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Effects of arbuscular mycorrhiza, soil sterilization, and soil compaction on wheat (*Triticum aestivum* L.) nutrients uptake

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ABSTRACT

The stress of soil compaction, because of using agricultural machinery, may provide conditions such as limiting nutrient uptake, not suitable for plant growth. Here we hypothesized that using arbuscular mycorrhiza (AM, plant symbiotic fungi), as a biological method, may overcome the stress of soil compaction on wheat (*Triticum aestivum* L.) growth by enhancing nutrient uptake. Soil surface layer of the Experimental Research Field of Soil and Water Research Institute in Karaj, Iran, was sieved, sterilized, and compacted at 10 kg pots in two experiments. At seeding wheat seeds were inoculated with different species of Glomus fungi with different origins. Shoot nutrient uptake of N, P, K, Fe, Mn, Zn, Cu was determined. Soil sterilization significantly increased the nutrient uptake of mycorrhizal wheat even at the highest level of compaction. Even under compacted conditions, increased P uptake, due to AM inoculation had an important role to alleviate the stress. This novel finding may indicate the important role of AM to overcome the stress of soil compaction on wheat nutrient uptake, the independency of AM origin on their functionality, and the great importance of managing soil biological communities in agricultural systems.

1. Introduction

1.1. Soil compaction and plant growth

Soil compaction, which is resulted by using agricultural machinery in the field, may adversely affect plant growth and hence yield production. The initial effects are on the root growth, i.e. limited nutrient uptake, which eventually influences the entire plant growth because of root to shoot signals (Passioura, 2002).

Some of the signs related to plant growth under field compacted conditions are decreased plant growth and height, pale leaf, cluster growth and pan cake like growth of roots (Miransari et al., 2006). Soil compaction influences soil structure and hence, soil porosity, through reducing macropores, while micropores are partially affected (Tardieu, 1994). This may result in the diminished movement of soil gases such as oxygen, necessary for plant and microorganisms activities, decreased nutrient uptake and, hence, plant growth (Nadian et al., 1997). In such a situation, the reduction of other electron receivers such as NO_3 results in the release of N_2 and hence the amount of N required for plant growth decreases (Soane and van Ouwerkerk, 1995). This is one of the main reasons why N efficiency is reduced in compacted soils and more N should be applied (particularly in organic form), which is of environmental and economical significance.

In addition, because of reduced oxygen and slow movement of gases, CO_2 (the product of cellular respiration) accumulates in the soil, which is eventually emitted from the soil as CO_2 or CH_4 (Soane and van Ouwerkerk, 1995).

1.2. Role of AM in nutrients uptake

Arbuscular mycorrhiza (AM) is soil fungi, developing symbiotic association with most terrestrial plants. When the soil conditions are suitable, the fungal spores germinate and through some signal communications (which is somehow similar to the signal exchange process between the rhizobia and legumes, Miransari and Smith, 2007, 2008, 2009) begin their symbiosis with the host plant (Boglárka et al., 2005). In the association between the AM fungi and the host plant, AM provide nutrients, especially P, for the host plant and receive the necessary C from the host plant (Jakobsen, 1995).

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Abbreviations: S0, unsterilized soil; S1, sterilized soil; C0, control; C4, 4 times compaction; C12, 12 times compaction; C20, 20 times compaction; G0, control; Gml, *Glomus mosseae* (Iranian); Gtl, *G. etunicatum* (Iranian); GmC, *G. mosseae* (Canadian).

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AM also increases the solubility of some immobile nutrients such as P, Zn and Cu by producing some enzymes such as phosphatase (Marschener and Dell, 1994). Usually AM performs best in soils with low or medium fertility, because under such conditions it is beneficiary for the host plant to develop symbiosis with the fungi.

1.3. AM and soil compaction

It is very important for the plant to adopt itself with conditions, such as compacted soils, for survival. In such a situation, due to increased soil resistance, plant root adjust the hormonal balance and hence, plant growth by sending root to shoot signals (Pardo et al., 2000).

Due to the unique properties of AM including their very thin and high volume of hypha, which is much finer even than root hairs (this can be very beneficial in a compacted soil), mycorrhizal plants can adsorb higher rate of nutrients, resulting in plant-enhanced growth. AM also enhances soil aggregate stability by its network of hypha, which may be very beneficiary in a compacted soil where the soil structure reduces considerably. In addition, AM produces a glyco protein called glomalin, which is able to bind soil particles and hence, improve soil structure and stability (Rillig and Mummey, 2006). These effects are all beneficiary to plant growth, resulting in the enhanced availability of nutrients to the plant.

1.4. AM and other soil microorganisms

There are different kinds of soil microorganisms in the soil, competing for soil resources (Calvet et al., 2002). Hence, it is very important to evaluate how AM may act in the presence or absence of other microorganisms under stressful conditions including soil compaction. Usually under stress-free conditions, the competition may be synergistic or antagonistic. However, under stressful conditions plant response to the competition between AM and other microorganisms may be different (Calvet et al., 2002). The results of this experiment will also address this question. Hence, we sterilized the soil to be able to recognize the functionality of AM under compacted conditions in the presence or absence of other soil microorganisms.

Since to our knowledge there is not any data on the effects of different species of AM with different origins on wheat nutrient uptake and, hence, growth in a compacted soil, under sterilized or unsterilized conditions, and with regard to the great properties of AM we hypothesized and conducted this research work. The objectives were to: (1) evaluate the stress of soil compaction on wheat nutrient uptake and, (2) evaluate whether inoculation of wheat seeds with different species of AM with different origin enhance plant growth in a compacted soil through enhancing nutrient uptake.

2. Materials and methods

2.1. Soil characteristics and measurements

Two experiments were conducted. In both experiments soil surface layer (0–30 cm) (S0), a Xeric Haplocalcids (Banaei, 2000), of the research field of Soil and Water Research Institute at Meshkin-Dasht, Karaj, Iran, was air dried and sieved. The Soil was then transferred to 10 kg pots, measuring 20 cm × 20 cm, while half of it was sterilized (S1) at 121 °C and at high vapor pressure for an hour using an autoclave (Toshihiro et al., 2004). Soil physical and chemical properties were determined (Miransari et al., 2008).

2.2. Soil treatments and measurements

Relative to the first experiment, 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., 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. It produces slight compaction gradient in the soil profile and hence plant roots behave very similar to the field conditions (Miransari et al., 2007, 2008, 2009).

The reason to use dry soil instead of moist soil was to avoid excessive hardness, which may be more stressful to the root growth. The compaction levels were selected according to Barzegar et al. (2000) and according to our own testing, meaning that the 20 times compaction was the highest likely compaction, we were able to create in the pots (Miransari et al., 2007, 2008, 2009). 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.

The pot soils were compacted using 2 kg weights, released from a 20 cm height. In the first experiment, the pot soils were subjected to the compaction levels of 4 (C4) and 12 times (C12) weight release and in the second experiment a 20 times compaction (C20) treatment was also applied. For both experiments a non-compacted soil, as control, (C0) was used (Miransari et al., 2007, 2008, 2009). 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.

The bulk densities of pot soils were measured. Soil bulk density was determined using a 100 cm^3 cylinder 3 times during the growing season and six measurements per replication (Miransari et al., 2007, 2008). The soil resistances at certain moisture were determined 3 times during the growing period for different pots using a penetrometer (Model Cernusco 20063). The tip of the penetrometer was 20 mm long and it had a maximum diameter of 12 mm. When measuring soil resistance, soil moisture was determined at 105 °C using an oven.

2.3. Experimental method

Experimental designs were 2 × 3 × 4 and 2 × 4 × 4 factorials based on completely randomized block in the first and second experiments, respectively. The duration of both experiments was four months. The first experiment was conducted in a growth chamber with an average temperature of 24 °C, in which plants received 14 h of florescent light, and since more space was required for the second experiment, the second experiment was conducted in a greenhouse, with a an average temperature of 27 °C, in which plants received natural light.

In the first treatments including: (1) non-sterilized and sterilized soils, (2) three levels of soil compaction with the bulk densities of 1.2, 1.34 and 1.41 g cm^{-3} and 3) wheat (*Triticum aestivum* L.) seeds inoculation with four levels of mycorrhizal species including control were tested. In the second experiment, the same treatments were used however; four levels of soil compaction with bulk densities of 1.18, 1.24, 1.39, and 1.54 g cm^{-3} were tested. Therefore, there were 24 and 32 treatments in four replicates in the first and second experiments, respectively. Four seeds of wheat were planted in each pot and were thinned to one plant after germination. At seeding mycorrhizal species, which had already been produced (Feldmann and Idczak, 1992) on sorghum roots in sterilized sand in a four month period, were added

underneath the seeds as much as 1.6 g, including 80 ± 10 active propagules (Toshihiro et al., 2004; Sood, 2003). Mycorrhizal treatments included control (without mycorrhiza) (G0), *Glomus mosseae* (GmI) and *G. etunicatum* (GtI) both isolated from the Iranian soils, and *G. mosseae* (GmC) received from GINCO (Glomales *In Vitro* Collection), Canada.

Before conducting the experiments, the total active propagules of mycorrhizal fungi in inoculums were determined using the most probable number (MPN) method (Feldmann and Idczak, 1992). Hence, using plastic bags to mix AM and sterilized sand thoroughly, 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 one month. Roots were stained to observe AM inoculation at different dilutions. Using microscopy observation and statistical tables the fungi active propagules were determined (Mahaveer et al., 2000).

Enough water was added to the pots so that excess water was drained 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 used twice for each pot.

2.4. Measurements of plant parameters

Wheat shoots were analyzed for the concentration 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 spectrophotometry) (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 Perkin Elmer 3110).

Nutrient uptake of N, P, and K was calculated using this formula: $(A \times B)/100$ in which A is shoot N, P, or K percentage and B is shoot dry weight. For Fe, Mn, Zn and Cu using this 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 shoot dry weight, nutrient uptake was calculated.

2.5. Statistical analysis

Using SAS (SAS Institute Inc., 1988) data were analyzed and 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).

3. Results

The effects of unsterilized and sterilized compacted soils and arbuscular mycorrhiza on soil resistance in the first and second experiments are presented in Table 1. Soil sterilization significantly increased the uptake of Mn in the first and the uptake of N, Mn, Zn and Cu in the second experiment (Table 2). AM enhanced N uptake at different levels of compaction in both experiments (Tables 3 and 4) and significantly for S1GtI in the first experiment (Table 3). Even with increasing the compaction levels (C12 and C20) in both experiments, different species of AM alleviated the stress. Although in the first experiment increased compaction suppressed the abilities of AM species to alleviate the compaction stress, soil sterilization resulted in enhanced N uptake by mycorrhizal wheat even at C12 (Tables 3, 4 and 6).

In the second experiment the situation was a little bit different, although increased compaction influenced AM ability (for example at S1C12) for nutrients uptake, species such as GmC in S0C20 and GmI in S1C20 enhanced wheat N uptake (Tables 3, 4 and 6). The highest increase was related to treatment S1C12GtI (81%) in comparison with control in the first experiment.

AM species increased P uptake in both experiments, significantly for S1GtI in the second experiment (Tables 3, 4 and 6). Similar to N, increased compaction (S0C12 and S1C4) reduced the ability of AM to enhance P uptake, but soil sterilization (removal of competing soil microorganisms) enabled the AM species to alleviate the stress at C12 in the first experiment (Tables 3, 4 and 6). In the second experiment, P uptake increased due to AM species at different levels of soil compaction, but at S0C20 only GmC was able to alleviate the stress, while at S1C20, species GmI and GtI resulted in enhanced P uptake. Like N, treatment S1C12GtI enhanced P uptake considerably (131%) in the first experiment and treatment S1C4GtI increased P uptake at the highest (142%), relative to control in the second experiment (Tables 3, 4 and 6).

While in the first experiment and in S1 soil GtI and GmC significantly increased K uptake at different levels of compaction (Table 3), in the second experiment AM species numerically enhanced K uptake by mycorrhizal wheat. At S0C12, increased compaction reduced K uptake by different species of AM and soil sterilization resulted in enhanced K uptake by mycorrhizal wheat, compared with control (Tables 3, 4 and 6). In the second experiment and in S0 soil AM inoculation increased K uptake, especially at the higher levels of compaction, though the

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

Level of compaction	SR1 (MPa)	SR2 (MPa)	SR3 (MPa)
First experiment, unsterilized soil			
C0	0.595 (0.07)	0.655 (0.16)	0.6575 (0.13)
C4	0.845 (0.18)	0.98 (0.22)	0.9225 (0.17)
C12	0.8925 (0.18)	0.9425 (0.28)	0.955 (0.17)
Sterilized soil			
C0	0.5625 (0.10)	0.6425 (0.15)	0.6575 (0.14)
C4	0.7525 (0.18)	0.9775 (0.33)	0.8925 (0.25)
C12	0.875 (0.16)	1.05 (0.23)	0.965 (0.13)
Second experiment, unsterilized soil			
C0	0.61 (0.01)	0.64 (0.07)	0.62 (0.05)
C4	0.78 (0.03)	0.75 (0.08)	0.76 (0.07)
C12	0.98 (0.06)	0.95 (0.07)	0.96 (0.04)
C20	1.13 (0.16)	1.08 (0.05)	1.07 (0.03)
Second experiment, sterilized soil			
C0	0.65 (0.04)	0.64 (0.07)	0.62 (0.05)
C4	0.80 (0.06)	0.75 (0.08)	0.76 (0.07)
C12	1.05 (0.07)	0.95 (0.07)	0.96 (0.04)
C20	1.24 (0.09)	1.08 (0.05)	1.07 (0.03)

C0: control, C4: 4 times compaction, C12: 12 times compaction, C20: 20 times compaction. SR: soil resistance.

Table 2
Mean comparisons of wheat nutrient uptake (per plant) in unsterilized and sterilized soils at all levels of compaction in the first ($n = 40$–44) and second experiments ($n = 57$–58).

Soil	N (mg)	P (mg)	K (mg)	Fe (mg)	Mn (mg)	Zn (mg)	Cu (mg)
First experiment							
S0	60a	7a	96a	0.44a	0.26b	0.18a	0.017a
S1	63a	6a	97a	0.57a	0.38a	0.25a	0.016a
LSD	14	2	24	0.22	0.07	0.08	0.005
Second experiment							
S0	58b	4a	142a	1.15a	0.23b	0.14b	0.061b
S1	77a	4a	140a	1.06a	0.37a	0.21a	0.069a
LSD	10.1	0.7	13	0.30	0.06	0.06	0.008

S0: unsterilized soil, S1: sterilized soil. Values within the same column followed by different letter(s) are statistically different using protected least significant difference (LSD) test at $P = 0.05$.

Table 3
Mean comparisons of wheat nutrient uptake (per plant) 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)	P (mg)	K (mg)	Fe (mg)	Mn (mg)	Zn (mg)	Cu (mg)
First experiment (S0)							
G0	57a	6.6a	90a	0.512a	0.244a	0.140a	0.018a
GmI	60a	6.9a	103a	0.449a	0.260a	0.225a	0.022a
GtI	60a	6.6a	90a	0.381a	0.244a	0.189a	0.015a
GmC	62a	7.6a	103a	0.426a	0.288a	0.170a	0.013a
LSD	33	3.6	57	0.332	0.114	0.124	0.011
First experiment (S1)							
G0	50b	5.3a	71b	0.544a	0.277c	0.182b	0.014a
GmI	58ab	5.9a	91ab	0.544a	0.350bc	0.188b	0.015a
GtI	74a	7.3a	107ab	0.556a	0.430ab	0.238ab	0.014a
GmC	70ab	6.4a	123a	0.599a	0.489a	0.408a	0.019a
LSD	27	2.9	41	0.423	0.152	0.199	0.010
Second experiment (S0)							
G0	58a	4.0a	137a	1.159a	0.233a	0.138a	0.058a
GmI	56a	3.8a	147a	1.097a	0.228a	0.135a	0.065a
GtI	57a	3.9a	140a	1.143a	0.246a	0.145a	0.062a
GmC	59a	4.1a	145a	0.809a	0.225a	0.155a	0.059a
LSD	13	1.4	23	0.48	0.052	0.034	0.013
Second experiment (S1)							
G0	82a	2.9a	140a	1.099ab	0.338a	0.169a	0.067a
GmI	74a	4.2a	143a	1.588a	0.378a	0.283a	0.071a
GtI	80a	4.6a	144a	1.113ab	0.381a	0.209a	0.069a
GmC	73a	3.5a	134a	0.819b	0.373a	0.175a	0.071a
LSD	27	1.8	29.4	0.660	0.147	0.151	0.016

S0: unsterilized soil, S1: sterilized soil. Values within the same column followed by different letter(s) are statistically different using protected least significant difference (LSD) test at P = 0.05. G0: control, GmI: *Glomus mosseae* (Iranian), GtI: *G. etunicatum* (Iranian), GmC: *G. mosseae* (Canadian).

Table 4
The effects of arbuscular mycorrhiza in unsterilized and sterilized compacted soils on N, P, and K uptake in wheat (*Triticum aestivum* L.), in the first experiment; means (SE, n = 3–4).

Level of compaction	AM	N (mg/plant)	P (mg/plant)	K (mg/plant)
Unsterilized soil				
C0	G0	50.1 (14)	5.4 (0.8)	76.9 (20)
	GmI	47.7 (22)	5.5 (2.3)	73.9 (31)
	GtI	45.2 (23)	5.2 (2.3)	68.6 (36)
	GmC	86.4 (61)	10.7 (8.8)	144.4 (111)
C4	G0	31.2 (15)	4.4 (1.8)	57.7 (25)
	GmI	66.9 (14)	7.9 (1.9)	119.5 (35)
	GtI	69.9 (7)	7.3 (1.8)	101.8 (37)
	GmC	34.8 (22)	4.2 (1.7)	58.6 (36)
C12	G0	82.0 (77)	9.9 (9.8)	135.3 (140)
	GmI	68.4 (26)	7.6 (2.0)	120.8 (56)
	GtI	69.8 (22)	7.5 (2.4)	110.3 (34)
	GmC	66.4 (13)	8.4 (0.1)	108.3 (40)
Sterilized soil				
C0	G0	42.2 (33)	4.1 (3.0)	67.3 (56)
	GmI	61.3 (42)	6.5 (3.9)	94.3 (80)
	GtI	67.9 (15)	5.9 (1.7)	93.5 (17)
	GmC	62.2 (10)	5.8 (1.6)	114.2 (38)
C4	G0	57.5 (21)	6.9 (3.2)	74.8 (16)
	GmI	47.3 (4)	5.0 (1.5)	78.2 (12)
	GtI	64.7 (28)	5.8 (1.9)	101.4 (44)
	GmC	65.4 (20)	5.8 (1.5)	109.1 (44)
C12	G0	49.2 (21)	4.5 (2.3)	69.7 (27)
	GmI	62.2 (27)	6.2 (2.1)	101.5 (48)
	GtI	89.1 (50)	10.4 (7.1)	125.4 (63)
	GmC	81.6 (26)	7.6 (1.7)	144.1 (67)
Model		n.s.	n.s.	n.s.
S		n.s.	n.s.	n.s.
C		n.s.	*	n.s.
M		n.s.	n.s.	n.s.
C × M		n.s.	n.s.	n.s.
S×M		n.s.	n.s.	n.s.
S×C		n.s.	n.s.	n.s.
S×C×M		n.s.	n.s.	n.s.
G0 vs GmI		n.s.	n.s.	n.s.
G0 vs GtI		n.s.	n.s.	n.s.
G0 vs GmC		n.s.	n.s.	*
LSD1		59.0	6.7	100.0
LSD2		43.0	4.6	70.3

C0: control, C4: 4 times compaction, C12: 12 times compaction. SR1-SR3 stand for soil resistance on the basis of Mega Pascal (MP). G0: control, GmI: *Glomus mosseae* (Iranian), GtI: *G. etunicatum* (Iranian), GmC: *G. mosseae* (Canadian). n.s.: not significant, *, ** and ***: significant at P = 0.1, 0.05 and 0.01, respectively. Values within the same column followed by different letter(s) are statistically different using protected least significant difference (LSD) test at P = 0.05 for unsterilized (LSD1) and sterilized (LSD2) soils.

interaction effect between AM and compaction was not significant. This was also the case in S1 soil but at C20, compaction suppressed AM ability to enhance K uptake, but not for GtI (Table 6). The highest increase in K uptake was related to treatment S1C12GmC (107%) in the first experiment (Table 4).

In the first experiment AM enhanced Fe uptake at C4, at both unsterilized and sterilized soils. The trend of interaction effect (P = 0.13) between AM and compaction is another indication for such increase (Tables 3 and 5). Similar trend was also observed in the second experiment where AM did not enhance Fe uptake at C12 and C20 in S0 and nor at C20 in S1 (with the exception of a slight increase due to GmI). The significant interaction effect of S × C is also another indication to this different behavior of AM at S0 and S1. The species GmI also (P = 0.12) affected Fe uptake in the second experiment. The highest increase in Fe uptake was related to treatment S1C12GmI (242%) in the second experiment (Table 6).

In the first experiment AM species increased Mn uptake in S0C0 and S0C4 and soil sterilization resulted in enhanced Mn uptake by mycorrhizal wheat even at C12. The significant effect of soil also indicates this difference. GtI and GmC significantly increased Mn uptake (Tables 3 and 5). In the second experiment in S0 soil, the ability of AM to enhance Mn uptake diminished with increasing compaction while in S1 soil even at the highest level of compaction AM (GmI) was able to enhance Mn uptake. This is also verified by the trend of S × C interaction effect (P = 0.14) (Table 7). Treatment S1C12GtI enhanced Mn uptake at the highest (92%) in comparison with control in the first experiment (Table 5).

In S0 soil in the first experiment AM increased Zn uptake, and soil sterilization resulted in significant enhancement of Zn uptake even at the highest level of compaction. The significant effect of soil and the trend of interaction effect between S × M (P = 0.17) is a verification to this. The species GmC significantly increased Zn uptake (Tables 3 and 5). In the second experiment AM increased Zn uptake at different levels of compaction, though the increase was at a lesser extent at C20 in both soils. Sterilization enhanced Zn uptake, verified by the significant effect of soil (Table 5). The highest increase was related to treatment S1C12GmI (369%), relative to control (Tables 3 and 7).

In the first experiment and in S0 soil, Cu uptake increased at C0 and C4 due to AM inoculation. In S1 soil although AM did not enhance Cu uptake at C4, soil sterilization resulted in enhanced Cu uptake by mycorrhizal wheat at C12 (Tables 3 and 5). In the second experiment AM enhanced Cu uptake at different levels of compaction but not at C20 in S1 (Tables 3 and 7). Treatment S1C12GmC in the first experiment enhanced Cu uptake at the highest (130%).

4. Discussion

Although under stress-free conditions AM and other soil beneficial microorganisms may be synergistic, it seems from the results of these experiments that under stress a different ecological environment may alter the nature of competition between AM and other microorganisms. When the soil is highly compacted the

Table 5
The effects of arbuscular mycorrhiza in unsterilized and sterilized compacted soils on Fe, Mn, Zn, and Cu uptake in wheat (*Triticum aestivum* L.), in the first experiment; means (SE, $n = 3–4$).

Level of compaction	AM	Fe (mg/plant)	Mn (mg/plant)	Zn (mg/plant)	Cu (mg/plant)
Unsterilized soil					
C0	G0	0.257 (0.09)	0.227 (0.05)	0.139 (0.03)	0.010 (0.003)
	GmI	0.250 ND	0.207 (0.09)	0.120 (0.09)	0.013 (0.001)
	GtI	0.345 (0.10)	0.231 (0.15)	0.162 (0.15)	0.011 (0.004)
	GmC	0.686 (0.50)	0.390 (0.23)	0.246 (0.14)	0.011 (0.001)
C4	G0	0.195 (0.06)	0.122 (0.07)	0.081 (0.04)	0.016 (0.011)
	GmI	0.415 (0.26)	0.294 (0.05)	0.343 (0.31)	0.027 (0.010)
	GtI	0.563 (0.33)	0.263 (0.05)	0.219 (0.10)	0.017 (0.006)
	GmC	0.167 (0.08)	0.155 (0.07)	0.083 (0.05)	0.013 (0.002)
C12	G0	1.338 (1.39)	0.383 (0.34)	0.199 (0.15)	0.035 (0.035)
	GmI	0.600 (0.09)	0.286 (0.08)	0.208 (0.17)	0.022 (0.008)
	GtI	0.295 (0.06)	0.236 (0.07)	0.184 (0.06)	0.017 (0.006)
	GmC	0.424 ND	0.348 (0.05)	0.192 (0.09)	0.016 (0.005)
Sterilized soil					
C0	G0	0.445 (0.30)	0.267 (0.12)c	0.155 (0.17)	0.015 (0.007)
	GmI	1.566 (0.06)	0.367 (0.15)abc	0.220 (0.12)	0.017 (0.013)
	GtI	0.398 (0.17)	0.328 (0.06)abc	0.201 (0.11)	0.012 (0.004)
	GmC	0.337 (0.18)	0.409 (0.07)abc	0.205 (0.07)	0.014 (0.002)
C4	G0	0.251 ND	0.289 (0.10)bc	0.198 (0.16)	0.019 (0.007)
	GmI	0.160 (0.05)	0.285 (0.05)c	0.100 (0.03)	0.009 (0.003)
	GtI	0.631 (0.35)	0.428 (0.24)abc	0.266 (0.19)	0.017 (0.002)
	GmC	0.796 (0.31)	0.507 (0.19)abc	0.439 (0.40)	0.018 (0.007)
C12	G0	1.035 ND	0.276 (0.13)c	0.194 (0.10)	0.010 (0.003)
	GmI	0.416 (0.20)	0.398 (0.19)abc	0.245 (0.16)	0.018 (0.003)
	GtI	0.692 (0.45)	0.535 (0.23)a	0.249 (0.11)	0.015 (0.009)
	GmC	0.583 (0.48)	0.531 (0.26)ab	0.527 (0.59)	0.023 (0.015)
Model		n.s.	*	n.s.	n.s.
S		n.s.	***	*	n.s.
C		n.s.	n.s.	n.s.	**
M		n.s.	**	$P = 0.12$	n.s.
C × M		$P = 0.13$	n.s.	n.s.	n.s.
S × M		n.s.	n.s.	$P = 0.17$	n.s.
S × C		n.s.	n.s.	n.s.	n.s.
S × C × M		$P = 0.14$	n.s.	n.s.	n.s.
G0 vs GmI		n.s.	n.s.	n.s.	n.s.
G0 vs GtI		n.s.	*	n.s.	n.s.
G0 vs GmC		n.s.	**	**	n.s.
LSD1		0.888	0.126	0.217	0.020
LSD2		0.738	0.243	0.352	0.013

C0: control, C4: 4 times compaction, C12: 12 times compaction. G0: control, GmI: *Glomus mosseae* (Iranian), GtI: *G. etunicatum* (Iranian), GmC: *G. mosseae* (Canadian). n.s.: not significant, *, ** and ***: significant at $P = 0.1$, 0.05 and 0.01, respectively. 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 at $P = 0.1$.

competition for soil resources among soil microorganisms increases. Also under conditions such as O_2 deficiency the soil microorganisms including AM may not be very beneficial, compared with a stress-free situation (Standish et al., 2007), because according to the results AM decreased wheat nutrients uptake at the highest level of compaction in the S0 soil (Johnson et al., 1997). Such results indicate the great role of AM under sterilized conditions where AM increased wheat nutrients uptake even at the highest level of compaction (Miransari et al., 2009). In addition soil sterilization may increase the solubility and hence, the availability of nutrients. These reasons may explain the better performance of AM to enhance nutrient uptake in a sterilized compacted soil (Miransari, 2005, PhD thesis; Miransari et al., 2007, 2008, 2009).

While soil compaction decreased N and P uptake at the highest level of compaction (Kristoffersen and Riley, 2005; Barzegar et al., 2006), AM in a compacted sterilized soil, where the soil pathogens are not present, could enhance plant growth through enhancing the N and P uptake. Also similar to the results of Troelstra et al. (2001) in sterilized soil P uptake is more enhanced relative to N and K uptake. Enhanced N and P uptake result in enhanced shoot and root growth, respectively (Miransari et al., 2007, 2008, 2009).

The Fungal spores may grow in the absence of the host plant but for the symbiosis to begin and continue there should be a host plant exchanging signals with the fungi (Boglárka et al., 2005). In such a situation, the AM hypha is able to extensively grow and substantially increases the root surface area resulting in increased water and nutrient uptake (Rillig and Mummey, 2006). This may be the reason why AM is able to enhance plant ability and, hence growth under stressful conditions such as water tension.

Under compacted conditions, since the ecological nature of the soil changes as a result of altered physical, chemical and biological properties there should be some unique abilities to compensate for the stress. AM owns many of these abilities, the most important of which, as stated, are the extensive network of hypha and also the ability of AM to improve soil structure by producing a glyco protein called glomalin (Rillig and Mummey, 2006).

AM increased N uptake even at the highest level of compaction, especially under sterilized conditions. This may be very advantageous to the plant under compaction, since decreased O_2 levels may result in N denitrification and reduce N efficiency. According to He et al. (2003) and Chalk et al. (2006) AM is also able to provide the plant with N, through adsorbing N from the soil, and the biochemical pathways, have been recently specified (Govindarajulu et al., 2005).

In addition to all these unique abilities, AM is also able to produce enzymes such as phosphatase and other enzymes that enhance the solubility and availability of immobile nutrients such

Table 6
The effects of arbuscular mycorrhiza, in unsterilized compacted soils, on N, P, and K uptake in wheat (*Triticum aestivum* L.), in the second experiment; means (SE, $n = 3–4$).

Level of compaction	AM	N (mg/plant)	P (mg/plant)	K (mg/plant)
Unsterilized soil				
C0	G0	41.1 (20)de	2.0 (1.4)e	147.3 (31)
	GmI	57.3 (24)bcde	3.1 (0.7)cde	161.8 (43)
	GtI	46.7 (6)cde	2.4 (1.6)de	135.1 (6)
	GmC	33.7 (11)e	1.8 (1.0)e	138.9 (14)
C4	G0	59.1 (18)bcde	4.2 (2.1)abcde	138.2 (30)
	GmI	48.6 (14)bcde	2.7 (1.3)cde	113.9 (35)
	GtI	63.5 (17)abcd	5.1 (2.3)abcd	139.2 (22)
	GmC	63.4 (19)abcd	4.1 (1.7)bcde	144.1 (37)
C12	G0	59.1 (31)bc	4.4 (3.1)abcde	121.6 (49)
	GmI	67.8 (11)abc	6.7 (2.4)ab	151.8 (30)
	GtI	67.8 (22)abc	5.4 (3.7)abc	152.0 (43)
	GmC	58.5 (11)bcde	4.3 (0.7)abcde	144.7 (18)
C20	G0	73.4 (24)ab	5.2 (2.8)abcd	139.9 (20)
	GmI	52.0 (4)bcde	2.6 (0.7)de	158.6 (20)
	GtI	50.3 (13)bcde	2.8 (1.1)cde	132.0 (30)
	GmC	88.2 (16)a	7.0 (1.7)a	154.4 (30)
Sterilized soil				
C0	G0	65.2 (17)b	2.7 (2.3)c	145.9 (17)
	GmI	62.4 (7)b	3.1 (1.5)c	144.1 (27)
	GtI	88.4 (27)ab	4.0 (1.8)bc	178.1 (42)
	GmC	64.5 (17)b	3.3 (1.5)c	116.5 (25)
C4	G0	73.6 (16)b	3.1 (0.9)c	132.1 (55)
	GmI	82.1 (27)ab	7.1 (4.5)ab	128.6 (20)
	GtI	98.3 (39)ab	7.5 (3.4)a	144.6 (55)
	GmC	90.3 (39)ab	4.8 (3.0)abc	123.1 (24)
C12	G0	125.3 (109)a	2.2 (2.0)c	129.8 (53)
	GmI	73.2 (11)b	2.5 (1.6)c	157.6 (40)
	GtI	70.3 (12)b	2.9 (1.1)c	139.1 (16)
	GmC	72.7 (25)b	2.6 (1.4)c	168.6 (53)
C20	G0	64.5 (8)b	3.6 (1.4)c	150.2 (25)
	GmI	78.8 (26)ab	4.2 (1.3)bc	140.1 (48)
	GtI	62.1 (31)b	3.9 (3.8)bc	115.6 (61)
	GmC	63.1 (23)b	3.4 (1.9)c	126.5 (52)
Model		*	**	n.s.
Block		n.s.	$P = 0.16$	n.s.
S		***	n.s.	n.s.
C		*	**	n.s.
M		n.s.	n.s.	n.s.
C × M		n.s.	n.s	n.s.
S × M		n.s.	n.s.	n.s.
S × C		n.s.	***	n.s.
S × C × M		n.s.	$P = 0.14$	n.s.
G0 vs GmI		n.s.	n.s.	n.s.
G0 vs GtI		n.s.	$P = 0.11$	n.s.
G0 vs GmC		n.s.	n.s.	n.s.
LSD1		26.2	2.8	44
LSD2		50.6	3.3	58.7

C0: control, C4: 4 times compaction, C12: 12 times compaction, C20: 20 times compaction. G0: control, GmI: *Glomus mosseae* (Iranian), GtI: *G. etunicatum* (Iranian), GmC: *G. mosseae* (Canadian). n.s.: not significant, *, ** and ***: significant at $P = 0.1$, 0.05 and 0.01, respectively. 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.

as P, Zn and Cu (Marschener and Dell, 1994). For example, enhanced P uptake is one of the most important benefits resulting from mycorrhizal association, for which plants have specific phosphate transporters (Eckardt, 2005).

Parameters such as root morphology, biochemistry and physiology significantly affect the efficiency of root P uptake (Marschner, 1995). P supply and distribution in the soil are the determining parameters in root growth and development (Forde and Clarkson, 1999; Forde and Lorenzo, 2001). This may be attributed to this interesting finding that AM results in enhanced wheat root growth at a higher rate, compared with shoot growth, under compacted conditions, as a result of increased P uptake, (Miransari et al., 2007, 2008, 2009).

Plant roots use different strategies (Bucher, 2007) to respond to P deficiency including alteration of root architecture (López-Bucio et al., 2003), increased root exudates (Neumann et al., 2000), improved P uptake at low concentrations by adjusting P transferring methods, and stablishing AM symbiosis to enhance nutrient uptake as a result of higher soil exploration by AM hypha (Smith and Gianinazzi-Pearson, 1988; Marschner, 1995).

The fungal hypha is able to grow into even the smallest micropores due to its very fine hypha (average diameter 3–4 μM), which is much finer than even the finest root hairs (10 μM) (Jakobsen, 1995). This may also be a big advantage for the host plant to grow more extensively in a compacted soil.

Another important parameter in determining the availability of nutrients in the soil is their chemical behavior. Despite P, Zn and Cu, which are not very soluble in the soil, N products are of high mobility and are easily subjected to chemical changes through oxidation and reduction (mineralization and denitrification) processes. K is actively adsorbed by the plant roots and the availability of Fe and Mn is determined by their oxidation/reduction potential.

Environmental stresses such as salinity, acidity, suboptimal root zone temperature and soil compaction may adversely affect plant growth and, hence yield (Miransari et al., 2007, 2008, 2009; Miransari and Smith, 2007, 2008, 2009). Determination and evaluation of mechanisms, envolved in plant adoptation and resistance under these conditions may greatly help the researchers to find solutions and suggestions, applicable to control the stresses.

It can be stated from the results of this experiment that nutrient uptake in wheat is less sensitive to the stress of soil compaction in comparison with corn (Miransari et al., 2007, 2008, 2009). This may be attributed to the different root architecture in these two plants. Corn roots extend much larger and are higher in diameter and would require to spend much more energy to grow in a compacted soil, while wheat roots develop less and since they are finer they grow more easily into micropores in a compacted soil. However. For both plants AM was very effective in alleviating the compaction stress through enhancing nutrients uptake (Miransari et al., 2009).

Also it is clear from the results that GtI and GmC species are more able to cope with the stress of soil compaction although there were situations where GmI was capable of handling the stress. Therefore, the origin of AM species may not affect their function, this can be very advantageous under different conditions (Miransari et al., 2007, 2008, 2009). Though many similarities were observed between the two experiments, the slight differences, may be attributed to the slight differences in growing conditions. These results are similar to the results of Daei et al. (in press) indicating that *G. etunicatum* and *G. mosseae* are the most efficient species to enhance wheat growth and nutrients uptake under field saline conditions.

While these results are very interestingly complementary to the corn experiments (Miransari et al., 2009) the similarities and differences may be used for the proper cultivation of corn and wheat under compacted conditions and hence higher crop production.

4.1. Conclusion

We can conclude that: (1) one of the main reasons that enables the mycorrhizal wheat to partially or completely overcome the stress of soil compaction is enhanced nutrient uptake, compared with non-mycorrhizal wheat, (2) soil sterilization significantly increased the nutrient uptake of mycorrhizal wheat even at the highest level of compaction, (3) even under compacted conditions increased P uptake, due to AM inoculation, had an important role to alleviate the stress, (4) this novel finding may indicate the role of

Table 7
The effects of arbuscular mycorrhiza in unsterilized and sterilized compacted soils on Fe, Mn, Zn, and Cu uptake in wheat (*Triticum aestivum* L.), in the second experiment; means (SE, $n = 3–4$).

Level of compaction	AM	Fe (mg/plant)	Mn (mg/plant)	Zn (mg/plant)	Cu (mg/plant)
Unsterilized soil					
C0	G0	0.703 (0.47)	0.165 (0.05)	0.105 (0.02)	0.066 (0.02)ab
	GmI	1.591 (1.02)	0.277 (0.09)	0.135 (0.02)	0.069 (0.01)ab
	GtI	1.331 (1.22)	0.216 (0.07)	0.126 (0.03)	0.068 (0.02)ab
	GmC	0.983 (0.71)	0.177 (0.09)	0.088 (0.03)	0.052 (0.01)b
C4	G0	0.693 (0.18)	0.203 (0.07)	0.143 (0.05)	0.059 (0.03)ab
	GmI	0.644 (0.22)	0.162 (0.03)	0.122 (0.01)	0.049 (0.02)b
	GtI	1.313 (0.70)	0.285 (0.06)	0.145 (0.03)	0.058 (0.01)ab
	GmC	0.731 (0.41)	0.204 (0.10)	0.184 (0.11)	0.062 (0.03)ab
C12	G0	1.379 (0.27)	0.252 (0.10)	0.136 (0.09)	0.044 (0.02)b
	GmI	0.730 (0.36)	0.185 (0.09)	0.162 (0.02)	0.058 (0.02)ab
	GtI	0.974 (0.53)	0.248 (0.15)	0.180 (0.09)	0.064 (0.02)ab
	GmC	0.728 (0.24)	0.260 (0.08)	0.159 (0.01)	0.052 (0.02)b
C20	G0	1.859 (2.07)	0.314 (0.22)	0.167 (0.03)	0.064 (0.03)ab
	GmI	1.424 (0.60)	0.287 (0.15)	0.119 (0.02)	0.086 (0.03)a
	GtI	0.954 (0.62)	0.234 (0.11)	0.127 (0.02)	0.059 (0.02)ab
	GmC	0.789 (0.24)	0.269 (0.09)	0.200 (0.04)	0.074 (0.02)ab
Sterilized soil					
C0	G0	1.098 (0.32)	0.336 (0.16)	0.174 (0.05)	0.072 (0.02)abc
	GmI	1.071 (0.56)	0.329 (0.12)	0.171 (0.05)	0.069 (0.02)abc
	GtI	1.725 (1.61)	0.434 (0.21)	0.221 (0.08)	0.088 (0.03)ab
	GmC	0.486 (0.07)	0.241 (0.09)	0.148 (0.05)	0.055 (0.01)bc
C4	G0	1.692 (0.74)	0.358 (0.11)	0.169 (0.03)	0.063 (0.03)bc
	GmI	2.529 (2.39)	0.349 (0.16)	0.192 (0.11)	0.064 (0.02)bc
	GtI	1.403 (1.08)	0.455 (0.26)	0.254 (0.09)	0.071 (0.02)abc
	GmC	0.772 (0.48)	0.435 (0.29)	0.199 (0.09)	0.069 (0.02)abc
C12	G0	0.471 (0.21)	0.362 (0.37)	0.161 (0.09)	0.063 (0.04)bc
	GmI	1.611 (1.42)	0.467 (0.23)	0.594 (0.82)	0.082 (0.03)abc
	GtI	0.816 (0.14)	0.372 (0.28)	0.176 (0.05)	0.066 (0.01)abc
	GmC	1.322 (0.60)	0.526 (0.17)	0.200 (0.04)	0.101 (0.04)a
C20	G0	1.133 (0.49)	0.295 (0.09)	0.171 (0.02)	0.069 (0.01)abc
	GmI	1.139 (1.13)	0.368 (0.22)	0.176 (0.05)	0.069 (0.04)abc
	GtI	0.507 (0.21)	0.261 (0.15)	0.187 (0.10)	0.051 (0.03)c
	GmC	0.696 (0.51)	0.291 (0.12)	0.153 (0.05)	0.060 (0.01)bc
Model		n.s.	*	n.s.	*
Block		**	**	n.s.	**
S		n.s.	***	**	**
C		n.s.	n.s.	n.s.	n.s.
M		$P = 0.12$	n.s.	n.s.	n.s.
C × M		n.s.	n.s.	n.s.	$P = 0.15$
S × M		n.s.	n.s.	n.s.	n.s.
S × C		*	$P = 0.14$	n.s.	**
S × C × M		n.s.	n.s.	n.s.	n.s.
G0 vs GmI		n.s.	n.s.	n.s.	n.s.
G0 vs GtI		n.s.	n.s.	n.s.	n.s.
G0 vs GmC		n.s.	n.s.	n.s.	n.s.
LSD1		1.126	0.125	0.073	0.03
LSD2		1.37	0.298	0.31	0.036

C0: control, C4: 4 times compaction, C12: 12 times compaction, C20: 20 times compaction.
G0: control, GmI: *Glomus mosseae* (Iranian), GtI: *G. etunicatum* (Iranian), GmC: *G. mosseae* (Canadian). n.s.: not significant, *, ** and ***: significant at $P = 0.1$, 0.05 and 0.01, respectively. Values within the same column followed by different letter(s) are statistically different using protected least significant difference (LSD) test at $P = 0.1$ for unsterilized (LSD1) and sterilized (LSD2) soils.

AM to overcome the stress of soil compaction on wheat nutrient uptake, the independency of AM functionality to their origin, and also the great importance of managing soil biological communities in agricultural systems.

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