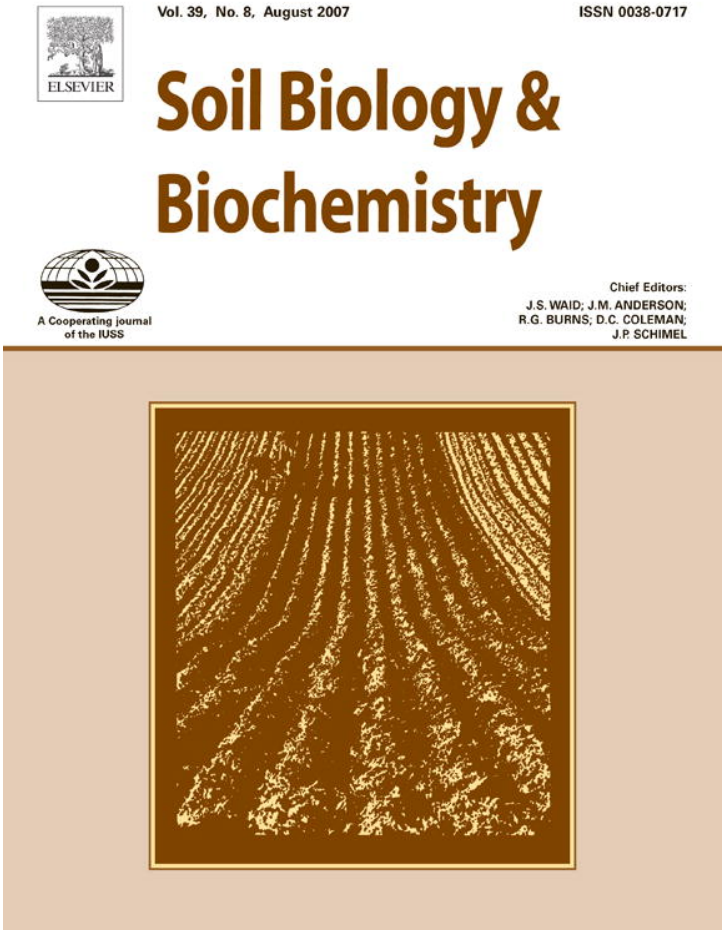

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Using arbuscular mycorrhiza to reduce the stressful effects of soil compaction on corn (*Zea mays* L.) growth

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Abstract

Soil compaction is of great importance in agriculture, because its high levels may adversely affect plant growth and the environment. Since mechanical methods are not very efficient and economical, using biological methods to alleviate the stress of soil compaction on plant growth may be beneficial. The objectives of this study were to: (1) evaluate the effects of soil compaction on corn (*Zea mays* L.) growth, and (2) test the hypothesis that applying arbuscular mycorrhiza (AM) with different origins can partially or completely overcome the stressful effects of soil compaction on corn growth under unsterilized and sterilized conditions. Corn was planted in unsterilized and sterilized compacted soils, while treated with three species of AM including, Iranian *Glomus mosseae*, Iranian *Glomus etunicatum*, and Canadian *Glomus mosseae*, received from GINCO (Glomales *in vitro* Collection), Canada. Plant growth variables and soil resistance parameters were determined. AM significantly increased root fresh (maximum of 94% increase) and dry (maximum of 100% increase) weights in the compacted soil. AM with different origins may improve corn growth in compacted soils, though its effectiveness is related to the level of compaction and also to the interaction with other soil microorganisms.

Keywords: Corn (*Zea mays* L.) growth; Origin of arbuscular mycorrhiza; Soil resistance; Unsterilized and sterilized compacted soil

1. Introduction

Although applying the new techniques (i.e., use of more sophisticated machinery in the field), to increase yield, can be useful, it may be harmful too resulting in the compaction of soil and hence the unfavorable ecological, environmental, and economical consequences. In a compacted soil, bulk density increases and soil porosity decreases (Arvidsson, 1998). Soil compaction results in the degradation of soil structure, reduced water potential, increased soil erosion, and reduced root growth, which eventually decreases plant growth (Bengough and Mullins, 1991; Horn and Lebert, 1994).

Increased soil strength in a compacted soil, which is quantified by measuring soil bulk density and soil resistance, reduces plant growth (Smit et al., 1989; Amato and Ritchie, 2002). The reduction in shoot growth is a result of chemical signals, produced by roots (Masle and Passioura, 1987; Pardo et al., 2000). According to Pardo et al. (2000), shoot growth is usually more reduced than root growth in compacted soils. Soil compaction affects the development and distribution of roots and increasing soil resistance causes the cluster growth of roots in parts of the soil, which are less resistant (Tardieu and Manichon, 1987; Amato, 1991; Pardo et al., 2000). As a result of cluster growth, root density decreases resulting in reduced water and nutrient uptake (Tardieu, 1987; Amato, 1991; Pardo et al., 2000). Since mechanical methods are not efficient and economical using biological methods to reduce soil compaction may be environmentally and economically useful leading to a sustainable agriculture system.

Lower levels of soil compaction may enhance corn growth through providing a suitable medium for seed growth, and also due to the improvement of soil structure resulting in decreased soil erosion under field conditions

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(Bouwman and Arts, 2000; Passioura, 2002; Miransari et al., 2004).

AM is able to make symbiotic relationships with many plants including important agricultural crops. AM inoculates the root surface of the host plant to acquire carbon and help the host plant take up phosphorous and other nutrients from the soil. This symbiosis is useful for the plant because phosphorous is necessary for plant growth and development especially under phosphorous deficient conditions (Harrison and van Buuren, 1995).

The process of root inoculation by the fungi is made of complex stages including spore germination, hypha differentiation, aprosurium formation, root penetration, intercellular growth, arbuscule formation and nutrient transfer (Harrier, 2001). Arbuscules are branched hypha, found inside root cells from where nutrient exchange takes place between fungi and the host plant (Van Duin et al., 1989; Entry et al., 2002; Troeh and Loynachan, 2003). As roots develop conditions for inoculation by AM improves. The carbohydrates are used by AM for growth (extension of the hypha).

AM may increase plant tolerance to biotic and abiotic stresses (Azcón-Aguilar and Barea, 1995; Newsham et al., 1995; Subramanian and Charest, 1997). One of the unique characteristics of AM, when in symbiotic relationship with plant roots, is the significant increase in surface area due to the production of extensive hypha helping plants grow under relatively harsh conditions, such as drought stress (Al-Karaki et al., 2004) and nutrient deficiency conditions (Marschener and Dell, 1994).

AM fungi improve soil properties through their extended hypha network (Bethlenfalvay and Schuepp, 1994). Therefore, these fungi are an important component of the ecosystem and can have significant applications in sustainable agricultural systems (Schreiner and Bethlenfalvay, 1995; Azcón-Aguilar and Barea, 1997). Since there is not any information on the effects of AM fungi on corn growth in compacted soils under sterilized and unsterilized conditions, these effects are evaluated in this study.

Mycorrhizal plants have a better growth compared with non-mycorrhizal plants. According to Levitt (1980) stress avoidance includes mechanisms by which an organism reduces the effects of stress while tolerance to stress allows the organism to resist the unfavorable conditions. The stress definition by Levitt may be modified so that includes every environmental factor that can cause physical and chemical (metabolic adjustment) changes, irrespective of the case that the change is useful or harmful for the organism (Entry et al., 2002).

The biochemicals, involved in the communications between the two partners, are usually made of flavonoid and phenolic compounds (Harrison, 1997b). Plants, inoculated with the mychorrhizal fungus, are more capable of resisting stressful conditions due to their complex molecular communications with the host plant. The recognition of these communicating molecules may be very helpful to understand the symbiotic process (Harrier, 2001). Just recently scientists have discovered the signals, strigolactones, responsible for hypha branching and arbuscule formation (Akiyama and Hayashi, 2006).

The hypha of AM, which are 2–3 times finer than even the finest root hairs (Bolan, 1991; Jakobsen, 1995) may penetrate very fine soil pores in compacted soils. At the higher levels of compaction AM may not be as effective as the lower levels because it would require adequate amount of oxygen (Arvidsson, 1999) for its activities and as soil compaction increases the amount of oxygen reduces. Also according to Yoo and Wander (2006), compared with other soil physical properties, clay content, bulk density and soil moisture, may collectively explain better the variations in soil biological activities such as soil organic C mineralization in a compacted soil.

Also the formation and activity of AM is influenced by the stresses caused by humans such as, soil compaction, metals and organic pollutants (Entry et al., 2002). These stresses affect AM by at least three mechanisms (1) direct effects on mycorrhizal roots, (2) through affecting the shoot altering carbon allocation to mycorrhiza and (3) nutritional factors that change carbon allocation to mycorrhiza.

Simple plant root exudates make the fungi and bacteria compete and develop antagonistic effects. For more complex organic compounds, e.g., cellulose and lignin, the interaction may be both competitive and mutualistic. There are also other types of interactions between fungi and bacteria including bacteria consuming fungal exudates and also endosymbiotic and mycophagous bacteria (de Boer et al., 2005).

The pathways, involved in plant gene induction, and hence, plant cell programs may be common between AM and soil bacteria. For example Sanchez et al. (2004) have stated that a fluorescent pseudomonas and *Glomus mosseae* may similarly induce genes, responsible for the symbiosis between the two partners.

In an agricultural system AM may affect the following active microbial populations; the bacteria solubilizing phosphate (Barea et al., 2002), the bacteria helping mycorrhization (Garbaye, 1994), the microbes transfering N (the authotrophic oxidizers of ammonium: Hodge et al., 2001), soil aggregating bacteria and fungi pathogenic to the roots (Graham, 2001).

Since soil compaction is of great concern in agriculture, in this study the effects of soil compaction on corn growth are evaluated and also the hypothesis that applying AM can partially or completely overcome the stressful effects of soil compaction on corn growth is tested.

2. Materials and methods

2.1. Soil characteristics and measurements

Surface layer soil, a Xeric Haplocalcids (Banaei, 2000), of the research field of the Soil and Water Research Institute, which is located in Meshkin Dasht Karaj, Iran,

Table 1a
The physical saturation and chemical properties of the soils, used

	PH	EC ($ds\,m^{-1}$)	Organic carbon (%)	Saturation percentage (%)	Total N (%)	P ($mg\,kg^{-1}$)
Experiment 1	7.86	0.60	0.48	29	0.05	10.4
Experiment 2	7.7	1.62	0.50	32	—	6.1
	K ($mg\,kg^{-1}$)	Fe ($mg\,kg^{-1}$)	Mn ($mg\,kg^{-1}$)	Zn ($mg\,kg^{-1}$)	Cu ($mg\,kg^{-1}$)	
Experiment 1	318	3.60	11.14	4.8	1.28	
Experiment 2	250	4.62	18.50	1.48	1.38	

was sieved and air-dried and half of it was sterilized at 121 °C for an hour using an autoclave (Toshihiro et al., 2004) and transferred to 10-kg round pots with a diameter and height of 20 cm, respectively. In the sterilization method high pressure and temperature may completely sterilize the soil. This temperature may not have any effects on the constant chemical properties of the soil such as mineralogical properties, but it may speed up the physico-chemical reactions, and also the biological potential of the soil, as mentioned, may be very much affected.

Soil physical and chemical properties to a 30-cm depth were determined (Table 1a). Nitrogen was measured using Kjeldahl method (Nelson and Sommers, 1973). phosphorus 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 Perkin Elmer 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 hydrometry method (Gee and Bauder, 1986). Soil moisture at field capacity (−33 Pa) and permanent wilting point (−1500 Pa) (Rhoades, 1982) were determined using pressure plates apparatus.

In the second experiment we used a texture with a higher rate of clay, as clear from the saturation percentages (Table 1a), to be able to create higher levels of compaction. Although in some papers it is mentioned that the soil may be compacted in layers, since in the field the soil become compacted non-uniformly, we compacted the soil in one layer. Although the role of soil water is of significance, since compacting a wet soil may create very hard layers in the soil that make the root growth very much limited more than expectation and also may enter some errors in the experiment, the dry soil was compacted in the pots. The compaction levels were selected according to some papers (Barzegar et al., 2000) and also according to our own testing, meaning that the 20-time compaction was the highest compaction level we could create in the pots.

Pots were treated with soil compaction levels using 2-kg weights, with an 18-cm diameter, released from a 20-cm height including four and 12 times compaction in the first experiment and a 20 times level was also included in the second experiment to more clearly study the role of AM at the higher levels of compaction on plant growth. The treatments also included a control level (without compaction). In the standard Proctor procedure a 2.5 kg rammer is released from a 30.5 cm height producing a 7.5 J energy and 7.3 kJ/m^3 compactive effort 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.

Soil bulk density was determined using a 100-cm^3 cylinder three times during the growing season and 6 measurements per replication. Soil resistance measurements were made three times during the growing season with a penetrometer (model Cernusco, 20063) at mean soil water contents 8.84, 14.28 and 6.34% in the first experiment and 11.84, 6.6 and 2.4% in the second experiment. The latter data were used to explain the variation in this measurement. The tip of the penetrometer was 20 mm long and it had a maximum diameter of 12 mm.

2.2. Experimental procedure

Experiments were designed as $2 \times 3 \times 4$ and $2 \times 4 \times 4$ factorial on the basis of a completely randomized block design. Therefore, there were 24 and 32 treatments 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 where plants received 14 h of florescent light. Since more space was required for the second experiment, it was conducted in a greenhouse where the plant received natural light only.

Treatments included unsterilized (S1) and sterilized (S2) soils, three levels of compaction with bulk densities of 1.18, 1.29 and 1.40 and four levels of compaction with bulk densities of 1.2, 1.27, 1.34 and 1.51 g/cm^3 in the first and second experiment, respectively, as well as AM species. Four corn seeds (var. 704) were planted in each pot and

Table 1b
The effects of unsterilized and sterilized compacted soils and arbuscular mycorrhiza on soil resistance in the first and second experiment (SD, $n = 3$–4)

Level of compaction	AM	SR1 (MPa)	SR2 (MPa)	SR3 (MPa)
First experiment, unsterilized soil				
C1	M1	0.83 (0.13)d	0.63 (0.16)de	0.73 (0.16)c
	M2	0.96 (0.07)d	0.69 (0.11)bcde	0.72 (0.12)c
	M3	1.16 (0.21)c	0.66 (0.16)cde	0.72 (0.05)c
	M4	0.89 (0.16)d	0.56 (0.17) e	0.64 (0.10)c
C2	M1	1.30 (0.13)abc	0.94 (0.24)ab	0.90 (0.18)b
	M2	1.24 (0.13)bc	0.99 0.24)a	0.91 (008)b
	M3	1.36 (0.18)ab	0.87 (0.25)abcd	0.91 (0.12)b
	M4	1.30 (0.15)abc	0.86 (0.25)abcd	0.89 (0.08)b
C3	M1	1.28 (0.12)abc	0.91 (0.16)abc	0.94 (0.10)b
	M2	1.41 (0.14)a	1.09 (0.31)a	1.10 (0.14)a
	M3	1.37 (0.04)ab	1.03 (0.19)a	0.93 (0.19)b
	M4	1.34 (0.15)ab	0.97 (0.20)a	0.96 (0.03)ab
Sterilized soil				
C1	M1	0.83 (0.09)d	0.59 (0.10)de	0.64 (0.12)e
	M2	0.99 (0.09)cd	0.48 (0.03)e	0.69 (0.10)de
	M3	0.97 (0.06)cd	0.52 (0.04)de	0.77 (0.12)bcd
	M4	0.96 (0.04)cd	0.61 (0.10)de	0.85 (0.14)abc
C2	M1	1.31 (0.22)a	0.84 (0.19)bc	0.75 (0.04)cde
	M2	1.23 (0.13)ab	0.88 (0.29)abc	0.88 (0.12)ab
	M3	1.31 (0.13)a	0.92 (0.05)ab	0.92 (0.10)a
	M4	1.09 (0.26)bc	0.71 (0.25)cd	0.94 (0.01)a
C3	M1	1.38 (0.20)a	1.04 (0.07)a	0.93 (0.11)a
	M2	1.33 (0.08)a	0.89 (0.15)abc	0.85 (0.06)abc
	M3	1.31 (0.14)a	0.97 (0.24)ab	0.92 (0.08)a
	M4	1.34 (0.09)a	0.94 (0.12)ab	0.95 (0.06)a
Model		***	***	***
LSD1		0.17	0.25	0.15
LSD2		0.17	0.19	0.11
Second experiment, unsterilized soil				
C1	M1	0.55 (0.17)b	0.59 (0.09)d	0.66 (0.04)d
	M2	0.55 (0.17)b	0.59 (0.09)d	0.66 (0.04)d
	M3	0.55 (0.17)b	0.59 (0.09)d	0.66 (0.04)d
	M4	0.55 (0.17)b	0.59 (0.09)d	0.66 (0.04)d
C2	M1	0.69 (0.1)b	0.85 (0.07)c	0.79 (0.04)c
	M2	0.69 (0.1)b	0.85 (0.07)c	0.79 (0.04)c
	M3	0.69 (0.1)b	0.85 (0.07)c	0.79 (0.04)c
	M4	0.69 (0.1)b	0.85 (0.07)c	0.79 (0.04)c
C3	M1	0.94 (0.12)a	1.00 (0.08)b	0.94 (0.02)b
	M2	0.94 (0.12)a	1.00 (0.08)b	0.94 (0.02)b
	M3	0.94 (0.12)a	1.00 (0.08)b	0.94 (0.02)b
	M4	0.94 (0.12)a	1.00 (0.08)b	0.94 (0.02)b
C4	M1	1.01 (0.12)a	1.12 (0.03)a	1.10 (0.03)a
	M2	1.01 (0.12)a	1.12 (0.03)a	1.10 (0.03)a
	M3	1.01 (0.12)a	1.12 (0.03)a	1.10 (0.03)a
	M4	1.01 (0.12)a	1.12 (0.03)a	1.10 (0.03)a
Sterilized soil				
C1	M1	0.56 (0.13)d	0.59 (0.09)d	0.66 (0.03)d
	M2	0.56 (0.13)d	0.59 (0.09)d	0.66 (0.03)d
	M3	0.56 (0.13)d	0.59 (0.09)d	0.66 (0.03)d
	M4	0.56 (0.13)d	0.59 (0.09)d	0.66 (0.03)d
C2	M1	0.79 (0.07)c	0.85 (0.07)c	0.79 (0.04)c
	M2	0.79 (0.07)c	0.85 (0.07)c	0.79 (0.04)c
	M3	0.79 (0.07)c	0.85 (0.07)c	0.79 (0.04)c
	M4	0.79 (0.07)c	0.85 (0.07)c	0.79 (0.04)c
C3	M1	1.03 (0.07)b	1.00 (0.08)b	0.94 (0.02)b
	M2	1.03 (0.07)b	1.00 (0.08)b	0.94 (0.02)b
	M3	1.03 (0.07)b	1.00 (0.08)b	0.94 (0.02)b
	M4	1.03 (0.07)b	1.00 (0.08)b	0.94 (0.02)b
C4	M1	1.18 (0.10)a	1.12 (0.03)a	1.10 (0.03)a
	M2	1.18 (0.10)a	1.12 (0.03)a	1.10 (0.03)a

Table 1b (*continued*)

Level of compaction	AM	SR1 (MPa)	SR2 (MPa)	SR3 (MPa)
	M3	1.18 (0.10)a	1.12 (0.03)a	1.10 (0.03)a
	M4	1.18 (0.10)a	1.12 (0.03)a	1.10 (0.03)a
Model		***	***	***
LSD1		0.15	0.09	0.04
LSD2		0.12	0.09	0.04

C1: control, C2: 4 time compaction, C3: 12 time compaction, C4: 20 time compaction. M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum,* M4: *G. mosseae* (Canadian). SR: Soil resistance. n.s.: not significant, *Significant at 10% probability, **Significant at 5% probability. Values within the same column, followed by the same letter(s) are not statistically different at $P = 0.1$.

Table 2
Mean comparisons of plant growth variables in unsterilized and sterilized soils at all compaction levels in the first ($n = 40$–44) and second experiment ($n = 57$–58)

Soil	Plant height (cm)	Leaf fresh weight (g)	Leaf dry weight (g)	Root fresh weight (g)	Root dry weight (g)	Root length (cm)
First experiment						
S1	103.8a	17.2b	3.1b	20.5a	2.5a	66.1b
S2	106.5a	18.3a	3.4a	21.5a	2.4a	71.5a
LSD	3.0	1.1	0.2	2.3	0.3	5.1
Second experiment						
S1	103.4a	27.8b	5.5b	38.7b	15.9b	63.6a
S2	103.1a	34.4a	6.7a	61.1a	19.9a	62.0a
LSD	3.1	1.9	0.4	11.6	3.2	3.4

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 at $P = 0.1$.

were thinned to one after germination. Pre-cultivated AM (Feldmann and Idczak, 1992) were placed under the seeds at planting using 1.6 g per pot containing about 80 (± 10) active fungus propagules (Toshihiro et al., 2004; Sood, 2003) including *Glomus mosseae* (M2), *G. etunicatum* (both isolated from the Iranian soils) (M3) and *G. mosseae* received from GINCO (Glomales *in vitro* Collection), Canada (M4). A control treatment (without mycorrhiza) (M1) was also included.

The inoculum was produced on the sorghum roots in sterilized sand in a 4-month period. Before conducting the experiment the total active fungus propagules in the inoculum was 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 propagules 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 season each pot was fertilized twice based on soil test at 1.48 g of N as urea, 0.46 g of P as triple super phosphate and 1.32 g of K as potassium sulfate.

2.3. Measurements of plant parameters

Plant height (cm) was measured and leaf samples were collected to determine the fresh and dry weights (g). At harvest root fresh and dry weights (g) as well as the longest root (cm) were measured.

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 LSD test the means were compared (Steel and Torrie, 1980).

3. Results

Measured soil resistances (Table 1b) at certain moisture verify that compaction treatments resulted in the compaction of pots and hence, increased soil bulk density.

In the second experiment increased compaction reduced plant height for control (without AM) treatments. The highest increase, as compared with control, is related to treatments S2C2M2 ($P = 0.17$) and S2C3M3 (by 9%) ($P = 0.18$) in the first experiment and treatment S1C4M4 (by 16%) in the second experiment ($P = 0.11$)

Table 3
Mean comparisons of plant growth variables, treated with 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	Plant height (cm)	Leaf fresh weight (g)	Leaf dry weight (g)	Root fresh weight (g)	Root dry weight (g)	Root length (cm)
First experiment (S1)						
M1	101.1b	16.9a	3.1a	20.3a	2.5a	66.2a
M2	102.9ab	17.0a	3.1a	20.6a	2.4a	56.1a
M3	103.7ab	17.8a	3.2a	21.2a	2.6a	70.5a
M4	107.4a	16.9a	3.1a	20.1a	2.3a	71.1a
LSD	6.2	1.7	0.3	3.6	0.5	9.8
First experiment (S2)						
M1	103.4a	17.3a	3.2a	17.2b	1.8b	68.9a
M2	108.4a	17.8a	3.2a	20.1ab	2.1b	70.7a
M3	108.2a	19.4a	3.5a	24.0a	2.5ab	75.4a
M4	105.8a	18.8a	3.6a	25.0a	3.1a	70.9a
LSD	6.4	2.4	0.5	5.6	0.7	10.1
Second experiment (S1)						
M1	100.6b	26.2a	5.3a	48.0a	17.7ab	63.8a
M2	103.3ab	28.1a	5.6a	28.44b	12.8b	59.3a
M3	100.9b	27.6a	5.6a	40.9ab	18.4a	66.8a
M4	108.8a	29.2a	5.7a	37.9ab	14.9ab	65.3a
LSD	6.1	3.3	0.8	19.4	5.2	7.8
Second experiment (S2)						
M1	100.8a	33.7a	6.3a	55.8a	19.0a	60.8b
M2	106.2a	36.4a	6.9a	65.7a	20.5a	66.1a
M3	105.0a	33.3a	6.5a	59.3a	22.8a	61.8ab
M4	100.9a	34.1a	7.1a	64.0a	17.7a	59.3b
LSD	6.6	4.7	1.1	25.4	7.5	5.2

S1: unstrilized soil, S2: sterilized soil. Values within the same column followed by different letter(s) are statistically different using protected Least Significant Difference (LSD) test at $P = 0.1$. M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum* (Iranian), M4: *G. mosseae* (Canadian).

Table 4
Mean comparisons of plant growth variables, treated with different species of arbuscular mycorrhiza at all levels of unsterilized and sterilized compacted soils in the first ($n = 20$–22) and second experiment ($n = 27$–30)

AM	Plant height (cm)	Leaf fresh weight (g)	Leaf dry weight (g)	Root fresh weight (g)	Root dry weight (g)	Root length (cm)
First experiment						
M1	102.2b	17.1a	3.1a	18.8b	2.2b	67.6ab
M2	105.9ab	17.5a	3.2a	20.3ab	2.3b	63.7b
M3	106.0ab	18.6a	3.4a	22.6a	2.6ab	73.0a
M4	106.6a	17.8a	3.3a	22.4a	2.7a	71.0a
LSD ($P = 0.1$)	4.2	1.5	0.3	3.2	0.4	7.1
Second experiment						
M1	100.7a	30.0a	5.8b	52.0a	18.4a	62.3a
M2	104.7a	32.1a	6.2ab	46.5a	16.3a	62.7a
M3	103.0a	30.4a	6.1ab	50.1a	20.5a	64.2a
M4	104.8a	31.8a	6.4a	51.9a	16.4a	62.1a
LSD ($P = 0.1$)	4.3	2.7	0.6	16.4	4.5	4.8

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 at $P = 0.1$.

(Tables 2–6). It is also clear that AM may differently affect plant growth in S1 and S2 soils according to the interaction between S and M ($P = 0.17$) (Table 6).

In the second experiment leaf fresh and dry weights were numerically reduced in control treatments with increasing compaction in S1 (Table 6). These variables were numerically increased at different levels of compaction

Table 5
The effects of unsterilized and sterilized compacted soils and arbuscular mycorrhiza on soil resistance, corn height, leaf, root fresh and dry weights and root length in the first experiment, (SD, $n = 3$–4)

Level of compaction	AM	Plant height (cm)	Leaf fresh weight (g)	Leaf dry weight (g)	Root fresh weight (g)	Root dry weight (g)	Root length (cm)
Unsterilized soil							
C1	M1	97.5 (11.8)	16.3 (4.2)	3.0 (0.9)	18.7 (9.6)b	2.2 (1.3)ab	62.3 (14.2)
	M2	102.0 (5.9)	16.3 (1.8)	3.0 (0.5)	16.3 (7.8)b	2.0 (0.9)b	56.1 (20.6)
	M3	100.0 (3.6)	17.4 (2.3)	3.2 (0.4)	18.6 (5.8)b	2.1 (0.8)ab	66.3 (7.9)
	M4	102.5 (7.5)	15.9 (2.1)	2.8 (0.5)	18.0 (4.3)b	2.1 (0.6)b	63.1 (9.9)
C2	M1	103.3 (7.6)	18.6 (2.6)	3.4 (0.6)	20.6 (4.0)ab	2.4 (0.3)ab	67.1 (15.9)
	M2	105.0 (8.9)	16.6 (2.4)	3.1 (0.5)	27.9 (9.4)a	3.1 (1.2)a	58.3 (21.8)
	M3	102.8 (14.0)	16.3 (5.0)	2.9 (1.1)	19.9 (2.3)b	2.5 (0.2) ab	69.0 (10.2)
	M4	111.0 (9.5)	16.6 (1.5)	3.1 (0.4)	21.6 (6.8)ab	2.4 (0.9)ab	74.2 (16.7)
C3	M1	103.0 (5.3)	16.3 (1.4)	3.0 (0.2)	21.6 (3.2)ab	2.9 (0.6)ab	69.5 (15.5)
	M2	102.0 (11.5)	18.4 (1.6)	3.2 (0.3)	18.9 (1.0)b	2.3 (0.4)ab	54.0 (4.4)
	M3	107.5 (8.2)	19.6 (2.5)	3.5 (0.5)	24.1 (4.3)ab	2.9 (0.7)ab	74.7 (11.3)
	M4	109.5 (3.9)	18.2 (2.2)	3.4 (0.3)	21.0 (7.4)ab	2.5 (0.8)ab	76.8 (6.2)
Sterilized soil							
C1	M1	103.8 (11.0)	17.4 (3.3)	3.2 (0.6)	16.8 (4.5) b	1.7 (0.6)c	75.5 (4.4)
	M2	105.5 (7.0)	16.2 (5.7)	3.0 (1.2)	19.4(14.7)b	2.1 (1.8)bc	60.7 (12.0)
	M3	105.3 (1.7)	20.0 (3.6)	3.6 (0.6)	25.4(5.4) ab	2.7 (0.6)abc	82.8 (27.5)
	M4	104.3 (8.5)	19.7 (1.3)	3.7 (0.2)	23.9(2.6)ab	2.7 (0.6)abc	69.2 (16.2)
C2	M1	100.3 (6.8)	16.9 (3.8)	3.1 (0.7)	16.0(11.3)b	1.8 (1.1)bc	72.1 (18.1)
	M2	109.8 (9.5)	19.0 (0.7)	3.4 (0.1)	22.6(8.3)ab	2.3 (1.0)bc	78.8 (7.9)
	M3	105.8 (4.8)	19.2 (3.5)	3.5 (0.7)	24.7(8.9)ab	2.8 (1.4)abc	69.0 (14.8)
	M4	105.7 (7.1)	17.6 (1.4)	3.5 (0.1)	31.0(10.7)a	3.6 (1.2)a	75.1 (5.5)
C3	M1	105.3 (15.3)	17.7 (3.6)	3.2 (0.8)	18.6(7.8)b	2.0 (1.0)bc	59.9 (14.2)
	M2	110.0 (14.9)	18.2 (4.5)	3.2 (1.0)	18.4(5.1)b	1.8 (0.6)bc	74.7 (14.0)
	M3	115.3 (1.5)	18.9 (2.2)	3.5 (0.3)	21.1(3.1)ab	2.1 (0.5)bc	73.9 (3.9)
	M4	107.0 (10.1)	19.1 (2.6)	3.6 (0.4)	21.3(1.4)ab	3.0 (0.7)ab	69.0 (5.4)
Model		n.s.	n.s.	n.s.	**	**	n.s.
S		$P = 0.11$	*	*	n.s.	n.s.	*
C		*	n.s.	n.s.	$P = 0.17$	$P = 0.18$	$P = 0.15$
M		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
C*M		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S*M		n.s.	n.s.	n.s.	n.s.	*	n.s.
S*C		n.s	n.s.	n.s.	n.s.	$P = 0.16$	n.s.
S*C*M		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
M1 vs M2		$P = 0.17$	n.s.	n.s.	n.s.	n.s.	n.s.
M1 vs M3		$P = 0.18$	$P = 0.16$	n.s.	$P = 0.17$	n.s.	n.s.
M1 vs M4		$P = 0.12$	n.s.	n.s.	*	*	n.s.
LSD1		11.2	3.5	0.8	8.0	1.0	18.0
LSD2		12.0	4.3	0.9	10.1	1.3	17.9

C1: control, C2: 4 time compaction, C3: 12 time compaction, M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum,* M4: *G. mosseae* (Canadian), SR: Soil resistance. n.s.: not significant, *Significant at 10% probability, **Significant at 5% probability. Values within the same column followed by the same letter(s) are not statistically different at $P = 0.1$.

due to AM in both experiments (Tables 5 and 6, Figs. 1 and 2). Leaf fresh weight increased the highest in treatment S1C3M3 (by 20%) ($P = 0.16$) in the first experiment (Table 5), and treatments S1C3M3 and S2C3M3 in the second experiment (by 27 and 28%, respectively) (Table 6). Compared with control in both experiments treatment S1C3M3 (by 17% and 22%, respectively) resulted in the highest increase in leaf dry weight (Tables 2–6). Soil effects (S1 or S2) on leaf fresh and dry weights were significant (Tables 5 and 6).

AM increased root fresh and dry weights in both experiments at different compaction levels. Although under unsterilized conditions at the highest level of compaction, C4, only M2 was able to increase leaf dry weight, interestingly sterilization made the AM species to perform much better as all species were able to reduce the stressful effects of soil compaction on leaf dry weight (Table 6).

Treatment S2C2M4 resulted in the highest increase in root fresh weight in the first (by 94%) ($P = 0.1$) and second experiment (by 87%), respectively. Contrast comparisons indicated that as compared with control, M4 significantly ($P = 0.1$) increased root fresh and dry weights in the first experiment (Tables 5 and 6).

Soil effect on root fresh weight was significant ($P = 0.05$). The highest increases in root dry weight in the first and second experiment were related to treatments S2C2M4

Table 6
The effects of unsterilized and sterilized compacted soil and arbuscular mycorrhiza on soil resistance, corn height, leaf, root fresh and dry weights and root length in the second experiment, (SD, $n = 3$–4)

Level of compaction	AM	Plant height (cm)	Leaf fresh weight (g)	Leaf dry weight (g)	Root fresh weight (g)	Root dry weight (g)	Root length (cm)
Unsterilized soil							
C1	M1	100.5 (3.5)	27.9 (2.6)ab	5.8 (0.3)	30.8 (19.3)abcd	11.6 (3.5)	62.8 (5.1)
	M2	95.8 (3.9)	26.1 (6.3)ab	5.4 (1.7)	17.5 (11.6)d	10.8 (3.9)	64.5 (5.9)
	M3	105.3 (9.2)	26.6 (8.9)ab	5.6 (1.5)	23.1 (12.4)cd	14.6 (4.6)	64.3 (21.5)
	M4	107.0 (2.0)	31.1 (0.4)a	5.8 (0.4)	32.3 (19.7)abcd	12.2 (2.7)	72.0 (2.6)
C2	M1	106.8 (7.1)	27.6 (3.5)ab	5.3 (0.4)	49.2 (42.0)abcd	21.7 (14.1)	69.5 (13.7)
	M2	105.0 (7.0)	28.0 (3.1)ab	5.7 (0.3)	26.2 (19.5)bcd	11.8 (4.6)	60.8 (11.4)
	M3	98.7 (16.5)	29.6 (12.1)ab	6.2 (2.5)	69.6 (46.7)a	29.9 (17.0)	70.0 (20.1)
	M4	106.8 (8.1)	29.7 (3.9)ab	5.9 (0.4)	30.3 (30.3)abcd	13.0 (4.8)	67.3 (12.1)
C3	M1	97.5 (7.2)	24.8 (6.5)ab	5.0 (1.3)	63.1 (60.9)ab	16.3 (9.0)	64.8 (14.3)
	M2	109.3 (10.7)	30.2 (5.1)ab	5.6 (1.0)	27.1 (14.4)bcd	12.7 (4.6)	56.0 (8.8)
	M3	104.5 (10.9)	31.6 (4.7)a	6.1 (1.7)	39.0 (24.0)abcd	18.9 (8.8)	74.8 (13.8)
	M4	108.3 (4.2)	28.7 (4.3)ab	5.9 (1.0)	59.3 (39.1)abc	19.1 (10.1)	64.8 (16.6)
C4	M1	97.5 (16..9)	24.5 (5.0)ab	5.2 (0.9)	52.6 (29.0)abcd	21.1 (5.9)	58.0 (9.8)
	M2	103.3 (12.1)	28.2 (6.2)ab	5.7 (1.4)	42.9 (38.4)abcd	16.0 (6.6)	56.0 (13.8)
	M3	95.8 (6.8)	23.3 (4.8)b	4.7 (1.6)	39.0 (45.0)abcd	13.0 (8.6)	58.3 (11.7)
	M4	112.8 (8.4)	27.8 (7.8)ab	5.1 (1.5)	31.8 (26.6)abcd	14.0 (5.4)	59.3 (16.5)
Sterilized soil							
C1	M1	102.8 (5.2)	33.4 (5.8)abcde	6.4 (1.1)	45.5 (35.4)	17.7 (15.2)	59.3 (10.3)
	M2	108.8 (1.5)	41.3 (3.5)a	7.4 (0.9)	50.4 (41.8)	21.3 (16.2)	67.0 (6.1)
	M3	106.5 (11.0)	33.2 (8.8)abcde	7.1 (2.1)	36.2 (25.4)	20.4 (9.4)	57.3 (11.2)
	M4	93.5 (6.7)	30.7 (5.5)bcde	6.5 (2.3)	43.7 (65.3)	14.9 (11.1)	55.3 (9.5)
C2	M1	104.0 (9.3)	37.3 (4.1)abcd	6.4 (0.8)	48.6 (36.0)	20.8 (3.4)	62.5 (5.3)
	M2	95.0 (35.4)	29.7 (14.2)cde	5.8 (3.4)	68.1 (96.9)	20.2 (18.1)	55.8 (10.2)
	M3	106.3 (12.3)	28.9 (5.5)de	5.3 (1.3)	61.6 (66.9)	23.2 (24.0)	64.3 (10.0)
	M4	102.5 (6.4)	38.1 (2.1)abc	7.7 (1.6)	91.1 (65.4)	22.8 (7.9)	68.3 (11.3)
C3	M1	95.5 (18.4)	27.6 (5.9)e	5.7 (1.3)	63.1 (47.5)	15.1 (10.7)	62.0 (9.3)
	M2	108.8 (9.1)	35.4 (6.3)abcde	6.6 (1.1)	64.4 (78.5)	14.4 (7.8)	74.8 (19.1)
	M3	106.0 (8.0)	35.4 (7.0)abcde	6.5 (1.3)	80.1 (32.6)	22.0 (2.0)	63.5 (8.1)
	M4	103.3 (9.5)	32.8 (10.0)abcde	6.8 (1.6)	61.2 (37.9)	15.6 (8.7)	58.0 (4.8)
C4	M1	101.0 (4.5)	36.6 (4.8)abcd	6.6 (0.9)	65.9 (55.3)	22.4 (8.5)	59.3 (3.4)
	M2	106.8 (11.5)	39.1 (6.8)ab	7.3 (1.3)	80.6 (56.4)	26.0 (3.5)	66.8 (11.6)
	M3	100.0 (11.3)	36.4 (7.5)abcd	7.3 (1.1)	59.2 (67.9)	26.3 (22.5)	62.3 (5.9)
	M4	105.3 (15.0)	35.3 (5.9)abcde	7.4 (1.9)	58.5 (51.1)	17.7 (14.8)	55.5 (3.7)
Model		n.s.	**	n.s.	**	n.s.	n.s.
S		n.s.	***	***	***	**	n.s.
C		n.s.	n.s.	n.s.	n.s.	n.s.	$P = 0.18$
M		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
C*M		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S*M		$P = 0.17$	n.s.	n.s.	n.s.	n.s.	*
S*C		n.s	n.s.	n.s	n.s.	n.s.	n.s.
S*C*M		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
M1 vs M2		n.s.	$P = 0.14$	n.s.	n.s.	n.s.	n.s.
M1 vs M3		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
M1 vs M4		$P = 0.11$	n.s.	$P = 0.14$	n.s.	n.s.	n.s.
LSD1		11.3	7.1	1.5	39.7	9.8	16.1
LSD2		14.1	8.6	2.0	67.9	16.3	11.5

C1: control, C2: 4 time compaction, C3: 12 time compaction, C4: 20 time compaction. M1: control, M2: *Glomus mosseae* (Iranian), M3: *G. etunicatum,* M4: *G. mosseae* (Canadian). SR: Soil resistance. n.s.: not significant, *Significant at 10% probability, **Significant at 5% probability. Values within the same column, followed by the same letter(s) are not statistically different at $P = 0.1$.

(by 100%) and S2C3M3 (by 31%), respectively. The interaction effect between soil and AM was significant ($P = 10\%$) (Tables 2–6).

Treatment S2C3M2 resulted in the highest increases in root length in the first (by 25%) and second experiment (by 21%). In the first experiment the effect of soil on root length was significant ($P = 0.1$). In both experiments the highest level of compaction decreased root length. The interaction effect of soil and AM is significant ($P = 0.1$) (Tables 2–6).

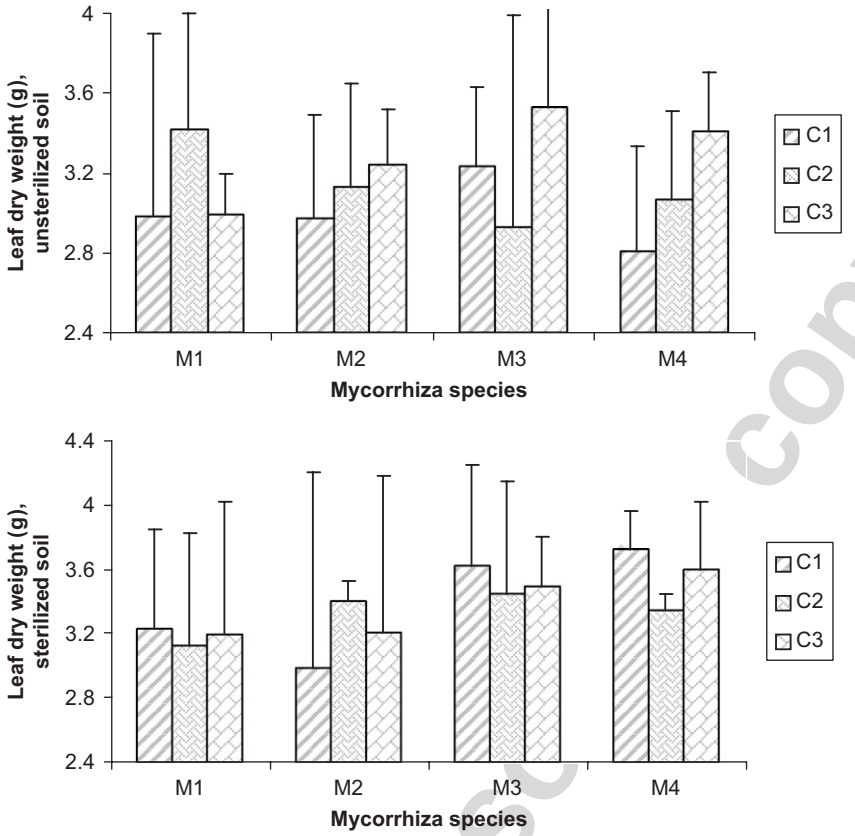

Fig. 1. The effects of different species of arbuscular mycorrhiza at different compaction levels on corn shoot dry weight (g) in the first experiment.

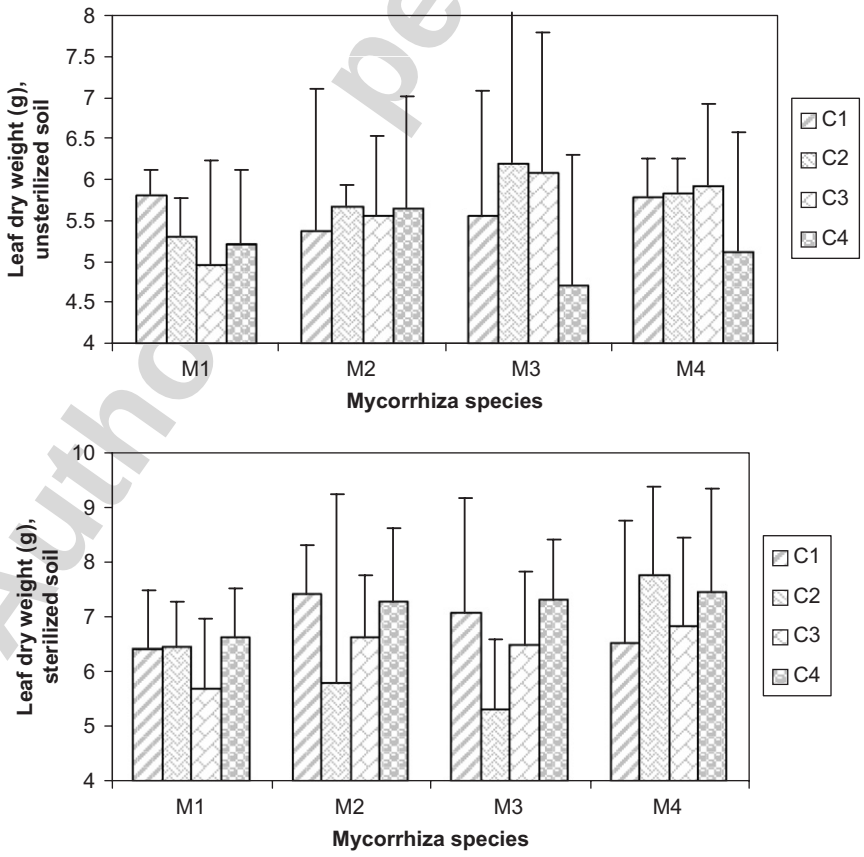

Fig. 2. The effects of different species of arbuscular mycorrhiza at different compaction levels on corn shoot dry weight (g) in the second experiment.

4. Discussion

4.1. Effects of soil moisture

Increasing moisture up to some level reduces soil resistance. The data shows that, in general, higher levels of moisture decreased soil resistance, which is in agreement with the findings of Whalley et al. (1995) and Passioura (2002).

4.2. Interactions between AM and other soil microorganisms

Sterilization significantly improved plant growth, which is in agreement with Passioura (2002). In addition to plant roots, microorganisms are also able to send inhibitory signals (for example abscisic acid) to plant shoots (Müller et al., 1989; Hartung et al., 1996). To prove the presence of inhibitory root to shoot signals scientists have stated that even through providing the plant with adequate amount of water and nutrients under stressful conditions still the signs of plant growth reduction appear (Passioura, 2002).

The interactions between AM and other soil microorganisms are very important due to their significant impact on sustainable agricultural systems via affecting soil fertility and, hence crop production (Johansson et al., 2004). The mechanisms, involved in the interactions between AM and bacteria are not very well understood yet. However, with the help of novel approaches such as PCR, isotopic and molecular markers methods the recognition of processes related to the activity, identity and also location of bacteria in the mycorrhizosphere has become likely (de Boer et al., 2005).

There are two ways by which AM may influence microbial community in the rhizosphere; the direct effects of AM hypha and its excreted products and the indirect effects of AM on microorganisms (Marschner and Baumann, 2003) through affecting rhizodeposition (Linderman, 1988). AM are able to affect microbial communities in the soil through providing high energy products via their hypha (Andrade et al., 1997), improving soil structure (Rillig and Mummey, 2006), competing for nutrient uptake (Ravnskov et al., 1999) and altering root exudates (Soderberg et al., 2002). Some soil bacteria such as *Bacillus* sp. are able to attach to AM hypha, and, hence interact with AM (Toljander et al., 2006).

In other words, the differences in plant growth at S1 and S2 soils at different compaction levels, treated with different AM species may be attributed to the competition and interaction effects between microorganisms. AM and soil beneficial microorganisms are synergistic (Belimove et al., 1999) and AM and soil pathogens are anthagonistic and this is another reason that AM enhances plant growth (Santhi and Sundarbabu, 1995). Since AM utilizes some root exudates and modifies root activities, microbial population in mycorrhizosphere and rhizosphere are different (Garbaye, 1991). Enhanced phosphorus uptake in mycorrhizal symbiosis reduces membrane permeability affecting the quantity and quality of root exudates (Mada and Bagyaraj, 1993) and hence results in substantial changes in rhizosphere microorganisms (Schwab et al., 1983).

Some bacteria may affect AM growth through stimulating processes, related to AM establishment such as spore germination and growth (Toljander et al., 2006). Researchers have stated that AM and soil bacteria are very much interactive (Soderberg et al., 2002), presumably through exchanging signal molecules and metabolite products (Toljander et al., 2006).

4.3. Effects of soil compaction

The effect of soil compaction on different plant parameters was significant. Different species of AM increased corn height, at different compaction levels in both experiments.

Root growth increased with increasing compaction. Usually under stressful conditions plants allocate more C to the roots and hence shoot growth is more affected. Also according to Jones et al. (1991) and Amato and Ritchie (2002) the increase in soil bulk density up to some level does not adversely affect root growth and higher levels of bulk density reduces root growth and distribution.

Root dry weight for S1 and S2 is the same but root length of S2 is significantly longer than that of S1. The reason is that root dry weight is related to the complete roots, but root length is related to the longest roots, re-verifying the effect of AM in sterilized soil on root growth and allocation of more C to the roots, specifically to the longest root.

Root dry weight for S1 is significantly less than that of S2 but root length of S2 is similar to that of S1. This may be attributed to the interference from other soil microorganisms for AM leading to higher root growth or higher C allocation to the roots under stress in S2, however AM, in a synergistic situation with other soil microorganisms, might have been able to increase root length in both soils.

Dry root weight of experiment 1 is probably significantly less than that of experiment 2 and yet the root length of experiment 1 is longer compared to that of experiment 2. The reason is that in the second experiment we increased the level of compaction to 20 times weight releasing, which might have limited the root growth.

AM significantly increased root growth, which is in agreement with Harrison (1997a) and AL Karaki and Clark (1998). This is because in mycorrhizal plants the fungal hypha increase root surface area resulting in exploring higher volume of soil and overcoming the water and nutrient depletion zones around the roots leading to increased water and nutrient uptake (Clark and Zeto, 2002). Mycorrhizal symbiosis also affects physiological parameters. These fungi increase the rate of photosynthesis and carbon allocation (Paul et al., 1984) and enhance the production of phytohormones such as cytokinins and

gibberellins (Barea and Azcon-Aguilar, 1982; Suresh and Bagyaraj, 2002).

Plants are able to develop mechanisms that are responsible for controlling root growth under different nutrient concentrations through their signaling and hence, sensing pathways. Plants are able to modify their root growth in a heterogeneous soil to more efficiently take up water and nutrients (Walch-Liu et al., 2006a). For example, Walch-Liu et al. (2006b) have stated that the exogenously applied signal molecule L-glutamate may be able to modify root growth and branching. However, it seems from our results that roots of a mycorrhizal plant may act more efficiently in this regard in a compacted soil.

Soil texture is an important parameter affecting soil compaction. Higher rates of clay may increase the compactability of soil to a higher extent. This is the reason we used a soil with higher clay, as clear from the saturation percentage (Table 1a), in the second experiment.

In a compacted soil, due to increased soil resistance, usually roots grow with a cluster distribution, limiting the uptake of water and nutrient. AM hypha (2–3 μM) are thinner even than the finest root hairs (<10 μM), enabling them to grow inside the very fine micro-pores in compacted soils, and hence increase water and nutrient uptake. This may be one of the main reasons explaining the important role of AM to alleviate the stress of compaction. Other reasons may be attributed to high volume of hypha and also the excretion of a glyco protein called glomalin by AM hypha, resulting in improved soil structure in compacted soils (Rillig, and Mummey, 2006).

For control treatments with increasing compaction root length decreased (Passioura, 2002), while for mycorrhizal treatments root length increased. These show the unfavorable effects of soil compaction on root length and the enhancing effects of AM on root length in compacted soils.

The second level of compaction increased corn root, shoot dry weight and root length and C3 and C4 decreased these parameters in the control treatments. The extent to which AM was able to overcome the stressful effects of soil compaction on corn growth was dependent on the level of compaction, which is in agreement with the results by (Entry et al., 1996; Nadian et al., 1997; Yano et al., 1998; Miransari et al., 2006 unpublished data).

4.4. Conclusion

While it is clear from our results that high levels of compaction may adversely affect plant growth (Passioura, 2002), AM may enhance plant resistance to compaction stress. The unique characteristic of AM may help the mycorrhizal plants grow better in compacted soils compared with non-mycorrhizal plants. This may also be attributed to the communications between the two partners through the exchange of signal molecules. Since AM and other soil microorganisms, are very much interactive, AM may behave differently in unsterilized and sterilized compacted soils. Although the Iranian *Glomus etunicatum* and Canadian *G. mosseae* performed better under stress, the Iranian *G. mosseae* was also able to cope with the stress in situations where the other two species were not able to. AM may overcome the stressful effects of soil compaction on corn growth, but its effectiveness may be dependent on the level of compaction.

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