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Benefit, cost and water-use efficiency of arbuscular mycorrhizal durum wheat grown under drought stress

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Abstract Arbuscular mycorrhizal fungi (AMF) living symbiotically with host plants enhance plant growth by improving the acquisition of mineral nutrients and water relations. This study determined the effects of AMF inoculation on growth, benefit/cost and water-use efficiency (grams dry matter produced per kilogram water evapotranspired) in two durum wheat genotypes (drought sensitive and drought tolerant) under water-stressed and well-watered conditions. Plants were grown in a low-P silty clay (Typic Xerochrept) soil mix in a greenhouse. Shoot and root dry matter (DM) and root AMF colonization were higher for well-watered than for water-stressed plants. The mycorrhizal plants were more water-use efficient than nonmycorrhizal plants. Shoot DM differences between mycorrhizal and nonmycorrhizal plants represent the benefit derived by plants from AMF-root associations. Shoot DM differences between mycorrhizal and nonmycorrhizal plants under similar conditions of water treatment represent the cost to the plant of AMF-root associations. Values of benefit/cost for AMF-root associations were highest when plants were water-stressed and decreased under well-watered conditions. Genotypic differences in calculated costs and benefits were pronounced. Benefit/cost analysis may be helpful in evaluating host plant genotypes in order to optimize efficiencies of AMF symbiosis under different environmental conditions.

Key words Mycorrhizae · *Triticum durum* · Water stress · Water use

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Introduction

A primary limitation of crop production in arid/semiarid regions is the lack of moisture and available nutrients, especially P. In these regions, most wheat is grown under rain-fed conditions where drought may occur at any time during the growing season. Incorporating or using factors which enable plants to better withstand drought stress would help improve crop production.

Arbuscular mycorrhizal fungi (AMF) associated with plant roots were found to enhance crop productivity under drought conditions by improving the mineral nutritional status (mainly P) (Al-Karaki and Al-Raddad 1997; Marshner and Dell 1994; Michelsen and Rosendahl 1990; Trimble and Knowles 1995). Root associations with AMF also appear to provide higher resistance to drought through enhanced water relations (Bethlenfalvay et al. 1988; Davies et al. 1992; Ellis et al. 1985; Ruiz-Lozano et al. 1995). Mycorrhizal plants have higher water uptake due to hyphal extraction of soil water (Allen 1982; Bethlenfalvay et al. 1988; Davies et al. 1992; Faber et al. 1991; Ruiz-Lozano et al. 1995) and higher root hydraulic conductivity (Auge and Stodola 1990; Safir et al. 1972) than nonmycorrhizal plants.

Through the associations of roots and AMF, host plants provide carbohydrates to AMF for development and growth. The interactions between roots and AMF which improve plant growth and at the same time nourish the AMF have been described in terms of benefit/cost analyses (Koide and Elliott 1989; Kucey and Paul 1982; Raju et al. 1990a). Carbon accumulation, P uptake, water uptake, and the loss of carbon due to respiration, exudation, and symbiotic organisms are the basis of such benefit/cost analyses.

The symbiotic interactions between AMF and host plants grown under drought conditions need to be studied in order to optimize beneficial effects of AMF. Potential decreases in biomass yield (cost paid) of crop plants supporting AMF associations also need to be un-

derstood. This present study determined the effects of AMF inoculation on growth, benefit/cost and water-use efficiency in durum wheat under water-stressed and well-watered conditions.

Materials and methods

Durum wheat (*Triticum durum* L.) genotypes CR006 'drought sensitive' and CR057 'drought resistant' (Jaradat 1992) were grown in 5-l plastic pots filled with silty clay (fine, mixed, thermic, Typic Xerochrept) soil mixed with sand (soil: sand, 1:1, v/v). The properties of the soil before mixture with sand were 7.5% sand, 43.5% silt, 46.0% clay, 1.21% organic matter, pH 8.0 (soil:water 1:1), and 8.2 g P kg^{-1} soil ($NaHCO_3$-extracted). The soil mix was fumigated with methyl bromide (Buttery et al. 1988) in air-tight plastic bags for 3 days and the fumigant allowed to dissipate for 10 days prior to planting. No P was added to the soil. Half of the pots received the AMF *Glomus monosporum* (Gerdemann and Trappe) by placing inoculum 3 cm deep in 10-cm-diameter holes in the center of the pots prior to planting. The AMF inoculum added consisted of root fragments [AMF colonized with chickpea (*Cicer arietinum* L.) roots] and spores mixed with soil to provide 58 spores per 100 g air-dried soil. Control treatments received no AMF inoculum. The experiment was conducted in a greenhouse under natural light and at 23±4 °C (January–March). Photosynthetic photon flux density at plant height ranged between 800 and 1350 μmol m^{-2} s^{-1}.

Five days after emergence, plants were thinned to 4 per pot and watered daily for 21 days until drought-stress treatments were initiated. Drought stress was imposed by withholding water from pots until a soil water potential of –0.13 MPa was achieved. Thereafter, water was maintained at this level by weighing pots daily and adding appropriate amounts of water. Pots with well-watered plants were maintained at a soil water potential of –0.04 MPa (near field capacity). The amount of water added to each pot was recorded to determine water evapotranspired. During the experiment, soil water potential was checked in three well-watered and three water-stressed pots without plants. Soil water potential was determined in the soil mix from a moisture retention curve using a pressure plate apparatus on four replicate samples for each pressure point. Soil water content was determined by weighing samples before and after drying at 110 °C for 24 h (US Department of Agriculture 1967).

The experiment was terminated by separating shoots from roots 55 days after planting (10- to 12-leaf stage). Shoots were oven dried at 80 °C for 24 h and weighed (shoot DM). Roots were rinsed free from soil, cut into 1-cm fragments and thoroughly mixed. Subsamples (1 g) were saved for determination of root colonization with AMF; the remainder of the roots were dried and weighed (root DM).

Root samples for determination of root colonization with AMF were cleared with 10% (w/v) KOH and stained with 0.05% (v/v) trypan blue in lactophenol as described by Phillips and Hayman (1970), and microscopically examined for colonization by determining percentage root segments containing arbuscules and vesicles using a gridline intercept method (Bierman and Linderman 1981). Roots used to determine AMF colonization were dried, weighed, and added to the total. Phosphorus was determined colorimetrically (Watanabe and Olsen 1965).

Potential shoot DM yields of nonmycorrhizal (nm) plants grown under the same drought-stress level as mycorrhizal (m) plants, and benefit/cost for plants with AMF-root associations were calculated according to formulas adapted from Raju et al. (1990a):

$$Potential\ DMnm = WUEnm/WUEm \times DMnm \quad (1)$$

where

WUE = water use efficiency (g DM kg^{-1} evapotranspired water)

$$Benefit = DMm - DMnm \quad (2)$$

$$Cost = potential\ DMnm - DMm \quad (3)$$

The experiment was randomized in complete blocks with two drought-stress levels (water-stressed and well-watered), two AMF inoculum treatments (inoculated and uninoculated), and two wheat genotypes to give a 2×2×2 factorial each with four replicates. 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, and LSDs ($P < 0.05$) were used to compare means.

Table 1 Root AMF colonization and shoot and root dry matter (*DM*) by nonmycorrhizal and mycorrhizal wheat genotypes grown with and without water stress (*WS* and *non-WS*)

Water status	AMF status	Genotype	Root colonization (%)	DM (g/plant)	
				Shoot	Root
NonWS	NonAMF	CR057	0	4.98	2.19
		CR006	0	4.68	2.89
	AMF	CR057	52	5.87	2.99
		CR006	38	5.09	3.83
WS	NonAMF	CR057	0	2.23	1.11
		CR006	0	1.93	1.16
	AMF	CR057	29	4.03	1.70
		CR006	24	3.32	1.58
LSD (0.05)			5	0.90	1.02
Significance					
Water stress (WS)			**	**	**
AMF			**	**	**
WS × AMF			**	*	NS
Genotype (G)			**	*	NS
WS × G			NS	NS	NS
AMF × G			**	NS	NS
WS × AMF × G			NS	NS	NS

* Significant at *P* 0.05
** Significant at *P* 0.01
NS Not significant

Results

Mycorrhizal wheat plants of both genotypes had higher shoot and root dry matter than nonmycorrhizal plants regardless of water-stress level (Table 1). Shoot and root DM were lower for both genotypes with water-stressed than with well-watered plants (Table 1). Reductions in shoot DM due to water stress was more pronounced in nonmycorrhizal than mycorrhizal plants.

Percent root AMF colonization ranged between 38 and 52% when plants were grown under well-watered conditions (Table 1). However, the degree of AMF colonization decreased considerably under water-stressed conditions. Significant genotypic differences for root AMF colonization and shoot DM were noted, but not for root DM (Table 1). The drought-resistant genotype CR057 had higher root AMF colonization and shoot DM than the drought-sensitive genotype CR006.

Both mycorrhizal genotypes had higher shoot P contents, but not concentrations, than nonmycorrhizal plants, regardless of water stress (Table 2). However, both mycorrhizal and nonmycorrhizal well-watered genotypes had higher P concentrations and contents than water-stressed plants. The mycorrhizal and nonmycorrhizal CR006 plants had higher P concentrations but not contents than CR057, regardless of water stress (Table 2).

The mycorrhizal plants used less water to produce one unit of shoot DM (i.e. a higher water-use efficiency, WUE) than nonmycorrhizal plants, but water-stressed and well-watered plants did not differ in WUE (Table 2). Both mycorrhizal and nonmycorrhizal CR057 plants had higher WUE when grown either under water-stressed or well-watered conditions than CR006.

The calculated benefit/cost values for wheat plants in response to AMF inoculation were higher under water-stressed than well-watered conditions (Table 3). Benefit/cost values for CR057 were higher than for CR006 when plants were grown under both well-watered and water-stressed conditions (Table 3).

Table 2 Water use efficiency (*WUE*), shoot P concentration and content of nonmycorrhizal and mycorrhizal wheat genotypes grown with and without water stress (*WS* and *nonWS*)

Water status	AMF status	Genotype	WUE (g DM/kg)	P concentration (mg/g)	P content (mg/plant)
NonWS	NonAMF	CR057	0.78	1.68	8.37
		CR006	0.63	2.10	9.84
	AMF	CR057	0.85	2.08	12.20
		CR006	0.71	2.45	12.47
WS	NonAMF	CR057	0.65	1.56	3.45
		CR006	0.58	2.08	4.01
	AMF	CR057	0.97	1.48	5.96
		CR006	0.89	1.78	5.82
LSD (0.05)			0.16	0.45	2.70
Significance					
Water stress (WS)			NS	**	**
AMF			**	NS	**
WS × AMF			**	*	NS
Genotype (G)			*	**	NS
WS × G			NS	NS	NS
AMF × G			NS	NS	NS
WS × AMF × G			NS	NS	NS

* Significant at *P* 0.05
** Significant at *P* 0.01
NS Not significant

Table 3 Potential shoot dry matter (*DM*) of nonmycorrhizal (*nm*) plants and AMF benefit/cost values of wheat genotypes grown with and without water stress (*WS* and *nonWS*)

Water status	Wheat genotype	Potential DM (g/plant)	Benefit		Cost	
			(g/plant)	(%)	(g/plant)	(%)
NonWS	CR057	4.57	0.88	17	1.30	26
	CR006	4.15	0.41	9	0.94	20
WS	CR057	1.49	1.80	100	2.54	136
	CR006	1.26	1.34	68	1.95	103
LSD (0.05)		0.60	0.26	20	0.50	28

Discussion

Mycorrhiza enhanced plant DM in both wheat genotypes tested under both well-watered and water-stressed conditions. Enhanced growth effects on mycorrhizal plants have been attributed to improved water relations resulting from enhanced P nutrition (Bethlenfalvay et al. 1988; Davies et al. 1992; Ellis et al. 1985; Ruiz-Lozano et al. 1995; Safir et al. 1972) and hyphal uptake of water (Allen 1982; Bethlenfalvay et al. 1988; Davies et al. 1992; Faber et al. 1991; Ruiz-Lozano et al. 1995). Shoot DM enhancements attributed to root AMF colonization decreased under water-stressed conditions. This may have occurred because of reduced AMF-root colonization under water-stressed conditions, with subsequent lower effects of AMF on plant growth. Similar observations were made in other wheat studies (Al-Karaki and Al-Raddad 1997; Ryan and Ash 1996).

The drought-resistant genotype CR057 generally had higher shoot DM and root AMF colonization than the drought-sensitive genotype CR006, regardless of water-stress level. Even though the enhancement DM was not proportional to AMF root colonization, the relationship was positive. However, increase in plant DM due to AMF colonization was sometimes unrelated to degree of root colonization, as reported in several studies (Ahiabor and Hirata 1994; Clark and Zeto 1996; El-Kherbawy et al. 1989; Medeiros et al. 1994).

AMF colonization increased total P uptake by both genotypes regardless of water-stress level. This likely occurred because mycorrhizal plants had enhanced root growth and thus a greater P absorption surface area (Raju et al. 1987, 1990b).

Higher WUE in mycorrhizal than nonmycorrhizal plants may indicate that AMF increased the ability of roots to absorb soil moisture, thus maintaining opened stomata in leaves and enhancing DM production. Enhanced water conductivity has been attributed to increased area for water uptake provided by AMF hyphae in soil (Bethlenfalvay et al. 1988; Hardie and Leyton 1981). Increased water transport by roots of mycorrhizal plants has been reported for different plant species (Ellis et al. 1985; Levy et al. 1983; Safir et al. 1972). The mycorrhizal wheat plants in this study produced more root DM than nonmycorrhizal plants. This might partially explain why mycorrhizal plants had higher WUE than nonmycorrhizal plants. The ability of AMF to increase root density is consistent with earlier investigations (Al-Karaki and Al-Raddad 1997).

Responses of the host plant, AMF, and soil environment to AMF symbiosis may be useful criteria for selecting "efficient" plants for water-stress conditions. These responses have sometimes been discussed in terms of "costs and benefits" to plants (Koide and Elliott 1989; Raju et al. 1990a). For the AMF-root symbiosis to be beneficial, plants colonized with AMF should have less biomass loss and produce more DM than nonmycorrhizal plants when grown under water stress (Ellis et al. 1985). The AMF hyphae absorb mineral nutrients, especially P, and water, which benefits the host plant. In turn, the host plant supplies carbohydrates and energy to the AMF. The AMF may thus act as respiratory and growth sinks and drain host plant resources (Raju et al. 1990a). The calculated benefit/cost values of AMF on host plant DM were higher for wheat grown under water-stressed than under well-watered conditions.

The values may have increased in water-stressed plants because of increased dependence of wheat on AM for mineral nutrient and water uptake when plant water relations improved due to AM colonization. However, the loss of C by plants (cost) was higher than the calculated benefit under water-stressed but not under well-watered conditions. This may have been because the AMF used C for development and growth and thus deprived the host plant. It should be emphasized, however, that the cost analysis for plant DM depression due to AMF-root association may only be temporary, since C loss by the plant may be compensated by enhanced photosynthesis and other metabolic processes (Allen et al. 1981; Brown and Bethlenfalvay 1988; Snellgrove et al. 1986). Host plant yield depression resulting from AMF-root association has been reported (Abbott and Robson 1984; Raju et al. 1988, 1990a).

In conclusion, benefit/cost analysis may help evaluate host plant genotypes to optimize efficiencies of AMF symbiosis under different environmental conditions.

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