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G. N. Al-Karaki [a] , A. Al-Raddad [b] & R. B. Clark [c]

[a] Department of Plant Production , Jordan University of Science and Technology , P. O. Box 3030, Irbid, Jordan

[b] Department of Plant Protection , University of Jordan , Amman, Jordan

[c] U. S. Department of Agriculture, Agricultural Research Service , Appalachian Soil and Water Conservation Research Lab , P. O. Box 400, Beaver, WV, 25813-0400

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Water Stress and Mycorrhizal Isolate Effects on Growth and Nutrient Acquisition of Wheat

G. N. Al-Karaki,[a] A. Al-Raddad,[b] and R. B. Clark[c]

[a]*Department of Plant Production, Jordan University of Science and Technology, P. O. Box 3030, Irbid, Jordan*
[b]*Department of Plant Protection, University of Jordan, Amman, Jordan*
[c]*Appalachian Soil and Water Conservation Research Lab, U. S. Department of Agriculture, Agricultural Research Service, P. O. Box 400, Beaver, WV 25813-0400*

ABSTRACT

Arbuscular mycorrhizal (AM) colonized plants often have greater tolerance to drought than nonmycorrhizal (nonAM) plants. Wheat (*Triticum durum* Desf.), whose roots were colonized with *Glomus mosseae* (Gms) and *G. monosporum* (Gmn), were grown in a greenhouse to determine effects of water stress (WS) on shoot and root dry matter (DM), root length (RL), and shoot phosphorus (P), zinc (Zn), copper (Cu), manganese (Mn), and iron (Fe) concentrations and contents. Mycorrhizal colonization was higher in well-watered (nonWS) plants colonized with both AM isolates than WS plants, and Gms had greater colonization than Gmn under both soil moisture conditions. Shoot and root DM were higher in AM than in nonAM plants irrespective of soil moisture, and Gms plants had higher shoot but not root DM than Gmn plants grown

under either soil moisture condition. Total RL of AM plants was greater than nonAM plants, but was consistently lower for plants grown with WS than with nonWS. The AM plants had similar shoot P and Mn concentrations as nonAM plants, but contents were higher in AM than in nonAM plants. The AM plants had higher shoot Zn, Cu, and Fe concentrations and contents than nonAM plants. The Gms plants grown under nonWS generally had higher nutrient contents than Gmn plants, but nutrient contents were similar for both Gms and Gmn plants grown under WS. The results demonstrated a positive relationship between enhanced growth and AM root colonization for plants grown under nonWS and WS.

INTRODUCTION

Symbiotic associations of plant roots with AM fungi often result in enhanced growth because of increased acquisition of P and other relatively low mobile mineral nutrients, especially Zn and Cu (Davies et al., 1992; Fitter, 1988; Kwapata and Hall, 1985; Marschner and Dell, 1994). Greater acquisition of Mn and Fe has also been reported in AM plants (Al-Karaki and Al-Raddad, 1997; Clark and Zeto, 1996b; Davies et al., 1992; Raju et al., 1987). Effective nutrient acquisition by AM plants is generally attributed to the more extensive external hyphal growth beyond the nutrient depletion zone surrounding roots (Brady, 1984). The AM fungal associations with plant roots may enhance not only growth and mineral nutrient acquisition, but also increase tolerance of plants to drought stress (Davies et al., 1992; Ellis et al., 1985; Ruiz-Lozano et al., 1995).

In many semiarid regions of the world, wheat production is limited by drought. Soil and crop management practices that increase availability of native or applied nutrients could enhance wheat production under these conditions. Symbiotic interactions between AM and roots of host plants grown under limited water could potentially enhance crop productivity. Plant growth responses to symbiotic root-AM fungi have been related to such factors as AM isolate, plant species/cultivar, and growing conditions (Bryla and Koide, 1990; Jakobsen et al., 1992; Ruiz-Lozano et al., 1995). Since individual AM isolates may infect wide ranges of unrelated plant species, the lack of AM specificity may result in considerable variation in symbiotic root-AM responses (Ianson and Linderman, 1991; Ruiz-Lozano et al., 1995). Knowledge about specific responses of given fungal isolates to plant productivity is important for successful utilization of symbiotic root-AM relationships. If tolerance of plants to drought differs with AM isolate with which plants are associated (Ruiz-Lozano et al., 1995), it is important to determine effective host plant root-AM fungal combinations for practical use in the field. Information is limited about effective host plant root-AM fungal combinations under drought conditions.

The objective of our study was to compare the effects of two AM isolates on growth and nutrient acquisition by wheat grown under nonWS and WS.

MATERIALS AND METHODS

A silty clay soil (fine, mixed, thermic, Typic Xerochrept) was thoroughly mixed with fertilizer (30 mg N kg^{-1} soil) and washed cement grade sand (soil:sand, 1:1), enclosed in air tight plastic bags, and fumigated with methyl bromide for 3 days. The bags were opened to the atmosphere (frequently stirred) to dissipate methyl bromide for 10 days, after which soil mixes were put in plastic pots (4.5 kg soil pot^{-1}) for plant growth. Properties of the soil before mixture with fertilizer and sand were 6.5% sand, 45.0% silt, and 48.5% clay; 1.2% organic matter; pH 8.1 (soil:water, 1:1); 8.0 P ($NaHCO_3$-extractable) in g kg^{-1} soil; and 25.7 Mn, 11.2 Fe, 1.5 Zn, 1.7 Cu (5 mM DTPA-extractable) in mg kg^{-1} soil. No additional P was added to soil mixes. The AM treatments were: *Glomus mosseae* [(Nicol. and Gerd.) Gerd. and Trappe] (Gms), *G. monosporum* (Gerd. and Trappe) (Gmn), and no inoculum (nonAM control). The AM inoculum consisted of root fragments [AM colonized with chickpea (*Cicer arietinum* L.) roots] and spores mixed with soil to provide 42 and 47 chlamydospores in 100 g dry soil for Gms and Gmn cultures, respectively. The AM inocula were placed 3 cm deep in 10 cm diameter holes in the center of pots prior to planting.

Seeds of the durum wheat cultivar (Hourani-27) were planted near the center of each pot and placed in a greenhouse for growth [natural light at 28±6°C (March-May)]. Seven days after emergence, seedlings were thinned to four per pot. Plants were watered daily until WS treatments were initiated 21 days after planting. The WS was imposed by withholding water from pots until a soil water potential of -0.13 MPa (40% of soil water holding capacity) was achieved. Pots with nonWS were maintained at soil water potential of -0.05 MPa (80% of soil water holding capacity) through daily weighing. Thereafter, water was maintained at this level by weighing pots daily and adding appropriate amounts of water. Soil water potential was determined with a pressure plate apparatus, and soil water content was determined by weighing samples before and after drying.

Experiments were terminated by severing shoots from roots 55 days after planting (10-12-leaf stage), and shoots were dried and weighed. Roots were rinsed free from soil, cut into 1 cm fragments, thoroughly mixed, and subsamples of fresh roots saved for determination of AM root colonization and total RL. The remainder of roots were dried and weighed.

Root samples for determination of AM root colonization were cleared with 1.78 M KOH and stained with 0.52 mM trypan blue in lactophenol (Phillips and Hayman, 1970), and microscopically examined for colonization by determining percentage root segments containing arbuscules+vesicles using a gridline intercept method (Bierman and Linderman, 1981). Total RL was determined using the gridline intersect method of Newman (1966). Roots used to determine colonization and RL were dried, weighed, and added to the total.

Dried shoot material was ground to pass 0.5 mm sieve in a cyclone laboratory mill, weighed into ceramic crucibles, ashed overnight at 550°C in a muffle furnace,

and the ash suspended in 2M HCl for determination of mineral nutrients. Phosphorus was determined colormetrically (Watanabe and Olsen, 1965), and Zn, Cu, Mn, and Fe were determined by atomic absorption spectroscopy.

The experimental design was randomized complete blocks with factorial arrangements of treatments with WS treatments (WS and nonWS) as main plots and AM isolates (Gms, Gmn, and nonAM) as sub-plots with four replications. Data were statistically analyzed using analyses of variance in the MSTATC (Michigan State Univ., East Lansing, MI). Probabilities of significance were used to indicate significance among treatments and interactions and LSDs ($P<0.05$) were used to compare means within and among treatments.

RESULTS AND DISCUSSION

Nearly all WS and AM treatment effects were significant for the growth and nutrient acquisition traits (Table 1), but the only significant WS×AM interaction was for AM colonization.

Root colonization did not occur for plants provided no AM inoculum. Substantial AM root colonization occurred for plants inoculated with the AM isolates, and plants grown under nonWS had higher colonization than plants grown under WS (Figure 1). Colonization was significantly higher for Gms than for Gmn plants grown under nonWS, but not under WS.

Shoot and root DM were higher for AM than for nonAM plants grown under both nonWS and WS (Figure 2). However, AM plants grown under WS had lower shoot and root DM than AM plants grown under nonWS. The Gms plants had higher shoot DM than Gmn plants grown under nonWS, but was similar when grown under WS. Root DM was similar for Gms and Gmn plants grown under either nonWS or WS. Shoot/root DM ratios were not significantly affected by AM colonization, but this ratio was higher for plants grown under WS than under nonWS (Figure 2). Total RL of AM plants was no different for nonAM plants grown under either nonWS or WS, but was higher for plants grown under nonWS than under WS (Figure 3).

Shoot P and Mn concentrations were similar for AM and nonAM plants grown under both nonWS and WS, while shoot concentrations of Cu and Fe were generally higher for AM than for nonAM plants grown under both nonWS and WS (Figure 4). Shoot concentrations of Zn were higher for plants grown under WS, but not under nonWS (Figure 4). In addition, shoot concentrations of Zn, Cu, and Fe were generally higher for AM plants grown under WS than under nonWS. Shoot concentrations P, Zn, Cu, Mn, and Fe were similar for Gms and Gmn plants grown under either nonWS or WS. Shoot contents of P, Zn, and Cu were higher for AM than for nonAM plants grown under nonWS, and shoot contents of P, Zn, Cu, and Fe were higher for AM than for nonAM plants grown under WS (Figure 4). Manganese contents were not significantly higher for AM compared to nonAM

TABLE 1. Probabilities of significance for growth traits, root colonization with mycorrhiza (AM), and mineral acquisition traits for wheat grown with and without water stress (WS).

Trait	WS	AM
Shoot dry matter (DM)	** *	**
Root DM	**	**
Shoot/root DM ratio	**	
Total root length (RL)	*	
AM colonization with roots	**	**
P concentration	**	
P content	**	**
Zn concentration		*
Zn content	**	**
Cu concentration	**	**
Cu content	*	**
Mn concentration	**	
Mn content	*	
Fe concentration	**	*
Fe content		*

*=significance at P=0.05 and **=significance at P=0.01.

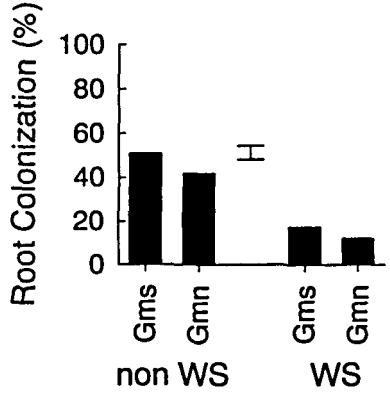

FIGURE 1. Percentage colonization of wheat roots with the arbuscular mycorrhizal isolates *G. monosporum* (Gmn) and *G. mosseae* (Gms) for plants grown in soil without water stress (nonWS) and with water stress (WS). The I represents LSD at P=0.05.

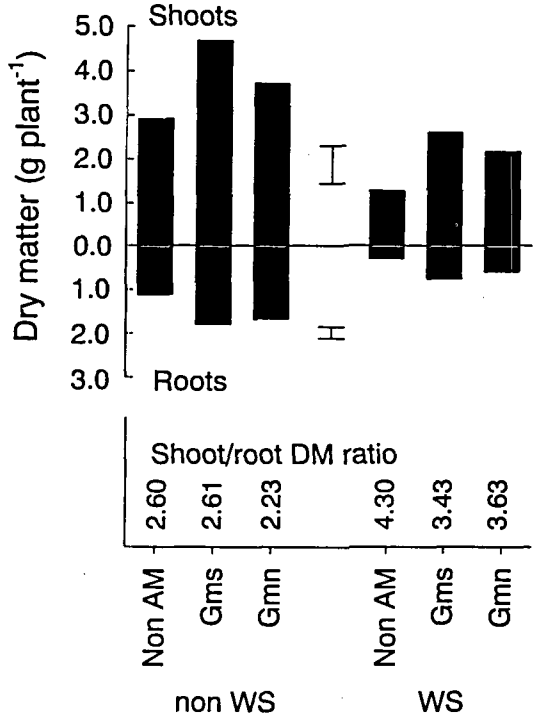

FIGURE 2. Shoot and root dry matter (DM) and shoot/root DM ratios of nonmycorrhizal (nonAM) and mycorrhizal (Gmn = *G. monosporum* and Gms = *G. mosseae*) wheat grown in soil without water stress (nonWS) and with water stress (WS). The I represents LSD at P=0.05.

plants grown under either nonWS or WS (Figure 4). For plants grown under WS and nonWS, contents of P, Zn, Cu, and Fe were generally higher for Gms than for Gmn plants.

Shoot and root DM were enhanced in AM wheat grown under both nonWS and WS even though the enhanced growth was not proportional to the AM root colonization. Nevertheless, a positive relationship was noted between DM enhancement and degree of root colonization. Enhancements in DM relative to increased percentage of AM root colonization are sometimes not related (Ahiabor and Hirata, 1994; Clark and Zeto, 1996a; Davis et al., 1983; El-Kherbawy et al., 1989; Hayman and Tavares, 1985; Medeiros et al., 1994). Even so, growth enhancements due to AM root colonization might be attributed to enhanced photosynthetic rates associated with increased P (Dietz and Foyer, 1986). The enhancement of shoot

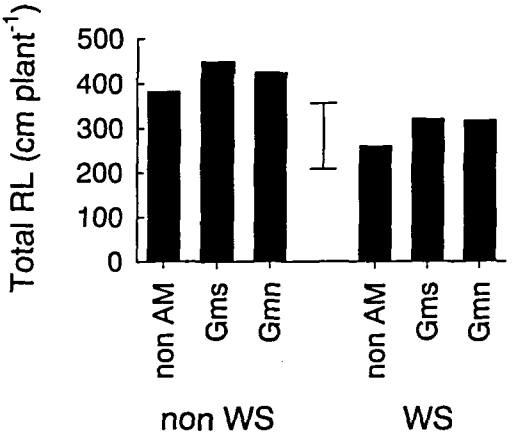

FIGURE 3. Total root length (RL) of nonmycorrhizal (nonAM) and mycorrhizal (Gmn = *G. monosporum* and Gms = *G. mosseae*) wheat grown in soil without water stress (nonWS) and with water stress (WS). The I represents LSD at P=0.05.

and root DM for plants with AM-root associations was lower under WS compared to nonWS in our study, and might be attributed to reduced AM root colonization and low P acquisition by plants grown under WS. Percentages of roots colonized by AM were considerably lower under WS than under nonWS. Decreased AM colonization of cowpea [*Vigna unguicula* (L.) Wolp subsp. *unguicalate*] roots under WS was also reported (Kwapata and Hall, 1985).

Several factors such as host plant, AM isolate, and soil environment can influence effectiveness of root-AM symbioses. It is important to understand and manipulate these factors to optimize plant growth responses to AM. It may also be necessary to select AM 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 (Clark and Zeto, 1996a; Fitter, 1985; Medeiros et al., 1994; Ruiz-Lozano et al., 1995). Specific AM isolates may be related to ability of AM to colonize with roots (Abbott and Robson, 1982) and for production of external hyphae to enhance P and water acquisition (Davies et al., 1992). Even though the AM isolates used in our study differed relative to root colonization, the differences in colonization between these isolates were significant only under nonWS conditions. Shoot and root DM of plants grown under WS and nonWS were improved by root colonization with either AM isolate used in our study. The Gms plants had higher percentages of root colonization than the Gmn plants, and the effectiveness in promotion of plant growth was also greater for Gms than for Gmn plants grown under nonWS. Al-Momany (1987) reported *G. mosseae* to have more favorable effects on plants than *G. monosporum* relative to shoot or total plant weight, and Ellis et al. (1985)

reported that *G. fasciculatum* had no advantage over *G. deserticola* relative to wheat grown under WS. No differences were noted between the two AM isolates used in our study for promoting plant growth under WS. However, our results demonstrated a positive relationship between plant growth and AM root colonization for plants grown under both WS and nonWS.

The AM plants generally had higher shoot P, Cu, Zn, and Fe contents than nonAM plants grown especially under WS. The enhanced accumulation of these nutrients might have been because of increased availabilities or transport (absorption and/or translocation) by AM hyphae. Enhanced acquisition of P, Zn, and Cu by AM plants has been commonly reported (Kwapata and Hall, 1985; Marschner and Dell, 1994; Trimble and Knowles, 1995). However, AM root colonization did not significantly affect Mn concentrations and contents in plants grown under nonWS or WS. The uptake and translocation of Mn might have been antagonized by P, Cu, and/or Zn (Olsen, 1972), whose contents are commonly enhanced by AM. Nevertheless, reduced acquisition of Mn (and Fe) by AM plants has been reported (Kothari et al., 1991; Mohammad et al., 1996). Zinc and Cu concentrations were affected little by AM root colonization under nonWS compared to WS, indicating that AM fungi appeared to be important for acquisition of Zn and Cu under dry soil conditions.

The AM fungal isolates used in our study may differ in ability to enhance nutrient acquisition and/or growth of host plants. The Gms plants had higher shoot mineral nutrient contents (and in some cases concentrations) than Gmn or nonAM plants regardless of soil moisture. This may have occurred because Gms plants had higher absorption surface areas offered by the fungal hyphae to enhance nutrient acquisition and increase root growth. That is, it might be assumed that higher AM root colonization would result in more extensive fungal hyphae out in the soil.

Shoot contents of most mineral nutrients could be accounted for by increased shoot DM. Changes in shoot contents of most mineral nutrients in AM plants compared to nonAM plants were similar to changes in shoot DM. Only Mn contents were not affected by AM root colonization. From these results, more effective P acquisition due to symbiotic interactions with effective root-AM could be a plausible explanation for the enhanced growth of Gms wheat grown under dry soil conditions. In addition, Gms plants accumulated higher total shoot P than Gmn plants grown under nonWS. Root colonization with either AM isolate did not influence shoot P concentrations of wheat grown under nonWS and WS. This probably occurred because of dilution from enhanced growth (Jarrell and Beverly, 1981). Even though P, Cu, Zn, Mn, and Fe contents in Gms plants were similar to Gmn plants grown under WS, P and Cu contents were greater in Gms than in Gmn plants grown under nonWS. Differences among AM isolates for enhanced mineral nutrients have been noted with different plant species (Clark and Zeto, 1996b; Medeiros et al., 1994; Raju et al., 1987; Ruiz-Lozano et al., 1995; Trimble and Knowles, 1995).

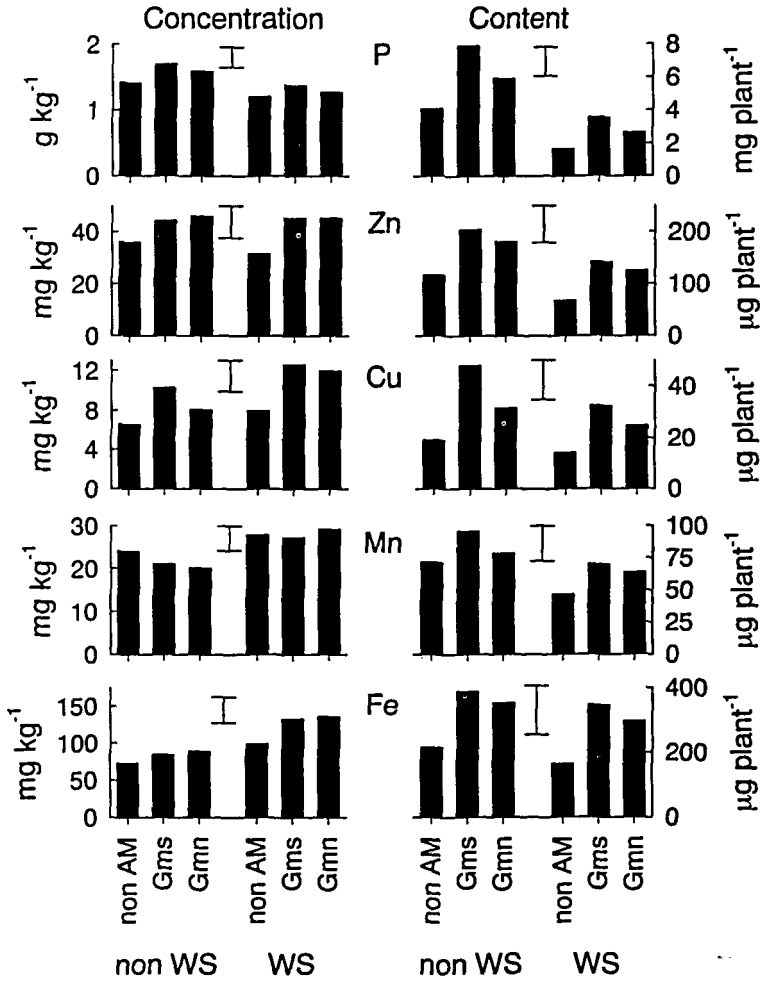

FIGURE 4. Shoot concentrations and contents of P, Zn, Cu, Mn, and Fe of nonmycorrhizal (*non*AM) and mycorrhizal (Gmn = *G. monosporum* and Gms = *G. mosseae*) wheat grown in soil without water stress (nonWS) and with water stress (WS). The I represents LSD at P=0.05.

The response of wheat to different AM isolates depended on soil moisture. The AM isolates may need to be evaluated under other soil environments to determine those that should be used to optimize beneficial effects on growth and productivity. In addition to soil moisture, environmental factors such as soil pH (Clark and Zeto, 1996a, 1996b; Medeiros et al., 1994) need to be evaluated for root-AM effectiveness. The results of our study illustrated that AM fungi are important for growth and nutrition of plants when grown under nutrient stress environments.

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