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Seasonal mycorrhizal colonization of winter wheat and its effect on wheat growth under dryland field conditions

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Abstract A field experiment was conducted to determine the seasonal patterns of arbuscular mycorrhiza (AM) in a dryland winter wheat (*Triticum aestivum* L.) system and to determine wheat growth and P uptake responses to inoculation with mycorrhizal fungus. Broadcast-incorporated treatments included (1) no inoculation with mycorrhizal fungus, with and without P fertilizer, and (2) mycorrhizal fungal inoculation at a rate of 5000 spores of *Glomus intraradices* (Schenck and Smith), per 30 cm in each row, with and without fertilizer P. Winter wheat was seeded within a day after treatments were imposed, and roots were sampled at five growth stages to quantify AM. Shoot samples were also taken for determination of dry matter, grain yield and yield components, and N and P uptake. No AM infection was evident during the fall months following seeding, which was characterized by low soil temperature, while during the spring, the AM increased gradually. Increases in wheat grain yields by enhanced AM were of similar magnitude to the response obtained from P fertilization. However, responses differed at intermediate growth stages. At the tillering stage, P uptake was mainly increased by P fertilization but not by fungal inoculation. At harvest, enhanced AM increased P uptake regardless of whether or not fertilizer P was added. The AM symbiosis increased with rising soil temperatures in the spring, in time to enhance late-season P accumulation and grain production.

Key words Winter wheat · Mycorrhiza · Phosphorus · Dryland

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Introduction

Phosphorus fertilizers constitute a significant cost in crop production (Cade-Menun et al. 1991) and when improperly managed can also contribute to environmental pollution. Arbuscular mycorrhiza (AM) fungi can improve the P uptake efficiency of crops, and are therefore considered a biotic fertilizer (Menge 1983). Many field crops support AM under a range of environmental conditions (Mosse 1986), especially when soil P availability is limited. The AM association with plant roots usually increases the growth of plants by enhancing water and nutrient uptake, especially P (Mohammad et al. 1995 Ortas 1996; Jacobson 1997). Mycorrhizal fungi have the potential to be considered as a major component of sustainable agroecosystems (Johnson and Pfleger 1992).

Winter wheat has an extensive root system, which makes it generally less responsive to AM (Mosse 1986). Colonization of winter wheat is generally not observed until spring (Hetrick and Bloom 1983; Jakobson and Nielson 1983; Hetrick et al. 1984). Hetrick et al. (1984) stated that the response of field-grown wheat to the AM fungal infection is doubtful because colonization occurs for a short time and late in the season. In contrast, other researchers observed that colonization can range from 1 to 40% within the 2 months of seeding winter wheat (Buwalda et al. 1985; Yocum et al. 1985; Dodd and Jeffries 1986). Saif and Khan (1975) have reported that more than 50% of root segments of winter wheat were mycorrhizal a month after seeding. Overall, it appears that the winter wheat response to AM is affected by site-specific environmental and agricultural conditions.

Mycorrhizal fungi can mitigate the severity of water stress in crop plants (Mohammad et al. 1995). For example, mycorrhizal fungal infection of field-grown onions under water stress conditions increased the dry weight and P concentration of shoots (Nelsen and Safir 1982). The higher level of P nutrition improved onion

plant tolerance to water stress. With the better P nutrition, total leaf area was increased and the roots developed better and penetrated deeper into the moist subsoil layers thus enhancing plant growth by avoiding the water stress caused by the dryness of the top surface soil layers (Saneoka et al. 1990). Moisture stress during wheat grain filling will negatively affect late-season P accumulation and grain yield (Pan and Hopkins 1991), and therefore AM colonization may occur at a critical stage of wheat growth (Passioura 1977).

The use of pesticides and insecticides, and the adoption of monoculture systems and long fallowing all contribute to the decline in mycorrhizal fungal populations in soils (Baltruschat and Dehne 1988; Harinikumar and Bagyaraj 1988). Mycorrhizal fungal inoculation has been shown to ameliorate long-fallow disorder (Thompson 1987), demonstrating that AM can be an important component of ecosystem restoration and reclamation (Miller and Jastrow 1992).

Plant responses to mycorrhizal symbiosis in the field are notoriously difficult to predict (Hayman 1983) due to difficulties associated with sterilizing the soil under field conditions (Hetrick 1989). There is relatively little information available on the role of AM in plant growth under non-sterilized field soil conditions. The objective of the present study was to determine the seasonal patterns of AM in a dryland winter wheat (*Triticum aestivum* L.) system and to determine wheat growth and P uptake responses to inoculation with a mycorrhizal fungus under non-sterilized field conditions.

Material and methods

Plot establishment

A field experiment was conducted during the 1991–1992 growing season at Lind, Wash., USA. The experiment was a randomized complete block design with four replications. Plot dimensions were 2.2 m × 4.5 m, with six wheat rows in each plot. The treatments included: (1) AM fungal inoculation with the addition of P fertilizer to the soil (I + P); (2) AM fungal inoculation without P (I–P); (3) no AM fungal inoculation with the addition of P (NI + P), and (4) no AM fungal inoculation or P additions (NI–P). The AM fungal inoculum was added at a rate of 5000 spores of *Glomus intraradices* (Schenck and Smith 1982) (Nutri-Link, Salt Lake City, Utah) per 30 cm in each row. Nitrogen was banded with the drill 10 cm below the seed at a rate of 80 kg ha^{-1} as ammonium nitrate (AN) (NH_4NO_3). Triple superphosphate (TSP) was applied at the rate of 30 kg P ha^{-1}. The P fertilizer and the AM inoculum were broadcast and incorporated in the top 10 cm of the soil surface with a rototiller the day before planting.

Plots were seeded with winter wheat (cv. Lewjain) on 11 September 1991, using a double disk drill. Before seeding, composite soil samples were taken to a depth of 30 cm and analyzed for major soil properties. Soil properties before seeding were pH 7.3 and 0.6 dS m^{-1} electrical conductivity in a saturation paste, 5.1 mg $NaHCO_3$-extractable P (Olsen et al. 1954), 1.1% organic matter by rapid oxidation (Nelson and Sommers 1982), and 11.2, 1.2, 0.8, and 6.6 mg DTPA-extractable Fe, Cu, Zn and Mn kg^{-1} soil, respectively (Lindsay and Norvell 1978). Soil temperature was predicted from air temperature as outlined by Parton (1984).

Shoot sampling and analysis

Plant samples were taken from 1 m of row at tillering, anthesis, and final harvest. Tiller density and dry matter accumulation were determined in each 1-m-row sample. Grain heads were threshed at harvest, and the dry weight of grain and chaff were determined. The number of heads per meter and the number of kernels per head were determined from the harvested plant samples. Kernel weight was determined by taking the average weight of 100 kernels taken randomly from seeds harvested within each plot. The grain and tissue samples were collected, air dried, weighed, and the straw yield was corrected based on oven-dried weights. Grain and tissue samples were analyzed for total N with a combustion analyzer (LECO CHN-600), and for total P using the method of dry-ash digestion with ascorbic acid-molybdate blue (John 1970). Following physiological maturity, grain yield was obtained from a 2-m section of the middle four rows from each plot with a plot combine.

Root sampling and analysis

Root samples were collected at the seven-leaf, late tillering, stem elongation, and midgrain-filling growth stages (15 November, 24 March, 28 April, and 2 June 1992, respectively). Root samples were excavated from one to two plants from the top 30 cm of one of the middle four rows of each plot. Roots were washed and subsamples were randomly taken from the root sample. The subsamples were fixed in a 90:5:5 (by volume) formaldehyde-acetic acid-ethanol solution (modified from Phillips and Hayman 1970). Root samples were cleared in 2% KOH, stained in trypan blue and cut into 1-cm pieces. From each root sample, ten 1-cm pieces were randomly selected and arranged parallel to each other on a microscope slide, and the mycorrhizal root infection determined microscopically at × 100 (Bierman and Linderman 1981). Five vision fields were examined in each 1-cm root section resulting in 50 fields examined for each sample, and a section was counted as infected when hyphae, vesicles, or arbuscules were observed. The infection percentage was calculated as the ratio of the number of infected sections to the total number of sections examined.

Statistical analysis

Analysis of variance (ANOVA) was used to determine the effect of each treatment. The experiment was analyzed as a randomized complete-block design. Multiple mean comparisons were performed using Fisher's least significance test at the 0.05 level of probability. Statistical analyses were performed with the Systat statistical program (Wilkinson 1990).

Results

The total precipitation during the growing season was 220.5 mm and the average temperature was 11.13 °C. The coldest temperatures (2–4 °C) occurred during November, December, and January. For the remainder of the growing season, the temperature began to rise to reach about 20 °C during June, July, and August, when the total precipitation was less than 60 mm. Most of the rainfall was received during November, February, and April, while the least rainfall was received during the summer months (Fig. 1). Soil surface temperature was low (0–10 °C) during winter months. After mid-March, the soil surface began to warm up and the soil temperature reached and remained above 15 °C.

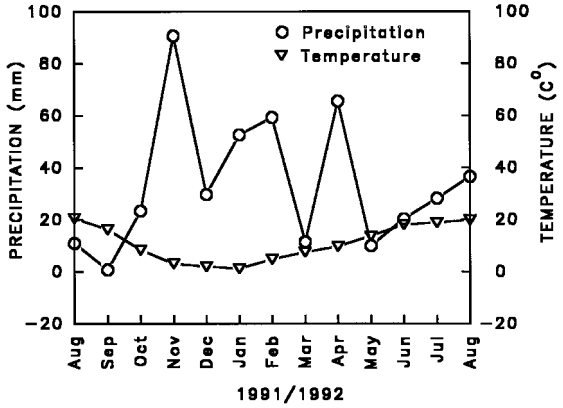

Fig 1 Precipitation and monthly average temperature during the 1991–1992 growing season at the study area, Lind,Wash

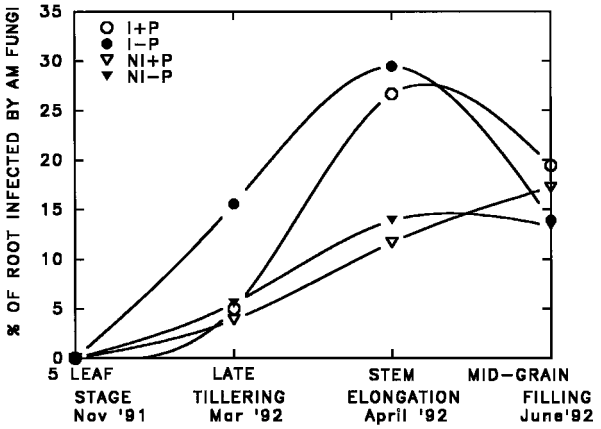

Fig 2 Mycorrhizal infection of plant roots as a function of arbuscular mycorrhiza (AM) fungal inoculation and P addition to the soil (*I+P* inoculation with P addition, *I–P* inoculation without P addition, *NI+P* no inoculation with P addition, *NI–P* no inoculation and no P addition

No AM fungi were observed in November 1991 when the plants were at the 7-leaf stage. Once established the level of infection increased with time, peaking at stem elongation in the AM-fungal-inoculated treatments. A subsequent decline in infection was observed between stem elongation and the midgrain-filling stage. The percentage infection was the highest when no P was added with the AM fungal inoculation during stem elongation (Fig. 2).

Addition of *G. intraradices* inoculum to the soil without P increased mycorrhizal infection by the late tillering stage and through stem elongation, but by the midgrain-filling stage, treatment differences were not observed. However, when P was added to the soil with the AM fungal inoculum, the increase in mycorrhizal infection was not observed until stem elongation. Seasonal infection by native mycorrhizal fungi was similar to that seen with the inoculated plants, increasing from late tillering through stem elongation, but at a lower rate compared to the inoculated plants.

There were no treatment effects on shoot dry matter at tillering and anthesis (Table 1). The enhanced AM fungal colonization increased the shoot dry matter by maturity, regardless of P status. Inoculation with the AM fungus increased grain yield by more than 25% when the P was not added to the soil compared to the non-inoculated plants (Table 2). The addition of P without the AM fungal inoculation increased the grain yield at the 0.1 level of probability compared to the no-P treatment. There were no significant differences among all other treatments. Kernel number per head was greater in the non-inoculated and without-P treatment. The head number per meter was increased by the enhanced AM colonization compared to the non-inoculated plants when P was not added.

Table 1 Shoot dry weight (g m^{-1}) as affected by P and arbuscular mycorrhiza (AM) fungal inoculation. Means in each column that have different letters are significantly different at the 0.05 level of probability. See legend to Fig. 2 for explanation of treatment abbreviations

Treatment	Growth stage		
	Tillering	Anthesis	Harvest
NI−P	213.6a	376.6a	443.1c
I−P	197.9a	414.2a	527.4a
NI+P	236.3a	357.5a	497.4b
I+P	248.5a	341.2a	549.9a
LSD 0.05	55.1	84.6	45.7

Table 2 Tiller number and yield components as affected by P and AM fungal inoculation. Means in each column that have different letters are significantly different at the 0.05 level of probability. See legend to Fig. 2 for explanation of treatment abbreviations

Treatment	Plant density (m^{-1})	Total tillers		Yield components			
		Tillering (m^{-1})	Anthesis (m^{-1})	Kernel number/head	Kernel weight (mg)	Head number (m^{-1})	Grain yield (kg ha^{-1})
NI−P	31.8a	314.2b	126.0c	19.4a	0.037a	175c	3236b
I−P	33.0a	314.5b	182.0a	18.6b	0.036a	211ab	4202a
NI+P	33.6a	362.9ab	178.6ab	17.5b	0.038a	205abc	4038ab
I+P	36.6a	432.1a	162.1abc	18.3b	0.038a	231a	3832ab
LSD 0.05	7.0	73.5	42.6	1.6	0.008	31	936

Table 3 N and P uptake as affected by the P and AM fungal inoculation. Means in each column that have different letters are significantly different at the 0.05 level of probability. See the legend to Fig. 2 for explanation of traetment abbreviations

Treatments	P (mg m^{-1})			N (g m^{-1})		
	Tillering	Anthesis	Harvest	Tillering	Anthesis	Harvest
NI – P	284.6b	400.2a	309.0c	2.9a	2.9a	3.7a
I – P	309.6b	484.1a	433.6b	2.8a	3.7a	3.9a
NI + P	425.7a	456.5a	351.3c	3.5a	3.4a	3.5a
I + P	437.4a	430.7a	510.2a	3.7a	2.4a	4.4a
LSD 0.05	80.9	87.1	67.4	1.1	1.8	2.4

Kernel weight and plant density were not differentially affected by the treatments. Tiller density was greater following AM fungal inoculation and with P compared to the no-P treatments at tillering (Table 2). By anthesis, erhanced AM colonization increased the tiller density compared to the non-inoculation when P was not added.

Phosphorus uptake was increased with P fertilization by the tillering stage (Table 3). The AM fungal inoculation increased P uptake regardless of whether or not P was added to the soil (Table 3). There were no significant differences among the treatments at any growth stage on N uptake.

Discussion

The absence of AM in plants sampled in November suggests that the infection rate of wheat is either naturally slow or that suboptimal soil conditions slowed colonization. Enhanced AM colonization by *G. intraradices* of spring wheat was observed 5 weeks after planting at the six- to eight-leaf stage under ideal temperature (22 °C) and moisture conditions in a growth chamber experiment (Mohammad et al. 1995). In the present experiment, the plants developed an extensive root system during warm September conditions, but lower soil temperatures in October and November (below 10 °C) likely delayed infection. Low infection during the winter has also been found by other researchers (Jakobsen and Nielsen 1983; Hetrick and Bloom, 1983; Hetrick et al. 1984; Buwalda et al. 1985; Yocum et al. 1985). Hetrick et. al. (1984) reported that while wheat was not colonized at 10 °C, infection was 7.8% at 25 °C. The low temperature may have prevented 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 infection of winter wheat. This increase was greater and earlier when P was not added to the soil. These data agree with the general observation that AM levels are greater at low P levels (Khan 1975; Hayman 1983; Dodd and Jeffries 1986). High P levels in soil have been shown to reduce mycorrhizal levels by decreasing root exudation, which is needed for root colonization to occur (Sparling and Tinker 1978; Daniels and Trappe 1980; Buwalda et al. 1985). The high level of P reduced AM fungal infection at tillering but not at later stages. This may be attributed to the decline in available soil P due to plant uptake and/or fixation by the soil with time. The average value of the sodium bicarbonate soil test of the post-harvest soil samples taken from the plots receiving P was 7.9 mg kg^{-1}. This soil P level is about half of the recommended level for normal growth. Therefore, the infection at stem elongation was increased even by the inoculation treatment with P addition. The early increase in AM fungal infection is very important for the growth and nutrient uptake by the plant. Plants at earlier stages of growth require more nutrients to complete their growth cycle.

In the present experiment, the high level of infection caused by AM fungal inoculation subsequently declined during the midgrain-filling stage, similar to the results reported by Cade-Menun et al. (1991). They suggested that as grain ripens, photosynthesis slows down and nutrients are translocated from the leaves to the grain (Karlen and Whitney 1980). Therefore, the level of photosynthate supply to roots may correspond to the decline in colonization observed during grain filling. Other researchers (Jakobsen and Nielsen 1983) have found that the AM levels off during the late stages of wheat growth. However, our results show that the level of infection of inoculated plants decreased at midgrain filling, but stayed higher than the infection at the early growth stages. In addition, the increase in AM levels by the AM fungal inoculation, compared to the non-inoculated treatments, may be due to the presence of a higher number of spores which may compete with native ones. It may also indicate that the introduced *G. intraradices* was more efficient then the native fungi, causing an earlier and higher infection of field-grown winter wheat. This suggests the potential for supplementing or improving native AM fungal populations to benefit plant growth.

The AM inoculation increased grain yield more than 25% only when P was not added to the soil. This suggests that low soil P availability can be compensated to a certain degree by AM inoculation. The increase in grain yield due to the addition of P indicated that the soil was low in available P. The rapid development of AM infection when P was not added to the soil and hence the beneficial effect of AM on nutrient uptake

may account for the increase in plant growth and grain yield.

The AM fungal inoculation increased shoot dry matter accumulation at harvest. Tiller density was increased by the inoculation with *G. intraradices* at both levels of P at tillering. Inoculation increased the tiller density compared to non-inoculation at both levels of P at anthesis. This suggests that more tillers survived to harvest after AM fungal inoculation. It is well documented that P enhances tillering; therefore, the effect of AM on tillering may be attributed indirectly to its effect on P uptake.

The increase in uptake by mycorrhizal plants is probably due to the extended soil network of AM hyphae which enables the mycorrhizal plants to explore more soil volume than the non-mycorrhizal ones (Kothari et al. 1991). Solubilization of unavailable forms of P through soil acidification by root exudates of mycorrhizal plants is also believed to enhance P uptake (Bolan et al. 1984), especially under ammonium fertilization regimes, as used here. Since P is relatively immobile in soil and transfer mainly occurs by diffusion to the root surfaces, AM fungi could greatly enhance nutrient uptake, particularly in water-stressed conditions (Allen and Boosalis 1983; Sieverding and Syverston 1983; Busse and Ellis 1985; Ellis et al. 1985). In the present field investigation, precipitation sharply decreased and temperature increased during the summer months. This suggests that the wheat suffered from water stress during later growth stages, and that AM symbiosis enhanced wheat growth, nutrient uptake and yield under these conditions.

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