.	n.s.	n.s.
S × C		n.s.	$P = 0.16$	$P = 0.12$	$P = 0.17$
S × C × M		n.s.	n.s.	n.s.	n.s.
M1 vs. M2		n.s.	n.s.	n.s.	n.s.
M1 vs. M3		n.s.	n.s.	n.s.	*
M1 vs. M4		n.s.	n.s.	n.s.	n.s.
LSD1 ($\alpha = 0.05$)		0.8	23	1.9	25
LSD2 ($\alpha = 0.05$)		0.9	27	2.9	34

C1: control, C2: 4 times compaction, C3: 12 times compaction. M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum* (Iranian), M4: *G. mosseae* (Canadian). n.s.: not significant. Values within the same column followed by different letter(s) are statistically different using protected least significant difference (LSD) test for unsterilized (LSD1) and sterilized (LSD2) soils. ***Significant at 0.01 level of probability.
* Significant at 0.1 level of probability.
** Significant at 0.05 level of probability.

In addition, the increased plant growth in a sterilized soil is related to the enhanced root growth, increased nutrients uptake (increasing photosynthesis as a result of higher leaf area and higher concentrations of N and P in the plant shoot), or both and the inhibition of soil pathogens as the process of soil sterilization can also affect the microbiological properties of the sterilized soil (Troelstra et al., 2001). Inoculation with AM under stress can also further contribute to such enhancement (Miransari et al., 2007, 2008) by increasing plant water and nutrients uptake.

Interestingly, is has been shown that sterilization increase plant P uptake (30–57% higher than P uptake in unsterilized sand) more effectively, than N and K uptake (Troelstra et al., 2001), which is in agreement with our results. This is also another indication that AM fungi can be more effective under sterilized conditions because N and P uptake were also increased by AM at the highest soil compaction (C4) in the second experiment. Although AM have the ability to alleviate the stress of soil pathogens under unsterilized conditions, however the suggested findings indicate that sterilized conditions are more ideal for optimal AM activities.

4.2. The effect of soil compaction on nutrient uptake and plant growth and the role of AM

Soil compaction resulted in decreased N and P uptake (Kristoffersen and Riley, 2005; Barzegar et al., 2006) at the highest levels of compaction (C3 and C4) and AM were able to alleviate the stress in S2 soil (Table 5). Increased denitrification rates and lower availability of oxygen and hence, decreased root activity may be the main reasons for diminished N uptake in compacted soils. Similar to our results other scientists have also found that AM are able to enhance plant nutrients uptake under non-stress (Khalil et al., 1994; Tobar et al., 1994; Marschner and Dell, 1994; Liu et al., 2000; Hodge et al., 2001; Tanaka and Yano, 2005) and stress conditions such as drought (Subramanian and Charest, 1997) and salinity (Tian et al., 2004; Al-Karaki, 2006; Daei et al., in press).

Shoot growth is usually more affected than root growth in a compacted soil (Munns and Cramer, 1996; Pardo et al., 2000; Miransari et al., 2004, 2006, 2007, 2008). This is because when N uptake is reduced, less cytokinin are produced in the roots and sent to the shoots. Lower amounts of cytokinin result in the reduction of cell division in the shoots while in the roots this may lead to neutralizing the suppressing effect of cytokinin on cell growth and development. Also transfer of more sucrose to the roots enhances root growth under these conditions (Van der Werf and Nagel, 1996).

Under compacted conditions shorter and wider cortical cells are produced. The root cap both protects the meristem and determines the interaction between the soil and the root at the time of root growth indicating that the pressure on a root cap decreases root growth in a compacted soil. One of the reasons is that root cap reduces the friction coefficient between the root and soil at the time of root growth (Amzallag, 1999). This may also be the reason for higher soil resistance in a dry soil compared with a wet soil (Bengough et al., 2006). The meristematic parts in root tips may determine the root architecture and, hence the volume of soil available to the plant root for uptake, and also for the production of plant signals (Harrison, 2005). This part of the root is very much affected in a compacted soil.

Although the main roles of the plant roots are: to strongly maintain the plant in the soil, to adsorb water and nutrients from the soil, and to interact with the soil microorganisms, they are also able to influence the soil structure through these five mechanisms: (1) soil penetration by roots, (2) soil water fluctuations, (3) rhizodeposition, (4) root degradation, and (5) root trapping of soil particles (Rillig and Mummey, 2006). By affecting plant growth (root/shoot ratio) AM may influence these activities (Miransari et al., 2007, 2008).

The results of the present study, which is in accordance with the results of our other research work (Miransari et al., unpublished data) indicates that one of the main reasons for such enhancing effects of AM on corn and wheat growth under compaction (Miransari et al., 2007, 2008) is increased nutrient uptake. Due to their extensive network of hypha and also increasing the volume of soil explored by the plant roots AM are able to enhance water and nutrient uptake in plants. In comparison with even the finest roots hairs ($\geq$10 μm in diameter) the hypha of AM are much finer (3–4 μm) enabling them to penetrate very fine pores (Bolan, 1991; Jakobsen, 1995), this may greatly help plant roots in compacted soils where the pore size substantially reduces. Also under the stress of soil compaction AM increases root growth more highly

Table 4
The effects of arbuscular mycorrhiza in unsterilized and sterilized compacted soils on Fe, Mn, Zn, and Cu uptake in corn (*Zea mays* L.), in the first experiment; means (S.E., $n = 3–4$).

Level of compaction	AM	Fe (mg/plant)	Mn (mg/plant)	Zn (mg/plant)	Cu (mg/plant)
Unsterilized soil					
C1	M1	0.299 (0.14)	0.250 (0.02)bcde	0.196 (0.15)	0.029 (0.007)
	M2	0.303 (0.07)	0.328 (0.03)a	0.241 (0.16)	0.031 (0.008)
	M3	0.351 (0.09)	0.297 (0.07)abcd	0.244 (0.07)	0.034 (0.009)
	M4	0.243 (0.03)	0.241 (0.05)cde	0.187 (0.09)	0.025 (0.003)
C2	M1	0.297 (0.05)	0.281 (0.05)abcd	0.268 (0.08)	0.030 (0.008)
	M2	0.300 (0.04)	0.227 (0.06)de	0.171 (0.07)	0.029 (0.003)
	M3	0.331 (0.03)	0.284 (0.05)abcd	0.229 (0.07)	0.032 (0.001)
	M4	0.280 (0.04)	0.199 (0.07)e	0.154 (0.05)	0.033 (0.011)
C3	M1	0.284 (0.02)	0.223 (0.03)de	0.162 (0.04)	0.028 (0.003)
	M2	0.316 (0.03)	0.314 (0.01)abc	0.226 0.04)	0.035 (0.010)
	M3	0.352 (0.03)	0.320 (0.06)ab	0.223 (0.10)	0.032 (0.004)
	M4	0.347 (0.05)	0.263 (0.05)abcde	0.200 (0.05)	0.034 (0.004)
Sterilized soil					
C1	M1	0.310 (0.07)	0.351 (0.1)	0.172 (0.04)	0.033 (0.008)
	M2	0.286 (0.11)	0.316 (0.08)	0.155 (0.08)	0.029 (0.009)
	M3	0.357 (0.07)	0.375 (0.12)	0.178 (0.05)	0.037 (0.008)
	M4	0.378 (0.03)	0.381 (0.10)	0.221 (0.07)	0.039 (0.003)
C2	M1	0.331 (0.11)	0.421 (0.08)	0.172 (0.05)	0.031 (0.008)
	M2	0.334 (0.02)	0.377 (0.1)	0.223 (0.06)	0.033 (0.003)
	M3	0.317 (0.07)	0.291 (0.04)	0.198 (0.03)	0.029 (0.006)
	M4	0.244 (0.19)	0.330 (0.13)	0.186 (0.02)	0.031 (0.001)
C3	M1	0.317 (0.10)	0.302 (0.02)	0.211 (0.14)	0.029 (0.011)
	M2	0.307 (0.10)	0.356 (0.08)	0.145 (0.07)	0.031 (0.008)
	M3	0.329 (0.03)	0.388 (0.11)	0.195 (0.02)	0.032 (0.008)
	M4	0.372 (0.02)	0.394 (0.03)	0.158 (0.02)	0.034 (0.001)
Model		n.s.	**	**	n.s.
S		n.s.	**	n.s.	n.s.
C		n.s.	n.s.	n.s.	n.s.
M		n.s.	n.s.	n.s.	n.s.
C × M		n.s.	n.s.	n.s.	n.s.
S × M		n.s.	n.s.	n.s.	n.s.
S × C		n.s.	n.s.	n.s.	$P = 0.16$
S × C × M		n.s.	n.s.	n.s.	n.s.
M1 vs. M2		n.s.	n.s.	n.s.	n.s.
M1 vs. M3		n.s.	n.s.	n.s.	n.s.
M1 vs. M4		n.s.	n.s.	n.s.	n.s.
LSD1 ($\alpha = 0.05$)		0.101	0.077	0.10.15	0.01
LSD2 ($\alpha = 0.05$)		0.130	0.130	0.098	0.01

C1: control, C2: 4 times compaction, C3: 12 times compaction. M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum* (Iranian), M4: *G. mosseae* (Canadian). n.s.: not significant. Values within the same column followed by different letter(s) are statistically different using Protected Least Significant Difference (LSD) test for unsterilized (LSD1) and sterilized (LSD2) soils. *Significant at 0.1 level of probability probability.
** Significant at 0.05 level of probability probability.

than shoot growth, which is partly due to increased P uptake (Miransari et al., 2007, 2008).

Under stressful conditions plant hormones, cytokinin (generally in root meristems) auxin (generally in shoot meristems), and gibberellins (generally in differentiating tissues) play a role in plant response by controlling meristem activity (Amzallag, 1999; Dodd, 2005). For example when P is deficient, auxin, ethylene and cytokinin induce morphological changes (i.e., increasing root surface, by producing more dense root hairs and cluster roots) in the plant to cope with the stress. In addition auxin is also able to influence the direct and indirect mobilization of soil P through increasing root exudates (Wittenmayer and Merbach, 2005). It has also been stated that AM alter the rate of plant hormones under stressful conditions (Suresh and Bagyaraj, 2002). It seems that the balance between the plant hormone alteration by the plant and AM may determine the final amount and role of plant hormones on regulating plant growth under stressful conditions.

Mineral nutrients determine the activity of plant signals involved in developmental processes (Dakora and Phillips, 2002). Under P deficient conditions shallow root corn was physiologically more efficient to uptake P compared with deep-rooted corn. Under these conditions AM changed corn root architecture in deep-rooted genotypes making it more shallow (Zhu et al., 2005). This can be one of the important mechanisms by which AM could have compensated for decreased P uptake under compaction in our research work.

Under N and P deficient conditions shoot growth, and under low K and Mn root growth are more affected. Carbohydrate stores are depleted from the roots when subjected to inhibitory conditions (Ericsson, 1995). With increasing compaction the oxidation status of Fe changes (due to reduced oxygen), this may affect the solubility of Fe and hence, its uptake by AM and the plant. At C4 in S1 soil the uptake of Fe by AM reduced compared with control but soil sterilization alleviated the stress.

Mn also behaved somehow similar to Fe, because like Fe its status and hence its availability is determined by the soil oxidation potential. The effect of soil on Mn and Zn uptake was significant, because the adsorbing activity of AM species in S1 and S2 was

Table 5
The effects of arbuscular mycorrhiza in unsterilized and sterilized compacted soils on N, P, and K uptake in corn (*Zea mays* L.), in the second experiment; means (S.E., $n = 3–4$).

Level of compaction	AM	Leaf dry weight (g)	N (mg/plant)	P (mg/plant)	K (mg/plant)
Unsterilized soil					
C1	M1	5.8 (0.3)	176 (10)	10 (2)	175 (19)
	M2	5.4 (1.7)	151 (40)	11 (4)	170 (70)
	M3	5.6 (1.5)	158 (40)	11 (2)	158 (36)
	M4	5.8 (0.4)	183 (10)	13 (3)	173 (12)
C2	M1	5.3 (0.4)	157 (20)	11 (3)	161 (32)
	M2	5.7 (0.3)	165 (10)	14 (2)	164 (2)
	M3	6.2 (2.5)	183 (80)	15 (8)	191 (101)
	M4	5.9 (0.4)	171 (20)	12 (2)	171 (24)
C3	M1	5.0 (1.3)	163 (20)	12 (1)	168 (20)
	M2	5.6 (1.0)	172 (50)	12 (4)	162 (53)
	M3	6.1 (1.7)	189 (50)	17 (4)	222 (71)
	M4	5.9 (1.0)	174 (30)	14 (2)	185 (35)
C4	M1	5.2 (0.9)	160 (30)	13 (1)	165 (14)
	M2	5.7 (1.4)	163 (30)	13 (1)	177 (45)
	M3	4.7 (1.6)	135 (40)	9 (2)	130 (29)
	M4	5.1 (1.5)	155 (50)	11 (4)	145 (52)
Sterilized soil					
C1	M1	6.4 (1.1)	185 (10)	14 (2)	196 (43)
	M2	7.4 (0.9)	231 (20)	15 (1)	223 (26)
	M3	7.1 (2.1)	221 (90)	15 (5)	209 (59)
	M4	6.5 (2.3)	197 (70)	12 (5)	199 (61)
C2	M1	6.4 (0.8)	199 (40)	14 (2)	201 (23)
	M2	5.8 (3.4)	180 (100)	11 (8)	169 (85)
	M3	5.3 (1.3)	177 (40)	11 (4)	160 (38)
	M4	7.7 (1.6)	249 (70)	15 (5)	246 (71)
C3	M1	5.7 (1.3)	172 (40)	10 (3)	161 (51)
	M2	6.6 (1.1)	212 (30)	12 (2)	207 (42)
	M3	6.5 (1.3)	210 (60)	14 (5)	199 (32)
	M4	6.8 (1.6)	240 (60)	16 (6)	227 (67)
C4	M1	6.6 (0.9)	200 (40)	12 (2)	211 (48)
	M2	7.3 (1.3)	239 (40)	16 (2)	226 (14)
	M3	7.3 (1.1)	237 (30)	14 (2)	235 (51)
	M4	7.4 (1.9)	238 (80)	15 (6)	223 (66)
Model		n.s.	n.s.	n.s.	n.s.
S		***	***	n.s.	***
C		n.s.	n.s.	n.s.	n.s.
M		n.s.	n.s.	n.s.	n.s.
C × M		n.s.	n.s.	n.s.	n.s.
S × M		n.s.	n.s.	n.s.	n.s.
S × C		n.s	n.s.	$P = 0.13$	$P = 0.13$
S × C × M		n.s.	n.s.	n.s.	n.s.
M1 vs. M2		n.s.	n.s.	n.s.	n.s.
M1 vs. M3		n.s.	n.s.	n.s.	n.s.
M1 vs. M4		$P = 0.14$	*	n.s.	n.s.
LSD1 ($\alpha = 0.05$)		1.5	55	5	68
LSD2 ($\alpha = 0.05$)		2.0	84	6	77

C1: control, C2: 4 times compaction, C3: 12 times compaction, C4: 20 times compaction. M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum* (Iranian), M4: *G. mosseae* (Canadian). n.s.: not significant. Values within the same column followed by different letter(s) are statistically different using Protected Least Significant Difference (LSD) test for unsterilized (LSD1) and sterilized (LSD2) soils. **Significant at 0.05 level of probability.
* Significant at 0.1 level of probability.
*** Significant at 0.01 level of probability.

Table 6
The effects of arbuscular mycorrhiza in unsterilized and sterilized compacted soils on Fe, Mn, Zn, and Cu uptake in corn (*Zea mays* L.), in the second experiment; means (S.E., $n = 3–4$).

Level of compaction	AM	Fe (mg/plant)	Mn (mg/plant)	Zn (mg/plant)	Cu (mg/plant)
Unsterilized soil					
C1	M1	0.766 (0.27)	0.685 (0.40)	0.222 (0.04)	0.065 (0.007)
	M2	0.723 (0.29)	0.466 (0.07)	0.173 (0.05)	0.053 (0.014)
	M3	0.639 (0.37)	0.499 (0.11)	0.190 (0.04)	0.069 (0.017)
	M4	0.750 (0.07)	0.530 (0.07)	0.219 (0.01)	0.082 (0.02)
C2	M1	0.727 (0.13)	0.476 (0.06)	0.183 (0.03)	0.065 (0.01)
	M2	0.636 (0.03)	0.533 (0.05)	0.169 (0.02)	0.059 (0.001)
	M3	0.714 (0.32)	0.534 (0.26)	0.249 (0.13)	0.100 (0.06)
	M4	0.903 (0.46)	0.487 (0.05)	0.177 (0.03)	0.068 (0.01)
C3	M1	0.727 (0.21)	0.537 (0.13)	0.195 (0.03)	0.062 (0.01)
	M2	0.639 (0.12)	0.513 (0.12)	0.192 (0.10)	0.065 (0.03)
	M3	0.799 (0.27)	0.549 (0.17)	0.225 (0.07)	0.077 (0.02)
	M4	0.739 (0.24)	0.521 (0.07)	0.184 (0.05)	0.063 (0.02)
C4	M1	0.617 (0.08)	0.435 (0.05)	0.194 (0.02)	0.071 (0.01)
	M2	0.583 (0.06)	0.502 (0.11)	0.203 (0.03)	0.066 (0.01)
	M3	0.536 (0.19)	0.413 (0.17)	0.137 (0.03)	0.052 (0.01)
	M4	0.539 (0.13)	0.441 (0.11)	0.162 (0.08)	0.057 (0.02)
Sterilized soil					
C1	M1	0.741 (0.14)	0.618 (0.18)	0.209 (0.03)	0.076 (0.02)
	M2	0.886 (0.17)	0.727 (0.23)	0.260 (0.08)	0.097 (0.007)
	M3	0.906 (0.42)	0.792 (0.30)	0.309 (0.10)	0.088 (0.03)
	M4	0.733 (0.28)	0.817 (0.29)	0.264 (0.11)	0.076 (0.03)
C2	M1	0.741 (0.15)	0.720 (0.10)	0.228 (0.07)	0.081 (0.03)
	M2	0.690 (0.39)	0.707 (0.43)	0.220 (0.14)	0.067 (0.04)
	M3	0.619 (0.14)	0.581 (0.20)	0.219 (0.08)	0.067 (0.02)
	M4	0.896 (0.32)	0.812 (0.30)	0.290 (0.07)	0.088 (0.02)
C3	M1	0.689 (0.12)	0.713 (0.23)	0.220 (0.13)	0.070 (0.01)
	M2	0.831 (0.13)	0.935 (0.25)	0.264 (0.04)	0.083 (0.02)
	M3	0.995 (0.15)	0.813 (0.29)	0.233 (0.08)	0.078 (0.02)
	M4	1.092 (0.56)	0.966 (0.27)	0.275 (0.07)	0.094 (0.03)
C4	M1	0.804 (0.21)	0.808 (0.07)	0.210 (0.02)	0.075 (0.02)
	M2	0.949 (0.13)	0.937 (0.28)	0.302 (0.12)	0.090 (0.01)
	M3	0.880 (0.13)	0.843 (0.11)	0.271 (0.03)	0.086 (0.01)
	M4	0.899 (0.24)	0.818 (0.29)	0.289 (0.11)	0.087 (0.03)
Model		n.s.	**	n.s.	n.s.
S		***	***	***	***
C		n.s.	n.s.	n.s.	n.s.
M		n.s.	n.s.	n.s.	n.s.
C × M		n.s.	n.s.	n.s.	n.s.
S × M		n.s.	n.s.	n.s.	n.s.
S × C		$P = 0.1$	$P = 0.16$	n.s.	n.s.
S × C × M		n.s.	n.s.	n.s.	$P = 0.12$
M1 vs. M2		n.s.	n.s.	n.s.	n.s.
M1 vs. M3		n.s.	n.s.	n.s.	n.s.
M1 vs. M4		n.s.	n.s.	n.s.	n.s.
LSD1 ($\alpha = 0.05$)		0.36	0.36	0.09	0.03
LSD2 ($\alpha = 0.05$)		0.38	0.35	0.14	0.03

C1: control, C2: 4 times compaction, C3: 12 times compaction, C4: 20 times compaction. M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum* (Iranian), M4: *G. mosseae* (Canadian). n.s.: not significant. Values within the same column followed by different letter(s) are statistically different using protected least significant difference (LSD) test for unsterilized (LSD1) and sterilized (LSD2) soils. *Significant at 0.1 level of probability.
** Significant at 0.05 level of probability.
*** Significant at 0.01 level of probability.

different at C4 being significantly higher in S2. Our results indicate that compared with other nutrients P and Zn are more sensitive under higher of compactions, which is in agreement with the results of Barzegar et al. (2006) who found that plant nutrient uptake of P and Zn decreased highly with increased compaction and addition of P and Zn compensate very much for such nutrients deficiency.

Cu behavior in comparison with other nutrients was somehow different, because not only the effect of soil on Cu uptake was significant, but the tendency of the three way interaction effect of S × C × M ($P = 0.12$) make it more complicated to evaluate the behavior of Cu under compacted conditions when AM is applied.

4.3. Comparison of different species of AM with different origin

Although it is clear from the results that M3 and M4 are the most effective AM species on corn nutrient uptake in a compacted soil, M2 showed to be able to efficiently compete with other microorganisms and increased nutrient uptake of P, K, Mn and Zn even at C4 under unsterilized conditions. These data also reverify that the origin of AM may not influence their performance under stressful conditions (Burleigh et al., 2002).

5. Conclusion

We may conclude that: (1) arbuscular mycorrhiza can alleviate the stressful effects of soil compaction on corn growth through enhancing nutrient uptake, (2) this role is very much dependent on the competition with other soil microorganisms, and (3) different species of arbuscular mycorrhiza, may be able to adopt themselves with different ecological and environmental conditions.

References

American Society for Testing Materials, 2000. Standard methods for laboratory compaction characteristics of soil using standard effort (12,400 ft-lbf/ft^3(600 kN/m^3)), in: American Society for Testing Materials, ASTM Standard in Building Codes. ASTM, West Conshocken, PA, pp. 1–11.

Amzallag, G.N., 1999. Regulation of growth: the meristem network approach. Plant Cell Environ. 22, 483–493.

Al-Karaki, G.N., 2006. Nursery inoculation of tomato with arbuscular mycorrhizal fungi and subsequent performance under irrigation with saline water. Scientia Horticalturae 109, 1–7.

Artursson, V., Finlay, R.D., Jansson, J.K., 2006. Interactions between arbuscular mycorrhizal fungi and bacteria and their potential for stimulating plant growth. Environ. Microbiol. 8, 1–10.

Arvidsson, J., 1999. Nutrient uptake and growth of barley as affected by soil compaction. Plant Soil 208, 9–19.

Baker, D.E., Amachar, M.C., 1982. Nickel, copper, zinc and cadmium. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. Part 2. 2nd ed. American Society of Agronomy, Madison, WI, USA, pp. 323–338.

Banaei, M.H., 2000. Soil Genesis and Classification Department. Soil and Water Research Institute, Tehran, Iran.

Barzegar, A.R., Asoodar, M.A., Ansari, M., 2000. Effectiveness of sugarcane residue incorporation at different water contents and the proctor compaction loads in reducing soil compactibility. Soil Till. Res. 57, 167–172.

Barzegar, A.R., Nadian, H., Heidari, F., Herbert, S.J., Hashemi, A.M., 2006. Interaction of soil compaction, phosphorus and zinc on clover growth and accumulation of phosphorus. Soil Till. Res. 87, 155–162.

Bengough, A.G., Bransby, M.F., Hans, J., McKenna, S.J., Roberts, T.J., Valentine, T.A., 2006. Root responses to soil physical conditions; growth dynamics from field to cell. J. Exp. Bot. 57, 437–447.

Bolan, N.S., 1991. A critical review on the role of mycorrhizal fungi in the uptake of phosphorous by plants. Plant Soil 134, 187–207.

Burleigh, S.H., Cavagnaro, T., Jakobsen, I., 2002. Functional diversity of arbuscualr mycorrhizas extends to the expression of plant genes involved in P nutrition. J. Exp. Bot. 53, 1593–1601.

Carpenter-Boggs, L., Loynachan, T.E., Stahl, P.D., 1995. Spore germination of *Gigaspora margarita* stimulated by volatiles of soil-isolated actinomycetes. Soil Biol. Biochem. 27, 1445–1451.

Daei, G., Ardekani, M., Rejali, F., Teimuri, S., Miransari, M, in press. Alleviation of salinity stress on wheat yield, yield components, and nutrient uptake using arbuscular mycorrhizal fungi under field conditions. J. Plant Physiol.

Dakora, F.D., Phillips, D.A., 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil 245, 35–47.

Díaz-Zorita, M., Perfect, E., Grove, J.H., 2002. Disruptive methods for assessing soil structure. Soil Till. Res. 64, 3–22.

Dodd, I.C., 2005. Root-to-shoot signaling: assessing the roles of 'up' in the up and down world of long-distance signaling *In Planta*. Plant Soil 274, 251–270.

Enkhtuya, B., Vosatka, M., 2005. Interaction between grass and trees mediated by extraradical mycelium of symbiotic arbuscular mycorrhizal fungi. Symbiosis 38, 261–277.

Ericsson, T., 1995. Growth and shoot: root ratio of seedlings in relation to nutrient availability. Plant Soil 168, 205–214.

Feldmann, F., Idczak, E., 1992. Inoculum production of vesicular arbuscular mycorrhizal fungi for use in tropical nurseries. Methods in Microbiology, Vol. 24. Academic Press Limited, pp. 339–357.

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, A. (Ed.), Methods of Soil Analysis. Part 1, 2nd ed., Vol. 9. Agron Monogr, ASA and SSSA, Madison, WI, pp. 383–411.

Harrier, L.A., 2001. The arbuscular mycorrhizal symbiosis: a molecular review of the fungal dimension. J. Exp. Bot. 52, 469–478.

Harrison, M.J., 2005. Signaling in the arbuscular mycorrhizal symbiosis. Ann. Rev. Microbiol. 59, 19–42.

Hodge, A., Campbell, C.D., Fitter, H.A., 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. Nature 413, 297–299.

Jakobsen, I., 1995. Transport of phosphorous and carbon in VA mycorrhiza. In: Varma, A., Hock, B. (Eds.), Mycorrhiza Structure, Function, Molecular Biology and Biotechnology. Springer-Verlag, Berlin, pp. 297–324.

Johnson, C.M., Ulrich, A., 1959. Analytical methods for use in plant analysis, Bulletin 766. University of California, Agricultural Experiment Station, Berkeley, pp. 26–78.

Johnson, N.C., Graham, J.H., Smith, F.A., 1997. Functioning of mycorrhizal associations along the mutualism–parasitism continuum. New Phytol. 13, 575–585.

Khalil, S., Loynachan, T.E., Tabatabai, M.A., 1994. Mycorrhizal dependency and nutrient uptake by improved and unimproved corn and soybean cultivars. Agron. J. 86, 949–958.

Knudsen, D., Peterson, G.A., Pratt, P.F., 1982. Lithium, sodium and potassium, in: Page, A.L., et al. (Eds.), Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties, ASA Monograph Number 9, pp. 225–246.

Kristoffersen, A., Riley, H., 2005. Effects of soil compaction and moisture regime on the root and shoot growth and phosphorus uptake of barley plants growing on soils with varying phosphorus status. Nutrient Cycl. Agroecosys. 72, 135–146.

Lindsay, W.L., Norvell, W.A., 1978. Development of a DTPA soil test for zinc, iron, manganese, and copper. Soil Sci. Soc. Am. J. 42, 421–428.

Liu, A., Hamel, C., Hamilton, R.I., Smith, D.L., 2000. Mycorrhizae formation and nutrient uptake of new corn (*Zea mays* L.) hybrids with extreme canopy and leaf architecture as influenced by soil N and P levels. Plant Soil 221, 157–166.

Liu, A., Wang, B., Hamel, C., 2004. Arbuscular mycorrhiza colonization and development at suboptimal root zone temperature. J. Environ. Exp. Bot. 14, 93–101.

Mahaveer, P.S., Singh, R., Adholeya, A., 2000. Laboratory Manual for Basic Techniques in Arbuscular Mycorrhizal Research. Center for Mycorrhizal Research, Tata Energy Research Institute, New Delhi.

Marschner, H., Dell, B., 1994. Nutrient uptake in mycorrhizal symbiosis. Plant Soil 159, 89–102.

Miransari, M., Bahrami, H.A., Malakouti, M.J., Smith, D., Rejali, F., 2004. Using mycorrhiza to reduce the stressful effects of soil compaction on corn (*Zea mays* L.). In: Proceedings of the 4th International Iran and Russia Conference "Agriculture and Natural Resources", Shahre Kord University, Shahre Kord, Iran.

Miransari, M., Bahrami, H.A., Rejali, F., Malakouti, M.J., 2006. Evaluating the effects of arbuscular mycorrhizae on corn (*Zea mays* L.) yield and nutrient uptake in compacted soils. Soil Water J. 1, 106–122 (In Persian, Abstract in English).

Miransari, M., Bahrami, H.A., Rejali, F., Malakouti, M.J., Torabi, H., 2007. Using arbuscular mycorrhiza to reduce the stressful effects of soil compaction on corn (*Zea mays* L.) growth. Soil Biol. Biochem. 39, 2014–2026.

Miransari, M., Bahrami, H.A., Rejali, F., Malakouti, M.J., 2008. Using arbuscular mycorrhiza to reduce the stressful effects of soil compaction on wheat (*Triticum aestivum* L.) growth. Soil Biol. Biochem. 40, 1197–1206.

Munns, R., Cramer, G.R., 1996. Is coordination of leaf and root growth mediated by abscisic acid? Plant Soil 185, 33–49.

Nadian, H., Smith, S.E., Alston, A.M., Murray, R.S., 1996. The effects of soil compaction on growth and P uptake by *Trifolium subterraneum*: interactions with mycorrhizal colonisation. Plant Soil 182, 39–49.

Nadian, H., Smith, S.E., Alston, A.M., Murray, R.S., 1997. Effects of soil compaction on plant growth, phosphorus uptake and morphological characteristics of vesicular–arbuscular mycorrhizal colonization of *Trifolium subterraneum*. New Phytol. 135, 303–311.

Nadian, H., Smith, S.E., Alston, A.M., Murray, R.S., Siebert, B.D., 1998. Effects of soil compaction on phosphorus uptake and growth of *Trifolium subterraneum* colonized by four species of vesicular–arbuscular mycorrhizal fungi. New Phytol. 140, 155–165.

Nelson, D.W., Sommers, L.E., 1973. Determination of total nitrogen in plant material. Agron. J. 65, 109–112.

Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon, and organic matter. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. Part 2. 2nd ed. American Society of Agronomy, Madison, WI, USA, pp. 539–573.

Olsen, R.S., 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. U.S. Department of Agriculture, No. 939.

Pardo, A., Amato, M., Chiaranda, F.Q., 2000. Relationship between soil structure, root distribution and water uptake of chickpea (*Cicer arietinum* L.). Plant growth and water distribution. Eur. J. Agron. 13, 39–45.

Pereira, J.O., Defossez, P., Richard, G., 2007. Soil susceptibility to compaction by wheeling as a function of some properties of a silty soil as affected by the tillage system. Eur. J. Soil Sci. 58, 34–44.

Piotrowski, J.S., Denich, T., Klironomos, J.N., Graham, J.M., Rillig, M.C., 2004. The effects of arbuscular mycorrhizae on soil aggregation depend on the interaction between plant and fungal species. New Phytol. 164, 365–373.

Porcel, R., Barea, J.M., Ruiz-Lozano, J.M., 2003. Antioxidant activities in mycorrhizal soybean plants under drought stress and their possible relationship to the process of nodule senescence. New Phytol. 157, 135–143.

Prokopy, W.R., 1995. Phosphorus in acetic acid extracts. QuikChem Method 12-115-01-1-C Lachat Instruments, Milwaukee, WI.

Rhoades, J.D., 1982. Soluble salts. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. Part 2. 2nd ed. American Society of Agronomy, Madison, WI, USA, pp. 167–178.

Rillig, M.C., 2004. Arbuscular mycorrhizae, glomalin and soil quality. Can. J. Soil Sci. 84, 355–363.
Rillig, M.C., Mummey, D.L., 2006. Mycorrhizas and soil structure. New Phytol. 171, 41–53.
Rivera-Becerril, F., Calantzis, C., Turnau, K., Caussanel, J.P., Belimov, A.A., Gianinazzi, Strasser, R.J., Cianinazzi-Pearson, V., 2002. Cadmium accumulation and buffering of cadmium-induced stress by arbuscular mycorrhiza in three *Pisum sativum* L. genotypes. J. Exp. Bot. 53, 1177–1185.
Ruser, R., Flessa, H., Russow, R., Schmidt, G., Buegger, F., Munch, J.C., 2006. Emission of N_2O, N_2 and CO_2 from soil fertilized with nitrate: effect of compaction, soil moisture and rewetting. Soil Biol. Biochem. 38, 263–274.
Sas Institute, Inc. 1988. SAS/STAT User's Guide. Version 6. 4th Ed., Statistical Analysis Institute, Inc., Cary, NC.
Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics. Soil Till. Res. 79, 7–31.
Smith, F.A., Jakobsen, I., Smith, S.E., 2000. Spatial differences in acquisition of soil phosphate between two arbuscular mycorrhizal fungi in symbiosis with *Medicago truncatula*. New Phytol. 147, 357–366.
Smith, F.A., Smith, S.E., 1997. Structural diversity in (vesicular)–arbuscular mycorrhizal symbiosis. New Phytol. 137, 377–388.
Smith, S.E., Read, D.J., 1997. Mycorrhizal Symbiosis. Academic Press, San Diego.
Sood, S.G., 2003. Chemotactic response of plant-growth-promoting bacteria towards roots of vesicular–arbuscular mycorrhizal tomato plants. FEMS Microbiol. Ecol. 45, 219–227.
Steel, R.G.D., Torrie, J.H., 1980. Principles and Procedures of Statistics: A Biometrical Approach, 2nd ed. McGraw-Hill Book Company.
Standish, R.J., Stokes, B.A., Tibbett, M., Hobbsa, R.J., 2007. Seedling response to phosphate addition and inoculation with arbuscular mycorrhizas and the implications for old-field restoration in Western Australia. Environ. Exp. Bot. 61, 58–65.
Subramanian, K.S., Charest, C., 1997. Nutritional, growth, and reproductive responses of maize (*Zea mays* L.) to arbuscular mycorrhizal inoculation during and after drought stress at tasselling. Mycorrhiza 7, 25–32.
Suresh, C.K., Bagyaraj, D.J., 2002. Mycorrhiza–microbe interactions: effects on rhizosphere. In: Sharma, A.K., Johri, B.N. (Eds.), Arbuscular Mycorrhiza, Interactions in Plants, Rhizosphere and Soils. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi, pp. 7–28.
Tanaka, Y., Yano, K., 2005. Nitrogen delivery to maize via mycorrhizal hyphae depends on the form of N supplied. Plant Cell Environ. 28, 1247–1254.
Tian, C.Y., Feng, G., Li, X.L., Zhang, F.S., 2004. Different effects of arbuscular mycorrhizal fungal isolates from saline or non-saline soil on salinity tolerance of plants. Appl. Soil Ecol. 26, 143–148.
Tobar, R.M., Azcón, R., Barea, J.M., 1994. The improvement of plant N acquisition from an ammonium-treated, drought-stressed soil by the fungal symbiont in arbuscular mycorrhizae. Mycorrhiza 4, 105–108.
Toshihiro, A., Maldonado-Mendoza, I.E., Dewbre, G.R., Harrison, M.J., Saito, M., 2004. Expression of alkaline phosphatase genes in arbuscular mycorrrhizas. New Phytol. 162, 525–534.
Troelstra, S.R., Wagenaar, R., Smant, W., Peters, B.A.M., 2001. Interpretation of bioassays in the study of interactions between soil organisms and plants: involvement of nutrient factors. New Phytol. 150, 697–706.
Van der Werf, A., Nagel, O.W., 1996. Carbon allocation to shoots and roots in relation to nitrogen supply is mediated by cytokinins and sucrose. Plant Soil 185, 21–32.
Wittenmayer, L., Merbach, W., 2005. Plant responses to drought and phosphorus deficiency: contribution of phytohormones in root-related processes. J. Plant Nutr. Soil Sci. 168, 531–540.
Wright, S.F., Upadhyaya, A., 1996. Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. Soil Sci. 161, 575–586.
Zhu, J., Kaeppler, S.M., Lynch, J.P., 2005. Topsoil foraging and phosphorus acquisition efficiency in maize (*Zea mays* L.). Funct. Plant Biol. 32, 749–762.