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Field response of wheat to arbuscular mycorrhizal fungi and drought stress

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Abstract Mycorrhizal plants often have greater tolerance to drought than nonmycorrhizal plants. This study was conducted to determine the effects of arbuscular mycorrhizal (AM) fungi inoculation on growth, grain yield and mineral acquisition of two winter wheat (*Triticum aestivum* L.) cultivars grown in the field under well-watered and water-stressed conditions. Wheat seeds were planted in furrows after treatment with or without the AM fungi *Glomus mosseae* or *G. etunicatum*. Roots were sampled at four growth stages (leaf, tillering, heading and grain-filling) to quantify AM fungi. There was negligible AM fungi colonization during winter months following seeding (leaf sampling in February), when soil temperature was low. During the spring, AM fungi colonization increased gradually. Mycorrhizal colonization was higher in well-watered plants colonized with AM fungi isolates than water-stressed plants. Plants inoculated with *G. etunicatum* generally had higher colonization than plants colonized with *G. mosseae* under both soil moisture conditions. Biomass and grain yields were higher in mycorrhizal than nonmycorrhizal plots irrespective of soil moisture, and *G. etunicatum* inoculated plants generally had higher biomass and grain yields than those colonized by *G. mosseae* under either soil moisture condition. The mycorrhizal plants had higher shoot P and Fe concentrations than nonmycorrhizal plants at all samplings regardless of soil moisture conditions. The improved growth, yield and nutrient uptake in wheat plants reported here demonstrate the potential of mycorrhizal inoculation to reduce the effects of drought stress on wheat grown under field conditions in semiarid areas of the world.

Keywords Arbuscular mycorrhiza · Drought stress · *Triticum aestivum* · Yield

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Introduction

In many arid and semiarid regions of the world, drought limits crop productivity. The incorporation of factors enabling plants to withstand drought stress would be helpful to improve crop production under drought conditions.

Inoculation of plant roots with arbuscular mycorrhizal (AM) fungi may be effective in improving crop production under drought conditions. Colonization of roots by AM fungi has been shown to improve productivity of numerous crop plants in soils under drought stress (Al-Karaki and Al-Raddad 1997; Al-Karaki and Clark 1998; Faber et al. 1990; Sylvia et al. 1993). Improved productivity of AM plants was attributed to enhanced uptake of immobile nutrients such as phosphorus, zinc and copper. In addition, other factors associated with AM fungal colonization may influence plant resistance to drought. These include changes in leaf elasticity (Auge et al. 1987a), improved leaf water and turgor potentials, maintenance of stomatal opening and transpiration (Auge et al. 1987b), increased root length and depth, and development of external hyphae (Ellis et al. 1985; Davies et al. 1992).

AM fungal colonization of roots has been shown to increase the drought resistance of wheat (Allen and Boosalis 1983; Ellis et al. 1985; Sylvia et al. 1993; Al-Karaki and Al-Raddad 1997; Al-Karaki and Clark 1998), as well as several other plant species (Davies et al. 1992; Ruiz-Lozano et al. 1995). However, most of these experiments were conducted under controlled (greenhouse) environments. Little is known about the participation of mycorrhizal inoculation on growth and productivity of crop plants in unsterilized soil, especially

under field conditions, where introduced AM fungi must compete with the indigenous AM fungi population. Therefore, field studies should be conducted to examine any advantage these organisms may have for plants under water-deficit conditions. The objective of this research was to examine the effects of mycorrhizal fungi on growth, nutrient uptake, and yield of field-grown wheat subjected to well-watered and water-stressed conditions.

Materials and methods

Inoculum production

Pot cultures of the AM fungi *Glomus mosseae* [Thaxter and Gerd. (Gerd. and Trappe)] (isolate UK125, INVAM) (Gms) and *Glomus etunicatum* Becker and Gerdemann (Gec) (isolate UT186, INVAM) were initiated on corn (*Zea mays* L.) in a greenhouse during the period September to December 2001. Pure starter cultures of both AM fungal species were provided by International Culture Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi (INVAM), Morgantown, W.Va. Soil used for production of mycorrhizal inoculum was collected from the field (where the experiment was to be executed) to a depth of 30 cm, air-dried, sieved through a 2-mm screen, mixed with sand (2:1, V:V), and steam-sterilized (twice on successive days) before it was put in plastic pots (5 l) for plant growth. Corn plants were harvested just prior to inoculation by excising and discarding shoots. Roots were removed from soil, cut into 1-cm lengths and then mixed back with the soil.

Cultural practices and experimental treatments

Field experiments were conducted during the 2001/2002 growing season on Amarillo fine sandy loam (fine-loamy, mixed, thermic aridic paleustalfs) soil at the Research Station of the United States Department of Agriculture, Lubbock, Texas. At the beginning of the season (fall of 2001), the experimental area was prepared with a moldboard plow followed by disking. The prior cropping system entailed cotton (*Gossypium hirsutum*) production. Composite soil samples were taken to a depth of 30 cm and analyzed for major soil properties and indigenous AM fungal spores. Soil properties before planting were 48.3% sand, 24.7% silt, and 27.0% clay; 1.3% organic matter; pH 7.3 (soil:water, 1:1); 20 P (Weak-Bray), 33 N-NO_3, 0.5 Zn, 7 Fe and 1.2 Cu in mg kg^{-1} soil. The experimental area was prepared thereafter with a chisel plough. Plot dimensions were 1 m×2.5 m with four wheat rows in each plot. Nitrogen was broadcast on all plots and incorporated below the soil surface at a rate of 75 kg N ha^{-1} as NH_4NO_3. No phosphorus was added to the plots in order to maximize the mycorrhizal benefit.

There were 12 treatments with three replicates. Treatments included two water regimes, three AM fungal levels and two wheat cultivars. AM fungal treatments included inoculation or no inoculation with the *G. mosseae* (Gms) or *G. etunicatum* (Gec). Before planting, furrows 0.25 m apart were opened to a depth of approximately 7–10 cm and mycorrhizal inoculum was evenly distributed along the bottom of the furrows of the whole plot. AM fungi inoculum was placed in the furrows below the wheat seeds and lightly covering with soil from the furrow on the day of planting. The inoculum consisted of AM-colonized root pieces and spores and hyphae mixed with soil (2 kg per row). The inoculum composed primarily of root pieces and hyphae was present in fritted clay, with spores a minor component (140±5 and 160±6 spores per kg soil for Gms and Gec, respectively). No inoculum was added to the control plots.

Seeds of the winter wheat cultivars Steardy (drought-sensitive) and TAM-105 (drought-tolerant) (Dave Marshall and Steve Baenziger, personal communications) were used in this study. Seeds were planted by hand in rows directly over the inoculum in furrows and covered with soil. Approximately 100 seeds were planted per row on 5 December 2001. Weeds were controlled by hand as required.

Water-management treatments were (i) water-stressed (WS) plants grown under rainfed conditions with 50 mm irrigation applied at planting, and (ii) well-watered (WW) plants grown under rainfed conditions with irrigation scheduled to prevent symptoms of water stress. The total seasonal irrigation for the WW treatment was 408.5 mm. Water was supplied to individual plots by a drip irrigation system. Rainfall during the period from planting to harvest was 238.1 mm.

Assessment of mycorrhizal development

The AM fungi spore count in native field soil was minimal (~3 spores 100 g^{-1} air-dried soil). Plant samples with their roots (five plants) from the top 30 cm of 0.5 m-segments of one of the outer two rows of each plot were randomly sampled 69 (4- to 5-leaf stage), 126 (late tillering), 149 (heading) and 175 (grain filling growth stage) days after planting for assessment of AM fungi root colonization. These samples were taken by a fork, fitted to excavate the soil volume under the area occupied by the plants. Roots were rinsed free of soil, cut into 1–2 cm fragments and thoroughly mixed, and subsamples (1 g) saved for determination of root colonization with AM fungi. These samples were cleared with 10% (w/v) KOH and stained with 0.03% (v/v) trypan blue in lactoglycerol according to the method of Phillips and Hayman (1970), and microscopically examined for colonization by determining percentage root segments containing arbuscules and vesicles using a gridline intercept method (Giovannetti and Mosse 1980).

Total crop biomass and grain yield

At maturity, plants from a 1.5 m-row segment of the two middle rows of each experimental plot were harvested. The harvested material was sun-dried, threshed manually, and weighed for total biomass and grain yield. Yield components (heads per plant, grains per head, and grain weight) were determined on five plants that were sampled together randomly from the two middle rows of each plot at maturity and added to the total.

Mineral analysis

Shoots of plants sampled for assessment of mycorrhizal development at stages of tillering, heading and grain filling were oven-dried, weighed and saved for mineral analysis. At harvest, grain samples from each treatment and replicates were selected randomly, oven-dried, and weighed. Dried shoot and grain samples were ground to pass a 0.5-mm sieve in a cyclone laboratory mill and analyzed for P, Zn, Cu and Fe by A & L Plains Agricultural Laboratories (Lubbock, Texas).

Experimental design and statistical analysis

The experiment was arranged in a split-plot and randomized in complete blocks with three replicates. Water regimes (WW and WS) were the main-plots with AM fungi inoculum treatments (control, Gms and Gec) and cultivars (TAM-105 and Steardy) as sub-plots. Data were statistically analyzed by analysis of variance with the MSTATC PROGRAM (Michigan State University, East Lansing, Mich., USA). Probabilities of significance were used to test for significance among treatments and interactions.

Table 1 Root colonization (%) as affected by arbuscular mycorrhizal fungi (AMF) (*Glomus* sp.) and water-stress treatments of two wheat cultivars (*C*) at different stages of growth (*WW* well watered, *WS* water stressed)

AMF	Cultivar	Leaf stage		Tillering		Heading		Grain-filling	
		WW	WS	WW	WS	WW	WS	WW	WS
Control	TAM-105	0	0	18.8	19.3	32.9	22.1	26.1	17.7
	Steardy	0	0	18.2	18.3	28.8	19.5	24.7	15.7
G.etunicatum	TAM-105	2	1	31.2	27.1	49.6	37.2	39.0	26.3
	Steardy	1	1	23.2	24.5	44.0	31.1	31.0	23.0
G. mosseae	TAM-105	1	2	27.5	23.7	45.6	37.9	37.2	24.9
	Steardy	1	1	25.8	22.2	40.7	35.4	33.9	22.3
Significance									
WS		>0.50		0.285		0.000		0.007	
AMF		0.062		0.000		0.000		0.000	
WS×AMF		>0.50		0.276		0.195		0.383	
C		>0.50		0.016		0.004		0.002	
WS×C		>0.50		>0.50		>0.50		>0.50	
AMF×C		>0.50		0.169		>0.50		0.232	
WS×AMF×C		>0.50		>0.50		0.045		>0.50	

Results

Soil and air temperatures and rainfall varied during the growth season (Fig. 1). The coldest air temperatures (5.2–5.4°C) occurred during December, January and February. For the remainder of the growing season, the temperature began to rise to reach about 24°C during May. Soil surface temperature was low (5–10°C) during winter months. After mid-March, the soil surface began to warm up and the soil temperature reached and remained above 15°C for the remainder of the growing season. Most of the rainfall was received during March, April and June, while the least rainfall was received during December and May.

Negligible root colonization with AM fungi were noted at the February sampling when the plants were at the 4- to 5-leaf stage in all plots. Once established, the level of root colonization with AM fungi increased with time, peaking at the heading stage in all plots regardless of water regime or AM fungal inoculation treatment in both cultivars (Table 1). A subsequent decline in root colonization with AM fungi was noted between heading and grain-filling stages in all plots. The percentage of root colonization with AM fungi was higher in the plots inoculated with AM fungal isolates than non-inoculated plots at all samplings. Mycorrhizal colonization of both wheat cultivars was higher in plants grown under WW than plants grown under WS conditions when averaged across all growth stages (Table 1).

Addition of Gec inoculum to the soil increased mycorrhizal colonization in roots of the drought-tolerant cultivar TAM-105 over roots of the drought-sensitive cultivar Steardy under both WW and WS conditions from the tillering until the grain-filling stage (Table 1). However, when Gms inoculum was added to the soil, differences in root colonization by AM fungi between the two cultivars were not significant except at heading stage under WW but not WS conditions.

Inoculation of plots with both AM fungal isolates increased biomass and grain yields of both cultivars regardless of water regime (Table 2). Water stress decreased biomass and grain yields in all plots. The Gec

Table 2 Wheat biomass and grain yield as affected by AMF (*Glomus* sp.) and water-stress treatments of two wheat cultivars (*C*) (*WW* well watered, *WS* water stressed)

AMF	Cultivar	Biomass yield kg ha^{-1}		Grain yield kg ha^{-1}	
		WW	WS	WW	WS
Control	TAM-105	10619	7139	1977	928
	Steardy	9985	6115	1657	614
G.etunicatum	TAM-105	12909	9396	2796	1165
	Steardy	11865	8418	2246	853
G. mosseae	TAM-105	11284	8569	2505	1127
	Steardy	10548	8040	1943	826
Significance					
WS		0.004		0.008	
AMF		0.000		0.024	
WS×AMF		0.121		0.357	
C		0.001		0.006	
WS×C		>0.50		>0.50	
AMF×C		>0.50		>0.50	
WS×AMF×C		>0.50		>0.50	

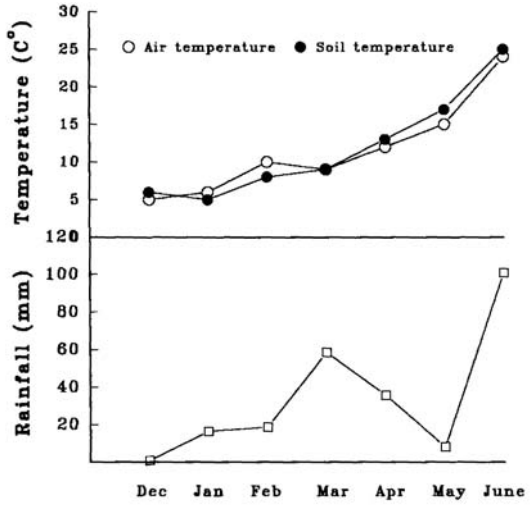

Fig. 1 Monthly average air-soil temperature and rainfall during the 2001–2002 growing season (planting to harvesting) at the study area in Lubbock, Texas

plants had generally higher biomass and grain yields than Gms plants grown under both WW and WS, even though grain yield was similar for Gec and Gms plants grown under WS for both cultivars. The overall effects of AM fungi inoculation on the wheat biomass and grain yields (percentage-wise) of plants grown under WW and WS conditions are summarized in Table 3.

Table 3 Percent change in biomass and grain yields due to AMF (*Glomus* sp.) inoculation of wheat cultivars (*C*) grown under WW and WS conditions (Yield $Y=Y_{AM}-Y_{nonAM}\times 100/Y_{nonAM}$) (*WW* well watered, *WS* water stressed)

Water regime	AMF	Cultivar	Biomass yield	Grain yield
WW	*G.etunicatum*	TAM-105	21.6	41.4
		Steardy	18.8	35.6
	G. mosseae	TAM-105	6.3	26.7
		Steardy	5.6	19.7
WS	*G.etunicatum*	TAM-105	31.6	25.5
		Steardy	37.7	38.9
	G. mosseae	TAM-105	20.0	21.4
		Steardy	31.5	34.5

The number of heads per plant was generally higher in the AM fungal inoculated plants than in the noninoculated plants. However, the Gec plants had significantly higher head number per plant than Gms and noninoculated plants regardless of water regime (Table 4). There were no significant differences in number of heads per plant between Gms and noninoculated plants in all plots. The number of heads per plant was similar for both cultivars grown under either WW or WS conditions. However, individual grain weight and grain number per head were generally higher in Gms plants than Gec and noninoculated plants, even though these differences were only significant for the TAM-105 cultivar grown under either WW or WS conditions.

Water management and AM fungal inoculation both had significant effects on shoot and grain nutrient concentrations. Water stress generally decreased the concentration of several nutrients in the shoots when averaged over the tillering, heading and grain filling stages, even though the effects of water stress were only significant for P and Zn at the grain-filling stage, and for Fe at the heading stage (Tables 5, 6, 7, 8). However, plants grown under WS had generally higher concentra-

Table 4 Wheat head number per plant, grain weight (mg), and grain number per head as affected by AMF (*Glomus* sp.) and water-stress treatments of two wheat cultivars (*C*) (*WW* well watered, *WS* water stressed)

AMF	Cultivar	Heads number		Grain weight		Grain number	
		WW	WS	WW	WS	WW	WS
Control	TAM-105	3.39	2.81	24.9	17.5	20.5	18.2
	Steardy	3.20	3.10	22.4	14.6	19.9	13.3
G.etunicatum	TAM-105	4.71	3.28	26.0	18.4	21.8	19.3
	Steardy	4.40	3.15	23.8	17.1	21.2	15.7
G. mosseae	TAM-105	3.60	2.94	30.7	19.1	24.0	20.1
	Steardy	3.26	2.92	27.1	16.7	20.2	16.1
Significance							
WS		0.008		0.014		0.033	
AMF		0.000		0.000		0.041	
WS×AMF		0.012		0.015		>0.50	
C		>0.50		0.000		0.000	
WS×C		0.228		>0.50		0.066	
AMF×C		>0.50		>0.50		>0.50	
WS×AMF×C		>0.50		>0.50		>0.50	

Table 5 Shoot and grain P concentrations (mg kg^{-1}) as affected by AMF (*Glomus* sp.) and water-stress treatments of two wheat cultivars (*C*) at different stages of growth (*WW* well watered, *WS* water stressed)

AMF	Cultivar	Tillering		Heading		Grain-filling		Harvest	
		WW	WS	WW	WS	WW	WS	WW	WS
Control	TAM-105	3267	3467	2700	2467	2790	2483	4633	5100
	Steardy	3300	3500	2700	2533	2800	2500	4666	4900
G.etunicatum	TAM-105	3667	3833	3033	2767	2967	2633	5200	5733
	Steardy	3800	3733	3100	2867	3167	2767	5433	5600
G. mosseae	TAM-105	3567	3833	2867	2600	2867	2600	4733	6200
	Steardy	3633	3800	2867	2667	2967	2767	5200	5100
Significance									
WS		0.261		0.120		0.036		0.294	
AMF		0.017		0.009		0.001		0.009	
WS×AMF		>0.50		>0.50		>0.50		>0.50	
C		>0.50		>0.50		0.022		>0.50	
WS×C		>0.50		>0.50		>0.50		0.038	
AMF×C		>0.50		>0.50		0.312		>0.50	
WS×AMF×C		>0.50		>0.50		>0.50		0.210	

Table 6 Shoot and grain Fe concentrations (mg kg^{-1}) as affected by AMF (*Glomus* sp.) and water-stress treatments of two wheat cultivars (*C*) at different stages of growth (*WW* well watered, *WS* water stressed)

AMF	Cultivar	Tillering		Heading		Grain-filling		Harvest	
		WW	WS	WW	WS	WW	WS	WW	WS
Control	TAM-105	295	230	248	193	289	242	67.7	76.7
	Steardy	285	217	233	176	222	191	78.0	82.3
G.etunicatum	TAM-105	351	317	299	252	732	583	64.3	73.7
	Steardy	333	268	292	241	678	467	72.7	84.3
G. mosseae	TAM-105	355	347	279	243	722	433	60.3	70.0
	Steardy	330	342	269	244	571	322	66.0	72.3
Significance									
WS		0.158		0.049		0.088		0.375	
AMF		0.000		0.081		0.000		0.143	
WS×AMF		0.165		>0.50		0.347		>0.50	
C		0.189		>0.50		0.085		0.065	
WS×C		>0.50		>0.50		>0.50		>0.50	
AMF×C		>0.50		>0.50		>0.50		>0.50	
WS×AMF×C		>0.50		>0.50		>0.50		>0.50	

Table 7 Shoot and grain Zn concentrations (mg kg^{-1}) as affected by AMF (*Glomus* sp.) and water-stress treatments of two wheat cultivars (*C*) at different stages of growth (*WW* well watered, *WS* water stressed)

AMF	Cultivar	Tillering		Heading		Grain-filling		Harvest	
		WW	WS	WW	WS	WW	WS	WW	WS
Control	TAM-105	38.0	31.7	30.7	27.0	30.0	22.3	45.3	56.3
	Steardy	36.7	27.3	30.7	26.3	30.0	18.0	45.7	57.0
G.etunicatum	TAM-105	42.7	38.0	34.3	31.7	33.7	26.7	52.0	56.0
	Steardy	38.7	36.0	33.3	31.3	35.7	23.7	46.3	56.0
G. mosseae	TAM-105	44.0	37.0	33.0	30.0	32.7	25.7	51.7	66.7
	Steardy	39.0	37.0	31.0	30.0	32.3	28.3	50.7	50.0
Significance									
WS		0.094		0.328		0.021		0.044	
AMF		0.026		0.150		0.018		0.222	
WS×AMF		>0.50		>0.50		>0.50		>0.50	
C		0.137		>0.50		>0.50		0.037	
WS×C		>0.50		>0.50		>0.50		>0.50	
AMF×C		>0.50		>0.50		>0.50		0.093	
WS×AMF×C		>0.50		>0.50		>0.50		0.043	

Table 8 Shoot and grain Cu concentrations (mg kg^{-1}) as affected by AMF (*Glomus* sp.) and water-stress treatments of two wheat cultivars (*C*) at different stages of growth (*WW* well watered, *WS* water stressed)

AMF	Cultivar	Tillering		Heading		Grain-filling		Harvest	
		WW	WS	WW	WS	WW	WS	WW	WS
Control	TAM-105	10.3	8.0	5.7	4.7	5.0	4.0	7.3	8.3
	Steardy	11.3	9.3	5.0	6.7	4.7	4.7	9.7	8.7
G.etunicatum	TAM-105	11.7	9.7	6.0	6.0	4.7	4.0	8.3	9.0
	Steardy	12.0	10.0	6.3	6.0	6.0	4.0	9.0	9.3
G. mosseae	TAM-105	10.0	10.3	6.3	6.0	5.0	4.0	8.0	7.3
	Steardy	11.3	11.3	6.3	6.3	5.0	5.0	10.0	8.0
Significance									
WS		0.086		>0.50		0.073		0.199	
AMF		0.021		0.174		>0.50		0.304	
WS×AMF		0.012		>0.50		0.347		0.065	
C		0.012		0.323		0.106		0.003	
WS×C		>0.50		0.194		>0.50		0.061	
AMF×C		>0.50		>0.50		0.138		>0.50	
WS×AMF×C		>0.50		0.174		>0.50		>0.50	

tions of P, Fe and Zn in the grain at harvest than plants grown under WW, but the differences were only significant for Zn. AM fungal inoculation increased concentrations of P and Fe in shoots (all samplings) and in grain for P (Tables 5, 6). AM fungal inoculation increased concentrations of Zn and Cu in shoots at tillering stage (Tables 7, 8). Shoot concentrations of P, Fe, Cu and Zn were similar for Gec and Gms plants except for Fe where Gms plants had higher Fe concentrations than Gec plants at tillering stage and grown under WS conditions

(Tables 5, 6, 7, 8). Grain concentrations of P were higher for Gec than Gms plants of TAM-105 cultivar grown under WW, but not under WS conditions (Table 5).

Discussion

The very low levels of AM fungi in plant roots sampled at the 4- to 5-leaf stage suggests that the infection rate of wheat with AM fungi is either intrinsically slow or that suboptimal (e.g., low temperature) soil conditions slow colonization. Low colonization with AM fungi during the winter has been found by other researchers (Hetrick et al. 1984; Buwalda et al. 1985; Yocum et al. 1985; Mohammad et al. 1998). Hetrick et al. (1984) reported that while wheat was not colonized at 10°C, colonization was 8% at 25°C. Low soil temperatures may prevent spore germination and subsequent colonization. Germination of mycorrhizal fungal spores occurs more slowly or is entirely inhibited at soil temperatures below 18°C (Daniels and Trappe 1980; Koske 1981).

AM fungal inoculation increased the level of colonization in the roots of both wheat cultivars. This increase was greater in plants grown under WW than under WS conditions. These data agree with the general observation that AM fungi levels are lower under WS than WW conditions (Ryan and Ash 1996; Al-Karaki and Clark 1998; Al-Karaki 1998). The highest level of colonization caused by AM fungal inoculation was attained at heading stage for both cultivars. The levels declined during the grain-filling stage under WW and WS conditions. Similar results were reported by Cade-Menun et al. (1991), who suggested that as grain ripens photosynthesis slows down and nutrients are translocated from the leaves to the grain, which reduces the photosynthate supply to roots and results in a decline in colonization observed during grain-filling.

In this study, inoculation with AM fungi provided an important enhancement to yield in both cultivars. The enhancement in grain and biomass yields due to inoculation with AM fungi was higher for wheat grown under WS than under WW conditions. The higher proportional increase in wheat grain and biomass yields in WS plants due to AM fungal inoculation might be attributed to the smaller size of WS plants (Sylvia et al. 1993) or to increased dependence of wheat on AM fungi for mineral and water uptake (Al-Karaki 1998). Enhanced plant growth and yield following AM fungal inoculation was related to improved uptake of P and Cu, especially under WS conditions (Sylvia et al. 1993; Al-Karaki 1998; Al-Karaki and Clark 1998). Mycorrhizal fungi may improve nutrient uptake by improving the exploration of the soil-pore space (Sylvia et al. 1993). Davies et al. (1992) found that external hyphal development and soil aggregation of mycorrhizal plants were enhanced by drought acclimation. O'Keefe and Sylvia (1993) observed that external hyphae adhere to soil particles, which would improve contact with the soil solution. Furthermore, they demonstrated that hyphae access smaller pore spaces than plant roots and root hairs. As soil water content decreases, the relative importance of these factors would increase.

The drought-tolerant cultivar TAM-105 generally had higher grain and biomass yields and root AM fungi colonization than the drought-sensitive cultivar Steardy, regardless of water regime. However, proportional grain yield enhancement due to AM fungal inoculation was higher in Steardy than in TAM-105 under WS but not under WW conditions, even though AM fungi colonization was higher in TAM-105 than in Steardy. It has been suggested that mycorrhiza are relatively more important to plant growth under dry conditions than when soil moisture is plentiful (Michelsen and Rosendahl 1990). The present results support this suggestion in the case of the Steardy cultivar.

Several factors such as host plant, AM fungal isolate, and soil environment can influence effectiveness of root-AM fungi symbioses. It is important to understand and manipulate these factors to optimize plant growth responses to AM fungi. It may also be necessary to select AM fungal isolates best adapted to the environment in which a plant species is to be grown. Isolates of AM fungi differ in ability to enhance plant growth (Ruiz-Lozano et al. 1995; Al-Karaki et al. 1998). Specific AM fungal isolates may be related to the ability of AM fungi to colonize roots (Abbott and Robson, 1982) and for production of external hyphae to enhance P and water acquisition (Davies et al. 1992). Even though the differences in root colonization between isolates used in this study were not significant at all samplings, the plant growth responses to these isolates were different in terms of grain and biomass yields. The enhancement in grain and biomass yields due to inoculation was higher with Gec than Gms for plants grown under both WS and WW conditions (Table 3). Fungal isolates have been reported to differ in their ability to ameliorate plant water stress. Isolates of *G. monosporum* have been shown to be less effective in relieving water stress on wheat in comparison to *G. mosseae* (Al-Karaki et al. 1998). Moreover, *G. fasciculatum* has been reported to increase drought resistance in several plant species (Allen and Boosalis 1983; Ellis et al. 1985).

The improved growth, yield, and nutrient uptake in wheat plants reported here demonstrate the potential of mycorrhizal inoculation to reduce the effects of drought stress on wheat grown under field conditions in semiarid areas of the world. However, the effectiveness of the AM fungal isolate to be introduced should be considered.

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