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Using arbuscular mycorrhiza to alleviate the stress of soil compaction on wheat (*Triticum aestivum* L.) growth

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

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Abstract

Since large areas of agricultural fields in the world become compacted every year, much effort has been made to reduce the adverse effects of soil compaction on plant growth. Mechanical methods to control soil compaction may be laborious and expensive; however, biological methods such as using arbuscular mycorrhiza (AM) may be more useful, economically and environmentally. The objectives of this study were: (1) to evaluate the effects of soil compaction on wheat (*Triticum aestivum* L.) growth, and (2) to evaluate if using AM of different origin can reduce the stressful effects of soil compaction on wheat growth. Unsterilized and sterilized soils, different levels of compaction and three species of arbuscular mycorrhiza were applied in four replicates. The experiments were conducted in the Soil and Water Research Institute, Karaj, Iran. Soil physical and chemical properties were determined. The AM increased wheat growth in both soils at different levels of soil compaction in both experiments. For root, shoot ($P = 0.1$) and grain ($P = 0.05$) dry weights increases were significant. AM enhanced root growth more than shoot growth under compaction (AM resulted in significant increase in root/shoot ratios, $P = 0.1$). Due to its unique characteristics, AM may reduce the stressful effects of soil compaction on wheat growth, though its effectiveness may decrease with increasing compaction.

Keywords: Arbuscular mycorrhiza; Glomus sp.; Soil compaction; Soil sterilization; Wheat (*Triticum aestivum* L.) growth; Rhizosphere

1. Introduction

Soil compaction, which is a result of using agricultural machinery in the field, is of great concern because of its environmental and economical consequences. Since large areas of agricultural fields in the world become compacted every year, much effort has been made to reduce the stressful effects of soil compaction on plant growth. Although low levels of compaction may be useful for plant growth, higher levels can be harmful (Motavalli et al., 2003).

Slight soil compaction may improve soil structure, reduce soil erosion and provide a more suitable medium for seed growth (O'Sullivan and Simota, 1995). High levels of compaction adversely affect soil root growth, resulting in decreased oxygen and nutrient uptake (Nadian et al., 1996). Soil compaction increases the emission of greenhouse gases, surface runoffs and transport of chemicals and pollutants into ground waters, resulting in higher requirements for energy and fertilizer (Soane, and van Ouwerkerk, 1995). Hence, soil compaction affects soil physical (Barzegar et al., 2000), chemical (Rillig and Mummey, 2006) and biological (Whalley et al., 1995) properties, leading to soil degradation.

The use of arbuscular mycorrhiza (AM) to reduce the stressful effects of soil compaction on plant growth can be useful, both environmentally and economically, compared with the mechanical methods (Miransari et al., 2007). AM is able to inoculate the roots of many plants for a mutual

Abbreviations: AM, arbuscular mycorrhiza; S1 and S2, unsterilized and sterilized soil, respectively; C1, C2, C3, C4, control, 4-, 12- and 20-time compaction; respectively; M1, M2, M3 and M4, control, Iranian *Glomons mosseae*, Iranian *Glomous etunicatum*, Canadian *Glomous mosseae*, respectively; RDW and SDW, root and shoot dry weight, respectively.

*Corresponding author. Tel.: +98 21 5277424; fax: +98 21 5277512.
E-mail address: Miransari1@Excite.Com (M. Miransari).

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symbiosis to enhance their growth in relatively harsh conditions (Bethlenfalvay, 1992; Sylvia and Williams, 1992). These fungi significantly increase the uptake of phosphorus (Smith and Read, 1997) and other nutrients through their hypha (Marschener and Dell, 1994) by increasing the effective root surface area in a greater volume of soil (Clark and Zeto, 2002). This may result in improved growth of plants in compacted soils (Miransari et al., 2007), where uptake of water and nutrients is usually reduced (Miransari et al., unpublished data; Hamblin, 1985; Amato and Ritchie, 2002).

Mycorrhizal plants in comparison with non-mycorrhizal plants have roots, which are greater in number and weight and longer in length (Hetrick et al., 1988). AM produces an extensive network of hypha and high amount of organic matter. The glomalin content, which is a glycoprotein, of organic matter is a source of C for other microorganisms. Production of organic matter protects soil structure through improving soil aggregation (Miller and Jastrow, 1992; Tisdall, 1994). Hence, AM can improve soil structure in compacted soils (Miransari et al., 2007) with degraded aggregates (Rillig and Mummey, 2006).

The effects of AM on the properties of rhizosphere are through indirect mechanisms including alterations in soil acidity (Li et al., 1991), increasing microbial population (Olsson, et al., 1998) and producing more root exudates (Laheurte et al., 1990). All these mechanisms affect the mobility of metals and their biological availability (Bi et al., 2003). AM considerably affects the chemical properties of root exudates (Marschner et al., 1997) and, hence, increases microbial populations in the rhizosphere (Wamberg et al., 2003).

Since to our knowledge there are not any data regarding the effects of AM fungi, of different origins, on the growth of wheat in unsterilized and sterilized compacted soils, this research work was conducted.

2. Materials and methods

2.1. Soil characteristics and measurements

The soil surface layer (0–30 cm) of the research field of the Soil and Water Research Institute at Meshkin-Dasht, Karaj, Iran was air dried, sieved and transferred to 10-kg pots. Half of the soil was sterilized (Miransari et al., 2007) at 121 °C and under high vapor pressure for an hour using an autoclave (Toshihiro et al., 2004). Soil physical and chemical properties were determined. Nitrogen was measured using the Kjeldahl method (Nelson and Sommers, 01973). Phosphorus was determined by sodium bicarbonate extraction (Olsen, 1954). Potassium was measured using a flame photometer (emission spectrophotometry) (Knudsen et al., 1982). Iron, manganese, zinc and copper were determined by the diethylenetriaminepentaacetic acid (DTPA) method (Baker and Amachar, 1982) using an 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 (−.033 atm) and permanent wilting point (−15 atm) were determined using a pressure plates apparatus. Table 1 presents soil analysis data.

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, released from a 20-cm height, including 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 control (C1) (Miransari et al., 2007). Using a 100-cm^3 cylinder, which was placed in the pots, the pot soil was taken and weighed and the bulk densities of pots were measured, three times during the growing season and six measurements per replication (Miransari et al., 2007). Pot soil resistances were determined during the growing period three times at soil moisture contents of 27.84%, 11.71%, and 11% for the first experiment and 9.04%, 3.35%, and 6.35% for the second experiment using a penetrometer (Model Cernusco 20063) (Table 2). When determining soil resistance, soil moisture was determined at 105 °C using an oven.

In the second experiment we used a soil with a higher rate of clay content, and hence higher saturation percentage, which led to higher levels of compaction (Table 1a). Although, according to literature, it may be a good idea to compact the soil uniformly, since the field soil is usually compacted non-uniformly, we compacted the soil in one layer (Miransari et al., 2007).

The reason for using dry soil was to avoid excessive hardness (Miransari et al., 2007). The compaction levels were selected according to Barzegar et al. (2000). It is also worth mentioning that the 20-time compaction (20 times release of the 2-kg weights from the 20 cm height) was the highest level at which the pots were compacted (Miransari et al., 2007).

2.2. Experimental method

Experimental designs were $2 \times 3 \times 4$ and $2 \times 4 \times 4$ 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, with an average temperature of 24 °C, in which plants received 14 h of fluorescent light. Since higher space was required the second experiment was carried out in a greenhouse, with an average temperature of 27 °C, where plants received natural light.

Treatments included unsterilized (S1) and sterilized (S2) soils, three levels of soil compaction with bulk densities of

Table 1
The physical and chemical properties of the soils

	pH	EC (dsm^{-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	

Table 2
Soil resistance (MPa) at different compaction levels, in the first and second experiment (SE, $n = 3$–4)

	SR1	SR2	SR3
First year			
Soil moisture (%)	27.84	11.71	11
Unsterilized soil			
C1	0.60 (0.07)	0.65 (0.16)	0.66 (0.14)
C2	0.85 (0.18)	0.98 (0.22)	0.92 (0.17)
C3	0.89 (0.18)	0.94 (0.29)	0.96 (0.17)
Sterilized soil			
C1	0.56 (0.10)	0.64 (0.15)	0.66 (0.14)
C2	0.75 (0.18)	0.98 (0.33)	0.89 (0.25)
C3	0.88 (0.16)	1.05 (0.23)	0.97 (0.13)
Second year			
Soil moisture (%)	9.04	3.35	6.35
Unsterilized soil			
C1	0.61 (0.01)	0.64 (0.07)	0.62 (0.05)
C2	0.78 (0.03)	0.75 (0.08)	0.76 (0.07)
C3	0.98 (0.06)	0.95 (0.07)	0.96 (0.05)
C4	1.13 (0.16)	1.08 (0.05)	1.07 (0.03)
Sterilized soil			
C1	0.65 (0.04)	0.64 (0.07)	0.62 (0.05)
C2	0.80 (0.06)	0.75 (0.08)	0.76 (0.07)
C3	1.05 (0.07)	0.95 (0.07)	0.96 (0.05)

SR1: first measurement, SR2: second measurement, SR3: third measurement, C1: control, C2: 4-time compaction, C3: 12-time compaction, C4: 20-time compaction.

1.2 (C1), 1.34 (C2) and 1.41 $g\,cm^{-3}$ (C3) in the first experiment and four levels of soil compaction with bulk densities of 1.18, 1.24, 1.39 and 1.54 $g\,cm^{-3}$ (C4) in the second experiment, respectively. Pots were also treated with mycorrhizal species. Therefore, there were 24 and 32 treatments in four replicates in the first and second experiment, respectively.

Four seeds of wheat (*Triticum aestivum* L., Shiraz cultivar) 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, 2004). Mycorrhizal treatments included control (without mycorrhiza) (M1), *Glomous mosseae* (M2) and *Glomous etunicatum* (M3) both isolated from the Iranian soils, and *Glomous mosseae* (M4) received from GINCO (Glomales *In vitro* Collection), Canada.

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). 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 (471 $kg\,ha^{-1}$) of urea, 0.46 g (146 $kg\,ha^{-1}$) of triple super phosphate and 1.32 g (420 $kg\,ha^{-1}$) of potassium sulfate were added twice to each pot.

2.3. Measurement of plant parameters

Before harvest plant heights were measured. At harvest grain fresh and dry weights were determined. Roots were separated from the soil by washing. Shoot and root fresh and dry weights (using an oven at 105 °C) were also measured.

2.4. Statistical analysis

Using SAS (Sas Institute, 1990) data were analyzed and significant differences between different treatments were determined. Using the GLM method and least significant difference (LSD) test the means were compared (Steel and Torrie, 1980).

3. Results

Soil resistance values are presented in Table 2, indicating the effectiveness of compaction treatments. AM increased plant height, shoot, root and grain dry weights in both S1 and S2 soils at different levels of compaction in both experiments. In the case of root ($P = 0.05$) and grain ($P = 0.1$) dry weights in the first experiment, these enhancing effects were significant. Soil sterilization had a significant effect on grain fresh and dry weights (Tables 3–5; Figs. 1 and 2).

Treatments S2C3M3 and S2C3M4 in the first experiment and treatments S2C1M3, S1C4M2, S1C4M4, and S2C3M4 in the second experiment resulted in the highest shoot dry weight. Treatment S1C2M1 in the first experiment and treatment S2C4M3 in the second experiment resulted in the lowest shoot dry weight (Tables 4 and 5). The highest level of compaction (C4) reduced plant height, root and grain

fresh and dry weights and root/shoot ratio in the unsterilized soil. In addition, C4 decreased plant height, shoot and root fresh weight and grain fresh and dry weight in sterilized soil in the second experiment. However, different species of AM were able to partially overcome the stress (Tables 4 and 5, Figs. 1 and 2).

Although the interaction effects between the fungi and compaction were not significant, AM in the first experiment in S2 (up to 38% increase in C1 and 67% increase in C3) and in the second experiment in S1 soil (up to 8% increase in C1 and 14% increase in C4) increased shoot dry weight at the highest levels of compaction more effectively, compared with C1. Shoot and root dry weights in S2 soil in the first and second experiment increased at C2 compared with C1 (Tables 4 and 5).

In both experiments at control treatments (without AM) and in unsterilized soil, increasing compaction resulted in reduced root dry weight. However, inoculation with AM resulted in significant and numerical enhanced root growth, compared with the control treatments, in the first and second experiment, respectively. The increases were significant for M2 and M3 at $P=0.1$, and for M4 at $P=0.05$. AM resulted in increased RDW/SDW at the highest level of compaction in both soils and in S1 soil in the first and second experiment, respectively (Tables 4 and 5).

In the first experiment in both soils and in the second experiment in S1 soil, increased compaction for control treatments decreased grain dry weight. In the first experiment AM increased grain dry weight significantly and the increases for M2 and M4 were significant at $P=0.1$ and $P=0.05$, respectively (Tables 4 and 5).

4. Discussion

AM significantly enhances wheat growth under controlled conditions (Vierheilig and Ocampo, 1991; Hetrick et al., 1992; Schweiger and Jakobsen, 1999). AM alters plant metabolism (Nemec and Meredith, 1981; Gupta, 2003) and modifies plant physiology by increasing the photosynthetic rate, altering the position of photosynthates in the shoot and root, and affecting the uptake of nutrients from the soil, resulting in altered nutrient concentrations in plants. These changes in the tissues result in the structural and biochemical alteration of root cells and also the membrane permeability, and hence affect the quality and quantity of root exudates (Linderman, 1992; Harrison, 1999).

AMs are capable of utilizing regulatory mechanisms in plant cells to use C for their own growth (Blee and Anderson, 1998). Under stressful conditions, although non-mycorrhizal plants employ mechanisms that may help

Table 3
Mean comparisons of wheat height, shoot, root, and grain fresh and dry weights and root/shoot ratio by different species of arbuscular mycorrhiza at 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)	Shoot fresh weight (*g*)	Shoot dry weight (*g*)	Root fresh weight (*g*)	Root dry weight (*g*)	Grain fresh weight (*g*)	Grain dry weight (*g*)	Root/shoot dry weight
First experiment (S1)								
M1	62.3b	8.6b	1.9a	0.88a	0.11a	1.65b	0.45a	0.071a
M2	69.5a	12.0a	2.1a	1.17a	0.16a	2.34a	0.63a	0.080a
M3	67.4ab	10.9ab	1.9a	1.15a	0.16a	2.12ab	0.57a	0.085a
M4	65.4ab	9.3ab	2.1a	0.98a	0.13a	1.77ab	0.52a	0.073a
LSD	6.1	2.8	0.9	0.31	0.05	0.64	0.19	0.021
First experiment (S2)								
M1	67.8ab	10.0b	1.76b	0.89b	0.12b	2.00b	0.52b	0.068b
M2	66.5b	11.0ab	2.04ab	1.06b	0.15b	2.55ab	0.71ab	0.072b
M3	66.3b	12.1ab	2.55a	1.02b	0.14b	2.32b	0.66ab	0.062b
M4	75.1a	13.6a	2.57a	1.45a	0.23a	3.20a	0.94a	0.091a
LSD	7.4	3.4	0.78	0.31	0.05	0.82	0.28	0.015
Second experiment (S1)								
M1	60.8a	8.4a	4.8a	5.3a	2.5a	10.6a	6.7a	0.50a
M2	61.2a	8.5a	5.0a	4.7a	2.0ab	11.3a	7.3a	0.40ab
M3	59.8a	8.3a	4.7a	5.6a	2.1ab	11.2a	6.9a	0.47ab
M4	61.2a	8.9a	4.8a	4.2a	1.7b	10.5a	6.8a	0.35b
LSD	2.7	1.2	0.6	1.8a	0.8	1.8	1.0	0.13
Second experiment (S2)								
M1	60.0a	8.5a	4.4a	5.3a	2.1a	9.7a	6.0a	0.47a
M2	59.3a	8.8a	4.5a	5.6a	1.5a	10.5a	5.9a	0.33b
M3	59.2a	9.3a	4.8a	4.8a	1.8a	9.6a	6.2a	0.36b
M4	56.9b	8.3a	4.5a	5.0a	2.1a	9.4a	5.7a	0.45a
LSD	2.1	1.9	0.8	1.7	0.7	1.9	1.0	0.09

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 $P=0.1$. M1: control, M2: *Glomus mosseae* (Iranian), M3: *Glomus etunicatum* (Iranian), M4: *Glomus mosseae* (Canadian).

Table 4
The effects of unsterilized and sterilized compacted soils and arbuscular mycorrhiza on plant measured parameters in the first experiment (SE, $n = 3$–4)

Level of compaction	AM	Plant height (cm)	Shoot fresh weight (*g*)	Shoot dry weight (*g*)	Root fresh weight (*g*)	Root dry weight (*g*)	Grain fresh weight (*g*)	Root/shoot dry weight
Unsterilized soil								
C1	M1	69.3 (7.6)	9.3 (1.7)	1.7 (0.3)	1.07 (0.3)ab	0.14 (0.06)ab	1.78 (0.7)abc	0.081 (0.030)
	M2	66.0 (8.2)	9.5 (3.4)	1.6 (0.8)	1.11 (0.6)ab	0.15 (0.10)ab	1.60 (1.1)bc	0.083 (0.021)
	M3	63.5 (5.7)	8.7 (4.5)	1.6 (0.8)	0.96 (0.6)ab	0.14 (0.08)ab	1.73 (0.10)abc	0.094 (0.027)
	M4	68.0 (8.5)	9.9 (2.6)	2.9 (1.9)	1.12 (0.6)ab	0.13 (0.10)ab	2.03 (1.2)abc	0.055 (0.044)
C2	M1	54.3 (7.1)	7.3 (3.3)	1.2 (0.5)	0.66 (0.3)b	0.09 (0.05)b	1.35 (0.8)c	0.079 (0.024)
	M2	71.5 (2.6)	14.1 (3.2)	2.5 (0.6)	1.24 (0.6)ab	0.17 (0.08)ab	2.78 (0.6)a	0.069 (0.027)
	M3	68.3 (6.3)	12.7 (3.4)	2.2 (0.5)	1.17 (0.3)ab	0.16ab	2.15 (0.3)abc	0.074 (0.029)
	M4	59.8 (12.6)	7.2 (4.6)	1.2 (0.7)	0.64 (0.3)b	0.10 (0.04)b	1.24 (0.8)c	0.087 (0.016)
C3	M1	63.3 (5.3)	9.3 (2.2)	2.8 (2.6)	0.90 (0.5)ab	0.11 (0.05)ab	1.83 (0.7)abc	0.053 (0.022)
	M2	71.3 (10.3)	12.4 (4.4)	2.1 (0.7)	1.16 (0.4)ab	0.18 (0.02)ab	2.76 (1.2)a	0.089 (0.028)
	M3	70.5 (8.2)	11.4 (5.5)	2.1 (0.1)	1.31 (0.7)a	0.18 (0.09)ab	2.60 (1.3)ab	0.087 (0.024)
	M4	71.5 (7.8)	12.2 (3.5)	2.4 (0.4)	1.40 (0.5)a	0.20 (0.04)a	2.33 (1.11)abc	0.082 (0.001)
Sterilized soil								
C1	M1	64.0 (7.2)	8.6 (7.2)	1.6 (1.3)	0.84 (0.65)bc	0.12 (0.09)cd	2.14 (1.84)ab	0.078 (0.016)
	M2	65.5 (10.2)	11.8 (7.5)	2.2 (1.4)	1.08 (0.72)abc	0.15 (0.11)bcd	2.66 (1.58)ab	0.065 (0.023)
	M3	65.3 (12.1)	12.2 (3.6)	2.1 (0.7)	1.01 (0.20)bc	0.13 (0.03)bcd	2.41 (1.14)ab	0.063 (0.022)
	M4	78.8 (4.6)	11.6 (3.4)	2.2 (0.5)	1.31 (0.27)abc	0.20 (0.03)bc	3.12 (0.44)ab	0.091 (0.011)
C2	M1	69.0 (13.3)	11.8 (5.2)	1.8 (0.8)	1.01 (0.40)bc	0.13 (0.07)bcd	1.75 (0.90)b	0.069 (0.023)
	M2	64.0 (14.0)	9.0 (0.9)	1.6 (0.4)	0.91 (0.27)bc	0.11 (0.04)cd	2.00 (0.92)ab	0.069 (0.011)
	M3	69.5 (10.5)	13.5 (6.4)	2.5 (1.1)	1.25 (0.58)abc	0.20 (0.09)bc	2.71 (1.04)ab	0.079 (0.020)
	M4	74.5 (13.8)	13.0 (5.3)	2.5 (1.1)	1.41 (0.59)ab	0.22 (0.12)ab	2.93 (1.42)ab	0.080 (0.027)
C3	M1	70.5 (7.9)	9.5 (3.9)	1.8 (0.8)	0.82 (0.49)bc	0.12 (0.07)cd	2.12 (0.95)ab	0.058 (0.026)
	M2	69.3 (4.3)	12.3 (5.3)	2.3 (0.9)	1.20 (0.71)abc	0.19 (0.09)bc	2.98 (1.59)ab	0.081 (0.008)
	M3	64.0 (11.2)	10.8 (5.6)	3.0 (1.6)	0.79 (0.06)c	0.10 (0.05)d	1.73 (0.79)b	0.043 (0.027)
	M4	72.0 (11.9)	16.0 (5.7)	3.0 (1.1)	1.62 (0.45)a	0.29 (0.02)a	3.53 (1.52)a	0.103 (0.034)
Model		n.s.	n.s	n.s.	**	**	**	n.s.
S		$P = 0.15$	$P = 0.11$	n.s.	n.s.	$P = 0.15$	**	n.s.
C		n.s.	n.s.	$P = 0.17$	n.s.	n.s.	n.s.	n.s.
M		n.s.	$P = 0.20$	n.s.	*	**	*	n.s.
C*M		n.s.	n.s.	n.s.	n.s.	$P = 0.16$	n.s.	$P = 0.13$
S*M		$P = 0.13$	n.s.	n.s.	$P = 0.12$	**	$P = 0.17$	*
S*C		n.s.	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.	n.s.
M1 vs M2		n.s.	$P = 0.13$	n.s.	*	*	**	n.s.
M1 vs M3		n.s.	*	$P = 0.19$	$P = 0.11$	*	n.s.	n.s.
M1 vs M4		**	**	$P = 0.13$	**	**	**	*
LSD1		9.9	4.6	1.4	0.62	0.09	1.16	0.034
LSD2		12.7	6.3	1.2	0.59	0.09	1.54	0.026

C1: control, C2: 4-time compaction, C3: 12-time compaction, M1: control, M2: *Glomus mosseae* (Iranian), M3: *Glomus etunicatum,* M4: *Glomus mosseae* (Canadian), S: soil, C: compaction, M: arbuscular mycorrhiza.
n.s.: not significant.
*significant at 10% probability.
**significant at 5% probability.
Values within the same column followed by the same letter are not statistically different at $P = 0.1$.

the plants to better control the stresses, mycorrhizal plants rely heavily on their symbiosis with AM. In other words, AMs are able to alter plant physiology in a way that confers the plant the ability to more efficiently grow under stressful conditions and cope with stresses.

The mean of shoot dry weight in the second experiment in S2C4 was reduced by 12.5% as compared with C1. In this case and also in the first experiment in S1C3 treatment, AM was not able to reduce the stressful effects of soil compaction. So it seems that increasing compaction level may turn the symbiotic relationship between the plant and fungi into a parasitic-like relationship (Standish et al., 2007) due to the unfavorable conditions, which result, especially, from reduced available oxygen (Arvidsson, 1999). These results are in agreement with those of Nadian et al. (1998) and Miransari et al. (2007), who stated that increasing compaction reduced the effectiveness of AM. Under compaction the expression of phosphate transporter

Table 5
The effects of unsterilized and sterilized compacted soils and arbuscular mycorrhiza on plant measured parameters in the second experiment (SE, $n = 3$–4)

Level of compaction	AM	Plant height (cm)	Shoot fresh weight (g)	Shoot dry weight (g)	Root fresh weight (g)	Root dry weight (g)	Grain fresh weight (g)	Root/shoot dry weight
Unsterilized soil								
C1	M1	61 (2.2)	7.4 (2.3)	4.9 (1.3)	6.80 (8.0)ab	3.31 (3.0)a	11.71 (1.2)	0.59 (0.41)a
	M2	63 (4.5)	8.5 (2.8)	5.3 (1.9)	4.94 (3.9)ab	2.24 (1.3)abc	10.84 (3.3)	0.42 (0.17)ab
	M3	59 (2.4)	6.8 (1.3)	4.4 (1.4)	3.15 (1.6)ab	1.39 (0.4)bc	9.95 (2.5)	0.32 (0.09)ab
	M4	61 (3.1)	7.0 (2.1)	4.0 (0.7)	3.15 (1.6)ab	1.30 (0.4)bc	9.55 (1.5)	0.33 (0.11)ab
C2	M1	62 (4.0)	8.5 (1.5)	4.9 (0.8)	5.25 (3.7)ab	2.21 (1.1)abc	11.21 (1.2)	0.47 (0.28)ab
	M2	61 (4.8)	6.4 (1.5)	4.0 (0.8)	1.91 (1.2)b	0.90 (0.3)c	11.42 (0.5)	0.24 (0.11)b
	M3	59 (1.7)	8.8 (1.6)	4.7 (0.3)	6.57 (0.6)ab	2.64 (0.9)abc	10.50 (2.4)	0.57 (0.22)a
	M4	63 (4.8)	9.3 (2.7)	4.9 (1.4)	5.31 (3.1)ab	1.65 (1.0)abc	12.06 (2.9)	0.33 (0.14)ab
C3	M1	62 (5.7)	8.2 (3.2)	4.5 (1.4)	4.23 (4.4)ab	2.18 (1.8)abc	8.74 (3.7)	0.44 (0.33)ab
	M2	60 (5.1)	9.8 (0.90)	5.0 (0.8)	5.29 (4.9)ab	2.31 (1.6)abc	9.58 (4.5)	0.43 (0.25)ab
	M3	62 (5.7)	9.6 (3.3)	5.1 (1.0)	7.14 (6.2)a	2.48 (1.3)abc	12.22 (1.7)	0.47 (0.21)ab
	M4	61 (5.3)	9.2 (1.7)	4.7 (0.8)	3.43 (3.2)ab	1.46 (0.7)bc	11.36 (4.1)	0.34 (0.21)ab
C4	M1	59 (4.0)	9.5 (2.3)	4.9 (1.0)	4.82 (4.8)ab	2.41 (1.8)abc	10.27 (1.9)	0.48 (0.34)ab
	M2	62 (1.0)	9.3 (1.9)	5.5 (0.9)	6.86 (4.3)ab	2.65 (1.0)ab	13.26 (2.2)	0.50 (0.30)ab
	M3	60 (1.9)	8.1 (2.0)	4.6 (1.1)	5.73 (3.0)ab	2.06 (0.8)abc	11.65 (3.6)	0.50 (0.29)ab
	M4	61 (1.2)	10.4 (0.7)	5.6 (0.5)	4.99 (5.2)ab	2.68 (2.4)ab	8.53 (4.5)	0.46 (0.38)ab
Sterilized soil								
C1	M1	61 (1.3)	8.9 (1.5)	4.3 (0.8)	5.19 (3.7)	1.87 (0.9)ab	9.13 (9.1)	0.43 (0.18)ab
	M2	59 (3.5)	8.7 (1.6)	4.3 (0.5)	3.53 (2.7)	1.27 (0.3)b	11.03 (3.0)	0.30 (0.08)b
	M3	60 (3.2)	10.7 (3.0)	5.8 (1.7)	6.51 (4.7)	2.26 (2.0)ab	11.48 (2.2)	0.35 (0.20)ab
	M4	55 (3.9)	6.4 (1.3)	3.7 (1.0)	5.17 (3.8)	1.73 (0.7)ab	8.69 (4.0)	0.46 (0.16)ab
C2	M1	61 (1.3)	9.6 (3.9)	4.9 (1.9)	6.91 (9.7)	3.11 (3.2)a	11.34 (4.4)	0.50 (0.33)ab
	M2	60 (4.6)	8.9 (2.6)	4.3 (1.1)	7.93 (2.8)	1.67 (0.9)ab	10.36 (3.1)	0.38 (0.09)ab
	M3	60 (4.3)	10.2 (5.2)	5.3 (2.1)	6.44 (5.4)	2.12 (1.9)ab	7.78 (1.8)	0.35 (0.18)ab
	M4	58 (1.6)	9.3 (3.3)	4.8 (1.7)	6.22 (8.2)	2.80 (2.4)ab	7.19 (2.0)	0.55 (0.40)a
C3	M1	59 (2.4)	8.1 (3.9)	3.9 (1.6)	5.18 (3.2)	1.97 (1.0)ab	10.01 (1.8)	0.49 (0.05)ab
	M2	61 (7.7)	9.2 (3.0)	5.1 (1.3)	6.92 (4.0)	1.79 (0.8)ab	11.60 (4.6)	0.34 (0.10)ab
	M3	58 (6.3)	8.4 (1.6)	4.5 (0.5)	3.25 (1.5)	1.51 (0.5)ab	9.98 (1.0)	0.34 (0.14)ab
	M4	57 (0.7)	10.4 (3.0)	5.6 (1.6)	4.35 (3.9)	1.98 (1.1)ab	12.29 (4.9)	0.31 (0.12)b
C4	M1	60 (1.3)	7.6 (1.1)	4.3 (0.5)	4.28 (2.8)	2.05 (0.9)ab	8.20 (3.1)	0.46 (0.17)ab
	M2	57 (6.8)	8.4 (3.3)	4.4 (1.5)	4.76 (7.0)	1.48 (1.2)ab	9.15 (2.6)	0.31 (0.17)b
	M3	59 (5.6)	7.9 (3.3)	3.6 (1.7)	3.39 (2.4)	1.38 (0.6)b	8.89 (3.8)	0.40 (0.17)ab
	M4	58 (3.1)	7.3 (2.9)	3.8 (1.2)	4.23 (3.7)	1.78 (1.3)ab	9.63 (2.7)	0.43 (0.18)ab
Model		n.s.	n.s.	n.s.	***	*	n.s.	**
S		**	n.s.	n.s.	n.s.	n.s.	*	n.s.
C		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
M		n.s.	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.	n.s.
S*M		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S*C		n.s.	$P = 0.14$	$P = 0.15$	$P = 0.22$	n.s.	$P = 0.20$	n.s.
S*C*M		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
M1 vs M2		n.s.	n.s.	n.s.	n.s.	*	n.s.	*
M1 vs M3		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
M1 vs M4		$P = 0.15$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
LSD1		5	2.6	1.2	5.04	1.75	3.57	0.31
LSD2		5	3.6	1.7	5.85	1.68	3.76	0.23

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

gene reduces, resulting in decreased concentration of root phosphate (Brown et al., 2006). Recently scientists have recognized the signals responsible for branching hypha and producing arbuscules (Akiyama et al., 2005; Akiyama and Hayashi, 2006). Researchers have also found that pre-incubation of N-fixing bacteria, *Bradyrhizobium japonicum*,

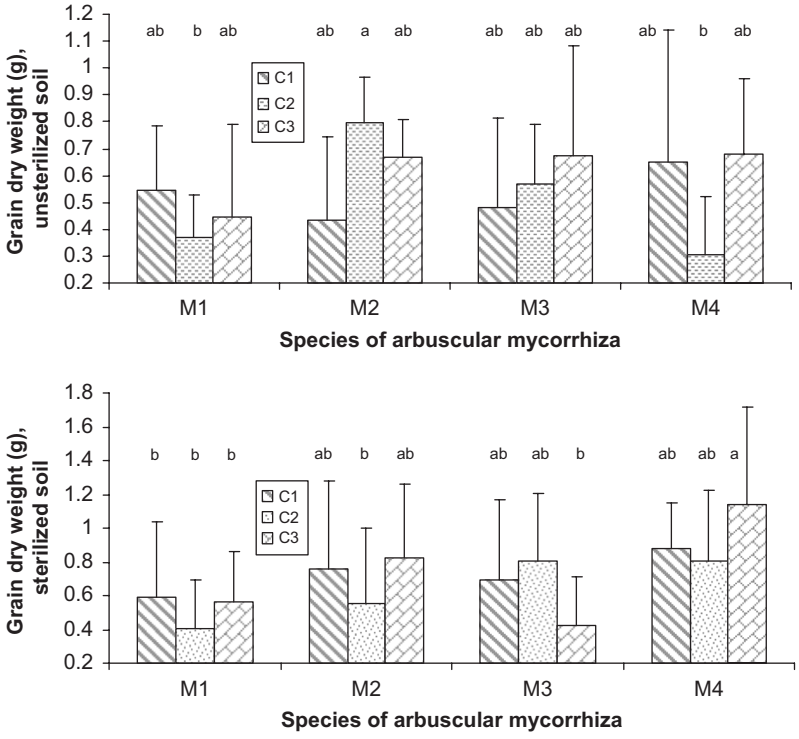

Fig. 1. Effects of different species of arbuscular mycorrhiza on grain dry weight (*g*) in unsterilized and sterilized compacted soils in the first experiment. The error bars indicate the standard error of means for $n = 3$–4.

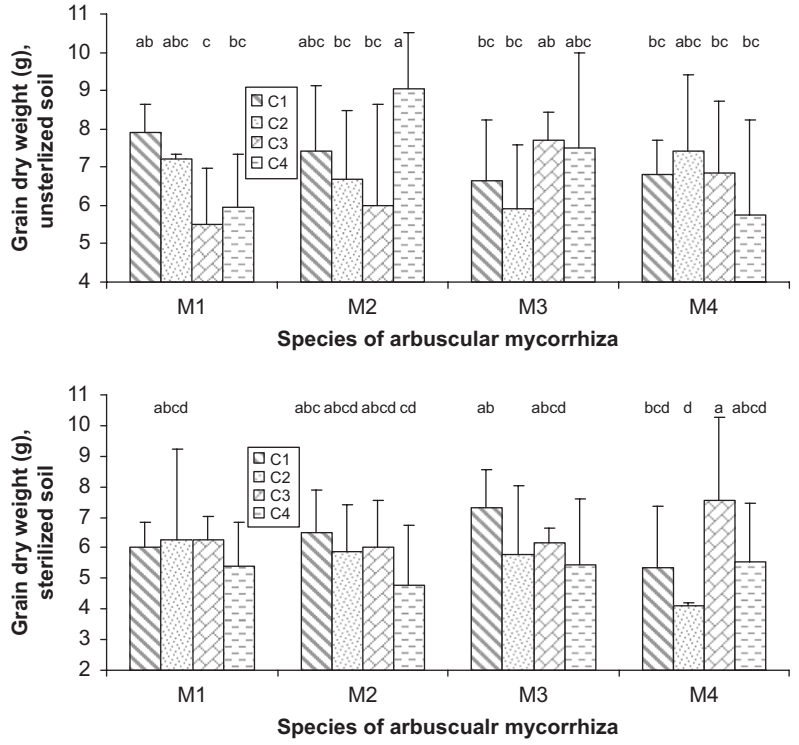

Fig. 2. Effects of different species of arbuscular mycorrhiza on grain dry weight (*g*) in unsterilized and sterilized compacted soils in the second experiment. The error bars indicate the standard error of means for $n = 3$–4.

with the important plant-to-bacterium signal, genistein, may reduce the inhibitory effects of soil stresses such as suboptimal root zone temperature (Zhang and Smith, 1995; Miransari and Smith, 2007b), acidity and salinity (Miransari and Smith, 2007a) on soybean nodulation, growth and yield.

Shoot and root dry weights in S2 soil in the first and second experiment increased at C2 compared with C1, which is in accordance with Bouwman and Arts (2000) and Passioura (2002), who mentioned that low levels of compaction may have enhancing effects on plant growth by providing a suitable medium for seed growth.

The interaction between C × M ($P = 0.16$) and also the significant interaction between S × M ($P < 0.05$) in the first experiment indicate that AM may behave differently under different compaction levels and in the presence or absence of other soil microorganisms. In other words, it is clear from the results that the effectiveness of AM on enhancing root growth increased with increasing compaction.

Many researchers have found that there is a significant interaction between AM and soil stress. This indicates that up to some level with increasing the stress the effectiveness of AM to alleviate the stress increases (Hildebrandt et al., 1999; Tian et al., 2004; Subramanian et al., 2006; Audet and Charest, 2006; Miransari et al., 2007).

The significant interaction between S × M shows that soil sterilization had significantly affected AM effectiveness (Passioura, 2002; Miransari et al., 2007). As soil mechanical resistance increases, higher rates of energy would be necessary for producing and maintaining roots (Sauerbeck and Helal, 1986). Root penetration strength in soil decreases as soil resistance increases, and hence roots explore less volume of the soil, though the total biomass of roots may stay constant (Boone et al., 1978). Under these conditions the uptake of water and nutrients, required for plant growth, decreases and roots influence shoot growth by sending signals.

AM resulted in increased RDW/SDW at the highest level of compaction in both soils and in S1 soil in the first and second experiment, respectively. Generally, under stressful conditions plants transfer higher amounts of photosynthates to roots (Yano et al., 1998; Mollier Pellerin, 1999; Miransari et al., 2007; Miransari and Smith, 2007a, b).

It seems that the enhancing effect of AM on wheat roots under stressful conditions is more pronounced than shoots. Except for the S2 soil in the second experiment, increasing compaction levels reduced RDW/SDW ratio in control treatments (without AM). In addition to the allocation of more C to the roots under stressful conditions, it is also clear from the results that AMs intensify this allocation and hence root growth (Miransari et al., 2007; Miransari and Smith, 2007a, b). This may greatly help the plant in a compacted soil to cope with the stress through enhancing water and nutrient uptake.

Also it is clear from the results that despite corn (Miransari et al., 2007) being grown in a compacted soil, soil microorganisms may enhance the performance of AM in symbiosis with wheat, which is also grown in a compacted soil. This may be attributed to different root exudates in corn and wheat and hence different combinations of microorganism population in the rhizosphere of the two plants.

Very fine hypha in AM (average diameter: 3–4 μm), compared with even the finest root hairs in plants (average diameter: $\geqslant 10$ μm), are able to penetrate very fine pores and be in contact with soil particles (Bolan, 1991; Jakobsen, 1995), and hence are more capable of penetrating compacted soils. In the first experiment all species of AM significantly increased root dry weight, compared with M1.

In the first experiment in both soils and in the second experiment in S1 soil increasing compaction in control treatments and also in SC4 (compared with SC1) decreased grain dry weight, which is due to limited root growth and hence decreased water and nutrient uptake in a compacted soil. In the first experiment AM increased grain dry weight significantly and the increases for M2 and M4 were significant at $P = 0.1$ and $P = 0.05$, respectively. The extensive AM hypha significantly increase plant root surface area, resulting in much greater root exploring of the soil and so increased water and nutrient uptake.

5. Conclusion

According to these results we may conclude that AM is able to reduce the stressful effects of soil compaction on wheat growth. In a compacted soil, AM enhances root growth at a higher rate than shoots, and hence through regulating root dry weight/shoot dry weight AM may alleviate the stress. Unlike corn (Miransari et al., 2007), soil sterilization may decrease AM efficiency for controlling the stress, which is also evident from the significant interaction between AM and the soil ($P < 0.05$). The performance of AM may enhance with increasing compaction up to a level, but at the high levels of compaction and due to unfavorable soil conditions (i.e. oxygen deficiency) AM may not be symbiotic to the plant and it may become parasitic to the plant (the interaction between AM and soil compaction, $P = 0.16$). Exotic species of AM may also be effective to reduce the stress.

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