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Dual inoculation with *Aspergillus fumigatus* and *Glomus mosseae* enhances biomass production and nutrient uptake in wheat (*Triticum aestivum* L.) supplied with organic phosphorus as Na-phytate

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Abstract

In a pot experiment, wheat was grown for 50 days in two heat-sterilized low-phosphorus (P) soils supplied with organic P as Na-phytate. Seed inoculation with the phosphatase-producing fungus (PPF) *Aspergillus fumigatus* or soil inoculation with the vesicular-arbuscular mycorrhizal (VAM) fungus *Glomus mosseae* increased shoot and root dry weight and root length, phosphatase activity in the rhizosphere and shoot concentrations of P and to a lesser extent of K and Mg. As a rule, the greatest effects on those parameters were most in the combined inoculation treatment (PPF+VAM). Shoot concentrations of Cu and Zn were only enhanced by VAM, not by PPF. At harvest, depletion of organic P in the rhizosphere soil increased in the order of: sterilized soil < PPF < VAM < PPF+VAM which corresponded with the enhanced P concentrations in the plants. The results demonstrate that organic P in form of Na-Phytate is efficiently used by VAM and that use of organic P can be increased by simultaneous inoculation with phosphatase-producing fungi.

Introduction

Vesicular-arbuscular mycorrhizal (VAM) fungi may enhance host plant growth by improving the supply of mineral nutrients of low mobility in the soil, phosphorus in particular, but also micronutrients like copper and zinc (Kothari et al., 1990; Li et al., 1991b; Tarafdar and Marschner, 1994b). Although it is generally assumed that VAM colonized plants take up phosphorus from the same labile pool as the roots (Bolan, 1991; Marschner and Dell, 1994), there is evidence for a particularly high efficiency of VAM to utilize organically bound phosphorus like RNA (Jayachandran et al., 1992) and phytate (Tarafdar and Marschner, 1994b). Jayachandran et al. (1992) suggest a possible role of VAM fungi in mineralization of organic phosphorus. In our earlier studies (Tarafdar and Marschner, 1994a,b) we demonstrated the production of phosphatase by VAM fungi and their efficiency in utilization of organic phosphorus.

Many soil fungi produce phosphatases as extracellular enzymes, and *Aspergillus fumigatus* has a particular high capacity to produces phosphatases (Tarafdar et al., 1988). Enhancement effects of this fungus on growth and mineral nutrition of mung bean and clusterbean are well documented (Tarafdar et al., 1992, 1995).

Synergistic effects of inoculation of legumes with VAMF and rhizobia in low P soils are well documented (Azimi et al., 1986; Brown et al., 1988; Subba Rao et al., 1986). There are also reports on synergistic interactions between VAM fungi and phosphatase solubilizing bacteria (Azcon et al., 1976; Sreenivasa and Krishnaraj, 1992). But to our knowledge, there are no reports on the co-inoculation of crops with VAM fungi and phosphatase producing fungi (PPF). The aim of the present study was to evaluate whether synergistic interactions existed between VAM fungi (*Glomus mosseae*) and PPF (*Aspergillus fumigatus*) in utilising an organic phosphorus source. For this purpose, a pot culture experiment was conducted with two

Table 1. Some characteristics of the soils used in the experiments

Characteristics	Bavendorf	Niger
Soil group	Cambisol	Psammentic Paleustalf
pH	6.9	5.9
Clay(%)	18.0	1.9
Extractable P (mg kg^{-1})[a]	14.9	7.8
Organic P (mg kg^{-1})	531.5	22.5
Total P (mg kg^{-1})	1066.5	137.5
Organic matter (%)	3.8	0.4
DTPA[c] extractable (mg kg^{-1}):		
Fe	1.4	1.7
Mn	1.8	1.6
Zn	0.1	0.1
Cu	0.2	0.1
Acid phosphatase activity (EU × 10^{-3})[b]	0.7	0.3
Alkaline phosphatase activity (EU × 10^{-3})	0.6	0.4

[a]Olsen-P (Bavendorf); Bray-P1 (Niger).
[b]EU = enzyme units.
[c]DTPA = Diethylenetriaminepentacetic acid.

phosphorus-deficient soils amended with Na-phytate as organic phosphorus source. Wheat seeds were inoculated with PPF (*Aspergillus fumigatus*) and the soil infested with VAM fungi (*Glomus mosseae*) and the dry matter production and nutrient uptake of wheat was studied during a 50 day growth period.

Materials and methods

A pot trial was conducted using two soils of different origin ('Bavendorf' and 'Niger'). Selected characteristics of the soils are given in Table 1. Earthern pots of 1 kg capacity were filled with 500 g of sterilized soil (except in unsterile control treatment). The soils were sieved (2 mm) prior to steaming (48 h two alternate days at 120°C). In all treatments mineral nutrients were mixed with soil to each pot at rates of 300 mg N (NH_4NO_3), 300 mg K (K_2SO_4), 100 mg Mg ($MgSO_4$), 2 mg Fe (Ferric ammonium citrate), 10 mg Zn ($ZnSO_4$) and 10 g Cu ($CuSO_4$) kg^{-1} soil. Phosphorus was supplied as Na phytate to all the pots at rate of 200 mg P kg^{-1} soil.

The mycorrhizal fungus used was *Glomus mosseae*, which had been propagated on maize grown in greenhouse for 8 weeks. Surface-sterilized spores(treated with 0.2% Chloramin-T and 0.02% streptomycin sulphate) were used as inoculum (Tarafdar and Marschner, 1994a). Mycorrhizal treatments received approximately 2000 surface-sterilized (infective spores) of 90–250 μm diameter. The inoculum was placed at 2 cm below the soil surface as a thin layer.

The PPF used was *Aspergillus fumigatus*, multiplied in PDA medium. Wheat seeds (*Triticum aestivum* L. var. Star) were surface-sterilized with ethanol (1 minute) followed by 30% H_2O_2 for 5 minutes and subsequently washed with distilled water. For the PPF treatment, seeds were treated with carrier-based (soil and charcoal in 1/3:2/3 proportion) inoculant of *Aspergillus fumigatus* with a population of 6.5×10^6 cells g^{-1} air dry carrier at the rate of 20 g 100 g^{-1} seed. The seeds were sown immediately after inoculation with *Aspergillus fumigatus*.

Four plants were grown in each pot. There were five treatments namely sterilized control, inoculated with PPF, inoculated with VAM, inoculated with PPF+VAM and unsterilized control. Each treatment had four replicates. Both control (sterilized as well as unsterilized) treatments received neither VAM inoculum nor the seed inoculum containing PPF. The upper surface of the soil was covered by a 2 cm layer of sterilized quartz sand (2 cm size) to minimize evaporation and contamination. The pots were then transferred to a growth chamber (20/15°C and 16/8 h day/night regime, 305 μmol m^{-2} sec^{-1} photon flux density). Measured amounts of sterilized water were supplied daily to the pots to maintain soil moisture content close to field capacity (about 20% W/W) during the growth period. The amount of water transpired by plants was measured gravimetrically. The water loss by evaporation from the pots was negligible because the top of pots was covered with sand.

Plants were harvested after 50 days of growth. At harvest the whole soil was almost surrounded by roots and designated as rhizosphere soil. The roots were carefully washed free from soil and samples of washed roots (50 g fresh weight) were stored in formalin-acetic acid-alcohol (FAA). Root length was measured, using the modified line intersect method (Tennant, 1975). The root samples were cleared using 8% KOH in an autoclave at 105°C for 5 minutes and stained with Trypan blue (Phillips and Hayman, 1970). The per cent root length colonized by VAMF was determined by the grid line intersect method (Giovannetti and Mosse, 1980).

After harvest, the soil in the pot was mixed and a part of it was stored in cold room (4°C). Fungal

hyphae length was determined by modified agar film method from Bääth and Söderström (1979), as adopted by Tarafdar and Marschner (1994a). A 0.5 g soil sample was dispersed in 100 mL deionized water in a blender for 1 min and fungal hyphae were separated by decantation and wet sieving. The separated fungal hyphae with 5 mL deionized water were transferred to a Petri dish containing 10 mL of agar solution (2%). Trypan blue (0.1%) was added, homogenized, dried and hyphal length was measured in the thin agar film by the line-intersection method under a microscope (16 ×). Acid and alkaline phosphatases were assayed by the method of Tabatabai and Bremner (1969), with an acetate buffer (pH 5.4) and a Borax-NaOH buffer (pH 9.4), respectively, using p-nitrophenyl phosphate as the substrate, after reaction 1 g soil for 1 h at 35°C. Phosphatase activity has been expressed in terms of enzyme units (EU). One unit is the amount of enzyme required to hydrolyse 1.0 μmol of p-nitrophenyl phosphate (p-NPP) at 35°C min^{-1} at a specific pH. Although we used sodium-phytate as an organic P source, phosphatase activity estimated by using p-NPP as the substrate also reflected the pattern of phytate hydrolysis (Tarafdar and Marschner, unpubl.). The extracted and organic P in soil was determined by standard methods (Jackson, 1967).

The plants (shoot and roots) were dried at 70°C for 72 h, taken dry weight and then ground. The ground samples were dry ashed at 500°C for nutrient analysis. Phosphorus was determined colorimetrically according to Gericke and Kurmies (1952). Potassium and Ca were analysed by flame photometer whereas Mg, Mn, Cu, Fe and Zn were analysed by atomic absorption spectroscopy.

Analysis of variance was carried out on the data, and means were separated by Student Newman-Keuls procedure for comparisons (Sokal and Rohlf, 1981).

Results

Significant differences in plant height were found between treatments from 4 weeks onwards (results not shown). At harvest, plant height and dry matter yield of shoots and roots were slightly higher in Bavendorf soil compared to Niger soil (Table 2). Irrespectively of these differences, the treatment effects were almost similar in both soils. Inoculation with PPF or VAM alone significantly increased plant height and dry matter yield, and the more positive effect on

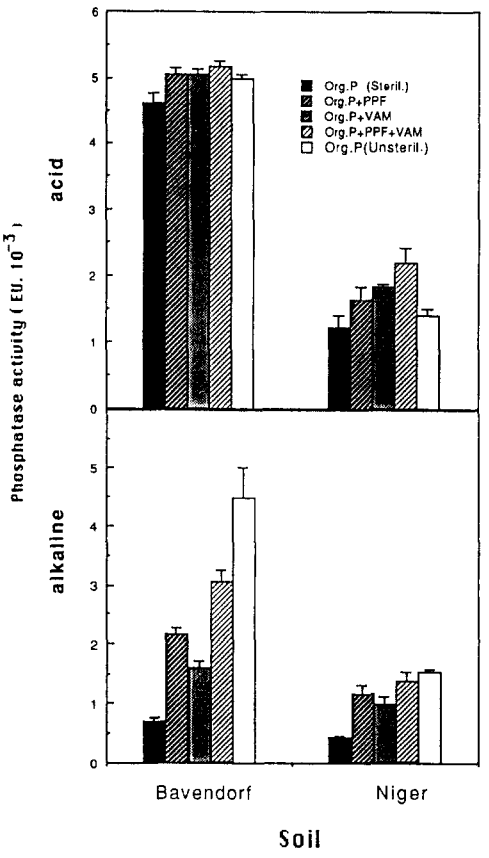

Fig. 1. Acid and alkaline phosphatase activity in the root-soil interface (I: LSD $p<0.01$).

shoot (23–38%) and root (39–92%) dry weight was observed in the combined treatment PPF+VAM. In general, water consumption of the different treatments followed the order of dry matter production. Nevertheless, despite its marked dry matter production in the PPF+VAM treatment about 6% more water was consumed, indicating a higher water use efficiency in this treatment.

Activity of acid and alkaline phosphatase at the soil root interface was higher in Bavendorf soil than in Niger soil (Fig. 1). Inoculation with PPF or VAM increased acid and alkaline phosphatase activity over control (Org. P steril.), particularly in the combined treatment PPF+VAM. The highest phosphatase activity was measured for acid phosphatase in the treatment PPF+VAM and for alkaline phosphatase in unsterilized soil.

Total root length per pot was higher in Bavendorf soil compared with Niger soil (Table 3) which corresponds with the dry weight data. Inoculation with PPF or VAM increased root length and the contri-

Table 2. Plant height, water uptake and dry matter yield as affected by inoculation with *Glomus mosseae* and *Aspergillus fumigatus* (B- Bavendorf soil; N- Niger soil). Figures followed by the same letter are not significantly ($p < 0.05$) different

Treatment	Plant height (cm)		Water use (mL plant^{-1})		Dry matter yield (g plant^{-1})			
					Shoot		Root	
	B	N	B	N	B	N	B	N
Org. P (Steril.)	51.7 a	47.4 a	1057 a	1017 a	5.0 a	4.4 a	1.8 a	1.3 a
Org. P+PPF	54.7 b	53.7 c	1073 a	1043 a	5.5 b	5.0 b	2.2 b	2.0 b
Org. P+VAM	55.3 c	53.4 c	1122 b	1075 b	5.5 b	5.1 b	2.4 b	2.1 b
Org. P+PPF+VAM	57.9 d	56.3 d	1127 b	1083 b	6.9 c	5.4 c	2.5 c	2.5 c
Org. P(Unsteril.)	54.0 b	51.8 b	1063 a	1033 a	5.6 b	4.8 a	2.0 a	1.6 a

Org. P- Organic phosphorus, PPF- Phosphatase producing fungi, VAM- Vesicular arbuscular mycorrhizal fungi, Steril.- Sterile, Unsteril.- Unsterile.

Table 3. Total root length, per cent root length infected by VAM and hyphal length density in wheat as affected by inoculation with *Glomus mosseae* and *Aspergillus funigatus* (B-Bavendorf soil; N-Niger soil). Figures followed by the same letter are not significantly ($p<0.05$) different

Treatment	Total root length (m pot^{-1})		Per cent infected root length		Hyphal length density (m cm^{-3} soil)	
	B	N	B	N	B	N
Org. P(Steril.)	123 a	106 a	0	0	0.1	0.1
Org. P+PPF	171 b	129 b	0	0	2.4 b	1.8 a
Org. P+VAM	184 b	136 c	47 b	42 b	2.6 c	2.2 b
Org. P+PPF+VAM	198 c	141 c	45 b	41 b	2.7 c	2.2 b
Org. P(Unsteril.)	188 b	127 b	3 a	1 a	2.0 a	1.5 a

Org. P- Organic phosphorus, PPF- Phosphatase producing fungi, VAM- Vesicular arbuscular mycorrhizal fungi, Steril.- Sterile, Unsteril,- Unsterile.

bution of PPF+VAM was the most effective among the treatment. Root length was also fairly high in the unsterilized control. No mycorrhizal infection was noticed in the sterile and PPF treatment (Table 3). The low mycorrhizal infection in the unsterilized control can be attributed to the presence of native VAM fungi in the soils. In the PPF+VAM treatments mycorrhizal infection was high and not affected by the presence of PPF. Hyphal length density was high in the non-sterile soil. Inoculation with PPF or VAM led to a slightly higher hyphal length density compared to the non-sterilized soil. There was no further increase in hyphal length density in the combined inoculation PPF+VAM. Despite precautions in the treatment with sterile soil, sterility could not be maintained until harvest. At harvest, the average microbial counts (most probable number) g^{-1} dry soil was 370 and the hyphal length density, 0.1 m cm^{-3} soil.

Table 4. Phosphorus fractions[a] (mg kg^{-1}) in the soil, after harvest, grown in two different soils supplied with Na-phytate (200 mg kg^{-1} soil). Figures followed by the same letter are not significantly ($p<0.05$) different

Treatment	Bavendorf		Niger	
	Org. P	Olsen-P	Org. P	Bray-P1
Org. P(Steril.)	652 a	8.4 a	189 a	4.4 a
Org. P+PPF	604 b	9.3 b	138 b	5.5 b
Org. P+VAM	584 c	10.2 c	120 c	5.0 b
Org. P+PPF+VAM	558 d	9.9 c	109 d	6.3 c
Org. P(Unsteril.)	609 b	12.7 d	142 b	8.2 d

Org. P- Organic phosphorus, PPF- Phosphatase producing fungi, VAM- Vesticular arbuscular mycorrhizal fungi, Steril.- Sterile, Unsteril.- Unsterile.

[a]Initial organic P concentration in soil before start of the experiment (after addition of Na-phytate) was 728 mg kg^{-1} soil in Bavendorf and 222 mg kg^{-1} soil in Niger.

The role of microbial phosphatases in the utilization of organic phosphorus by the wheat plants is shown in

Table 5. Concentration of mineral nutrients in the shoot dry matter of wheat grown in two soils supplied with Na phytate (200 mg P kg^{-1}). Figures followed by the same letter are not significantly ($p<0.05$) different

Soil	Treatment	P	K	Ca	Mg	Cu	Zn	Fe	Mn
		(mg g^{-1})				($\mu g\ g^{-1}$)			
Bavendorf	Org. P(Steril.)	0.8 a	8.4 a	2.8 a	1.8 a	5.4 a	41.5 a	67.0 a	25.9 a
	Org. P+PPF	1.3 c	9.4 b	2.9 a	2.3 b	5.8 a	44.5 a	73.0 a	24.9 a
	Org. P+VAM	1.6 d	9.5 b	3.0 a	2.2 b	7.2 b	80.9 b	68.1 a	23.1 a
	Org. P+PPF+VAM	1.8 d	9.9 b	2.9 a	2.3 b	7.9 b	83.1 b	72.1 a	23.0 a
	Org. P(Unsteril.)	1.1 b	8.8 a	3.1 a	2.1 a	5.9 a	52.1 a	73.5 a	24.1 a
Niger	Org. P(Steril.)	0.6 a	7.3 a	2.9 a	1.7 a	4.8 a	38.2 a	71.0 a	25.0 a
	Org. P+PPF	1.2 b	8.1 b	3.1 a	2.2 b	5.1 a	41.3 a	73.9 a	24.2 a
	Org. P+VAM	1.4 b	8.2 b	3.2 a	2.1 b	6.7 b	76.8 b	72.5 a	23.5 a
	Org. P+PPF+VAM	1.7 c	8.9 c	3.4 a	2.3 b	6.9 b	80.5 b	73.5 a	23.2
	Org. P(Unsteril.)	0.9 a	8.0 a	3.2 a	2.0 a	5.3 a	45.3 a	80.9 a	24.8 a

Org. P-Organic phosphorus, PPF- Phosphatase producing fungi, VAM- Vesticular arbuscular mycorrhizal fungi, Steril.- Sterile, Unsteril.- Unsterile.

Table 4. Depletion of organic phosphorus was similar in the soils of the non-sterilized control and the soil inoculated with PPF. Maximum depletion of organic phosphorus was noticed in PPF+VAM treatment. Interestingly, VAM or PPF alone contributed relatively more to the depletion than the mixed inoculation. This result is in accordance to the lack of increase in hyphal length density in this mixed treatment compared to VAM or PPF alone (Table 3).

Inoculation with PPF or VAM significantly increased shoot concentrations of phosphorus, potassium and magnesium (Table 5). In contrast, concentrations of calcium, iron and manganese were not significantly affected. Shoot concentrations of phosphorus were highest in the combined treatment PPF+VAM. Shoot concentrations of copper and zinc were only enhanced by VAM and not affected by PPF.

Discussion

The present experiment confirms that utilization of organic P is enhanced by VAM. This enhancement effect could be due to both increase in surface area and phosphatase activity of the extraradical hyphae (Li et al., 1991a; Tarafdar and Marschner, 1994a). Inoculation with the PPF increased phosphatase activity in the rhizosphere and utilization of organic P and dual inoculation had no additional effect (Table 4, Fig. 1). The enhanced effect of PPF and VAM on utilization of organic P however, cannot be exclusively attributed to higher phosphatase activity or hyphal uptake as root growth was enhanced also (Table 2 and 3). In view of the fairly high activity of acid phosphatase at root surfaces (Chhonkar and Tarafdar, 1981) and root apical zones in particular (Dinkelaker and Marschner, 1992), increase in root growth will also have favourable effects on utilization of organic P. Compared to the sterile treatment, root length was also significantly greater in the non-sterile control (Table 3), but utilization of organic P was less enhanced in the treatment with PPF (Table 4 and 5) in spite of similar root length in both treatments. Thus, the high phosphatase activity of PPF had a particular enhancement effect an utilization of organic P by wheat plants compared to the native soil microflora.

Shoot concentrations of K and Mg were also higher in the inoculated plants (Table 5), most likely as results of enhanced root length. The shoot concentrations of Cu and Zn were only enhanced in VAM plants (Table 5). It is well documented that Zn and Cu can be absorbed and translocated through VAM hyphae and then released to the host (Kothari et al., 1991b; Li et al., 1991b). In general, Fe and Mn concentrations were slightly decreased. Lower shoot concentration in Fe and Mn in mycorrhizal wheat plants are in accordance with the results of Pacovsky (1986) in soybean and Kothari et al. (1990, 1991a) in maize.

Linderman (1988) suggested that mycorrhizal plant responses involve the entire mycorrhizosphere, not just

the fungus alone. Companion fungi or bacteria present in the mycorrhizosphere, may promote plant growth through a variety of mechanisms. The microbial community may stimulate the devolopment of hyphae and rhizomorphs or decrease the growth of pathogens.

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References

Azcon R, Barea J M and Hayman D S 1976 Utilization of rock phosphate in alkaline soils by plants inoculated with mycorrhrzal fungi and P solubilizing bacteria. Soil. Biol. Biochem. 8, 135–138.

Azimi S, Gianinazzi-Pearson V and Gianinazzi S 1980 Influence of increasing soil phosphorus levels on interactions between vesicular-arbuscular mycorrhiza and *Rhizobium* in soyabeans. Can. J. Bot. 58, 2200–2205.

Bääth E and Söderström B 1979 Fungal biomass and fungal immobilization of plant nutrients in Swedish coniferous forest soils. Rev. Ecol. Biol. Sol 16, 477–489.

Bolan N S 1991 A critical review of the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant and Soil 134, 189–207.

Brown M S, Thamsurakul S and Bethlenfalvay G J 1988 The *Glycine-Glomus-Bradyrhizobium* symbiosis.IX. Phosphorus-use efficiency of CO_2 and N_2 fixation in mycorrhizal soybean. Physiol. Plant. 74, 159–163.

Chhonkar P K and Tarafdar J C 1981 Characteristics and location of phosphatases in soil-plant system. J. Indian Soc. Soil Sci. 29, 215–219.

Dinkelaker B and Marschner H 1992 In vivo demonstration of acid phosphatase activity in the rhizosphere of soil grown plants. Plant and Soil 144, 199–205.

Gericke S and Kurmies B 1952 Die kolorimetrische phosphorsäurebestimmung mit ammonium-vanadat-molybdat und ihre Anwendung in der Pflanzenanalyse. Z. Pflanzenernähr. Düng. Bodenkd. 59, 235–247.

Giovannetti M and Mosse B 1980 An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infection in roots. New Phytol. 84, 489–500.

Jackson M L 1967 Phosphorus. *In* Soil Chemical Analysis. pp 134–182. Prentice-Hall of India, Delhi.

Jayachandran K, Schwab A P and Hetrick B A D 1992 Mineralization of organic phosphorus by vesicular-arbuscular mycorrhizal fungi. Soil Biol. Biochem. 24, 897–903.

Kothari S K, Marschner H and George E 1990 Effect of VA-mycorrhizal fungi and rhizosphere microorganisms on root and shoot morphology, growth and water relations in maize. New Phytol. 116, 303–311.

Kothari S K, Marschner H and Römheld V 1991 a Contribution of the VA-mycorrhizal hyphae in acquisition of phosphorus and zinc by maize grown in a calcareous soil. Plant and Soil 131, 177–185.

Kathari S K, Marschner H and Römheld V 1991b Effect of vesicular-arbuscular mycorrhizal fungus and rhizosphere micro-organisms on manganese reduction in the rhizosphere and manganese concentrations in maize (*Zea mays* L.). New Phytol. 117, 649–655.

Li X-L, George E and Marschner H 1991a Extention of the phosphorus depletion zone in a VA-mycorrhizal white clover in a calcareous soil. Plant and Soil 136, 41–48.

Li X-L, Marschner H and George E 1991b Acquisition of phosphorus and copper by VA mycorrhizal hyphae and root to shoot transport in white clover. Plant and Soil 136, 49–57.

Linderman R G 1988 Mycorrhizal interactions with the rhizosphere microflora: The mycorrhizosphere effect. Phytopathol. 78, 366–371.

Marschner H and Dell B 1994 Nutrient uptake in mycorrhizal symbiosis. Plant and Soil 159, 89–102.

Pacovsky R S 1986 Micronutrient uptake and distribution in mycorrhizal phosphorus fertilized soybeans. Plant and Soil 95, 379–388.

Phillips J M and Hayman D S 1970 Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhrzal fungi. Trans. Br. Mycol. Soc. 55, 158–161.

Sokal R R and Rohlf F J 1981 Biometry-The Principles and Practice of Statistics in Biological Research, 2nd, ed. Freeman, New York.

Subba Rao K V, Tilak B R and Singh G S 1986 Dual inoculation with *Rhizobium* sp. and *Glomus fasciculatum* enhances nodulation, yield and nitrogen fixation in chickpea (*Cicer arietinum* Linn.). Plant and Soil 95, 351–359.

Sreenivasa M N and Krishnaraj P U 1992 Synergistic interaction between VA mycorrhizal fungi and a phosphate solubilizing bacterium in chilli (*Capsicum annuum*). Zentralbl. Mikrobiol. 147, 126–130.

Tabatabai M A and Bremner J M 1969 Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. Soil Biol. Biochem. 1, 301–307.

Tarafdar J C, Rao A V and Bala K 1988 Production of phosphatases by fungi isolated from desert soils. Folia Microbiol. 33, 453–457.

Tarafdar J C, Rao A V and Praveen-Kumar 1992 Effect of different phosphatase producing fungi on growth and nutrition of mung bean (*Vigna radiata* (L.) Wikzek) in arid soil. Biol. Fertil. Soils 13, 35–58.

Tarafdar J C and Marschner H 1994a Phosphatase activity in the rhizosphere and hyposphere of VA mycorrhizal wheat supplied with inorganic and organic phosphorus. Soil Biol. Biochem. 26, 387–395.

Tarafdar J C and Marschner H 1994b Efficiency of VAM hyphae in utilization of organic phosphorus by wheat plants. Soil Sci. Plant Nutr. 40, 593–600.

Tarafdar J C, Rao A V and Praveen-Kumar 1995 Role af phosphatase producing fungi on growth and nutrition of clusterbean (*Cyamopsis tetragonoloba* (L) Taub). J. Arid. Environ. (*In press*).

Tennant D 1975 A test of a modified line intersect method of estimating root length. J. Ecol. 63, 995–1001.

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