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Effects of mycorrhizae and phosphorus on growth and nutrient uptake of millet, cowpea and sorghum on a West African soil

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SUMMARY

Despite numerous reports on the positive effects of vesicular arbuscular mycorrhizae (VAM) on plant growth in temperate soils, surprisingly little data exist on the importance of VAM for crop growth on acid sandy soils of West Africa. A pot experiment conducted with local genotypes of pearl millet (*Pennisetum glaucum* L.), sorghum (*Sorghum bicolor* L. Moench) and cowpea (*Vigna unguiculata*) with and without phosphorus (P) application in a sterilized sandy soil from a farmer's field in Niger showed large growth-enhancing effects of VAM. Phosphorus application led to 18- and 24-fold increases in pearl millet root and shoot dry matter independently of VAM, whereas the shoot and root dry matter of sorghum and cowpea depended largely on the interaction between P application and VAM. With P, VAM increased total uptake of P, K, Ca, Mg and Zn by 2·5- to 6-fold in sorghum and cowpea. On severely P deficient West African soils P application can lead to large increases in early root growth, a prerequisite for early mycorrhizal infection and a subsequent significant contribution of VAM to enhanced plant growth and nutrient uptake.

INTRODUCTION

Vesicular arbuscular mycorrhizal (VAM) fungi can play an important role for plant nutrient uptake, particularly on soils with low phosphorus (P) availability. The hyphal mycelium increases the total absorption surface of infected plants and thus improves its access of immobile elements such as P, copper (Cu), zinc (Zn) (Lambert *et al.* 1979; George *et al.* 1994; George *et al.* 1996; Ortas *et al.* 1996) and cadmium (Cd) (Guo *et al.* 1996) in areas beyond the root's depletion zone. Furthermore, mycorrhizal fungi may permit some plant-to-plant transport of nitrogen (N) (Bethlenfalvay *et al.* 1991). Nitrogen released from senescing roots of one plant may be taken up by mycorrhizal hyphae and transported to other plants (Hamel *et al.* 1991*a*, *b*). Mycorrhizal fungi can also absorb N from NH_4^+-N mineral fertilizers and transport it to the host plant (Ames *et al.* 1983; Johansen *et al.* 1993). Some evidence also suggests that mycorrhizal fungi may contribute to the water uptake of the host plants and consequently improve their drought resistance (Ibrahim *et al.* 1990; Michelsen & Rosendahl 1990; Davies *et al.* 1992). However, George *et al.* (1992*a*, *b*) did not find any evidence for direct water transport by VAM hyphae to plants. The effect of mycorrhizae on plant growth can be direct, such as when hyphae can take up nutrients and translocate them to the host, or indirect, such as when an infection of the root system by the fungi causes morphological and physiological changes in the host plant (George *et al.* 1992*a*).

Compared with the vast work on VAM effects in temperate soils, little information is available for millet, sorghum and cowpea grown on acid sandy soils from semi-arid Sudano Sahelian West Africa. Because it is well known that nutrients, particularly P and to a lesser extent N, severely limit crop growth on many of these soils (Bationo *et al.* 1990, 1992; Bationo & Mokwunye 1991), VAM associations may have a large effect on plant growth. This study was therefore undertaken to examine whether early growth and nutrient uptake of millet, cowpea and sorghum may benefit from VAM inoculation of a West African soil from which indigenous VAM fungi have been

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eliminated. Large-scale field sterilizations to obtain non-mycorrhizal 'control' plants are often unsuccessful and in addition can lead to drastic changes in soil nutrient availability (Weber *et al.* 1993). Therefore, the potential contribution of VAM fungi to early nutrient uptake of the plants in this study was examined under controlled conditions in a growth chamber.

MATERIALS AND METHODS

Local genotypes of pearl millet (*Pennisetum glaucum* L.), sorghum [*Sorghum bicolor* (L.) Moench] and cowpea (*Vigna unguiculata*) were grown in a sandy, siliceous, isohyperthermic Psammentic Paleustalf soil (West *et al.* 1984) collected from a farmer's field in Niger (Table 1). The air-dried soil was analysed as follows: for pH ratios of 1:2·5 of water and 1:2·5 of 0·01 M KCl were used; for organic carbon (C_{org}) the method of Walkely & Black (1934) was followed; extractable P was measured as Bray P (Olsen & Sommers 1982); and exchangeable aluminium (Al) was determined according to McLean (1982). Exchangeable bases were extracted with 1 M NH_4 acetate, and cations were determined by atomic absorption spectrophotometry (Ca and Mg) and by flame emission spectrophotometry (K and Na). To obtain a mycorrhizal-free substrate and minimize chemical changes by autoclaving, the soil was dry heated at 80 °C in the oven for 48 h. A total of 2·5 kg of soil was filled into each of 48 pots of 3 litre volume. Treatments consisted of two levels of P (0 and 10 mg/kg soil) and two mycorrhizal treatments: uninoculated (−VAM) and inoculated (+VAM). Phosphorus was applied as KH_2PO_4 powder mixed thoroughly with the soil. In all treatments mineral nutrients were uniformly added to the soil at rates of 150 mg N (NH_4NO_3), 150 mg K (K_2SO_4), 50 mg Mg ($MgSO_4$), 2 mg Fe (Fe_2SO_4), 5 mg Zn ($ZnSO_4$) and 5 mg Cu ($CuSO_4$) per kg of soil. Possible benefits to plant growth from VAM inoculation were examined with *Glomus mosseae* (isolate BEG 107) because this species had been found in preliminary experiments to provide satisfactory mycorrhizal colonization in all three plant species used in this study. The inoculum consisted of colonized maize roots and adhering soil and it was homogenized and added at a rate of 30 g/kg to the soil of the mycorrhizal treatments. Sterilized inoculum and an inoculum filtrate were added to non mycorrhizal treatments. The inoculum was thoroughly mixed with the entire soil of each pot.

Seeds of millet, cowpea and sorghum were surface-sterilized with 10% H_2O_2 for 5 min and then washed with deionised water before planting. Each treatment was replicated four times. To maintain an adequate soil moisture level during the course of the experiment, pots were weighed daily and the water content was adjusted to approximately 60% field capacity, equivalent to a water content of 6% (w/w). The experiment was conducted in a growth chamber with respective day and night temperatures of 35 °C and 25 °C in a cycle of 14 h days and 10 h nights and a photon flux density of 480 $\mu E/m^2$ per s in the day. Every 3 days, all pots were moved to new, randomly assigned positions in the growth chamber.

The plants were harvested after 8 weeks of growth. Roots were carefully washed from the adhering soil using tap water, and the total fresh weight was determined. From each pot a subsample of approximately 2 g fresh roots was removed and cut into small segments of 10 mm length. They were then transferred into staining tubes, and cleared with 10% KOH for 1 h at 60 °C. Subsequently the KOH was removed, roots were washed three times using demineralized water and acidified with 2 N HCl for 30 min. After removal of the acid, roots were stained with 0·05% trypan blue in lactoglycerol and destained in lactic acid. The per cent mycorrhizal colonization was measured with a line intersection method (Kormanik & McGraw 1982). For this purpose, all parts of mycorrhizal colonization in the roots (vesicles, arbuscules and hyphae) were counted.

To determine root length density, 5 g of fresh roots were sampled. Root length was determined as described by Tennant (1975). The remaining roots were oven dried to measure their dry weight. The ratio of fresh to dry weight of roots was determined and this ratio was used to calculate total root dry weight. Total above-ground dry weight was determined after drying shoot biomass at 65 °C for 48 h. Then the shoot material was ground to determine N, P, K, calcium (Ca), magnesium (Mg) and Zn

Table 1. *Chemical characteristics of the surface soil (0 to 0·2 m depth) from Niger used for the pot trial*

pH (H_2O)	pH (KCl)	C_{org} (g/kg)	P_{Bray} (mg/kg)	CEC*	Na^+	k^+	Ca^{2+}	Mg^{2+}	Al^{3+}
				mmol(+)/kg					
5·60	4·60	1·1	4·10	5·2	0·2	0·8	2·3	1·1	0·4

* Cation exchange capacity. Cations were extracted with 1 M NH_4 acetate.

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concentrations. For the analysis of these mineral elements, samples were dry ashed for 4 h at 500 °C in a muffle furnace and the ash dissolved in 1:30 (v/v) diluted HCl. Potassium and Ca were determined by flame emission spectrophotometry using an Eppendorf Elex6361, Mg, Zn and Cu by atomic absorption spectrophotometry using a UNICAM 939 and P calorimetrically using a Hitachi U-3000 spectrophotometer according to the vanado-molybdate method (Gericke & Kurmies 1952).

The AM infection ratings were compared with those in millet-cowpea rotation trials conducted on sandy soils of Niger. For this comparison, millet root samples were taken at maturity in September of 1996, and in July and September of 1997, and processed in the same way as described previously. All data collected in this study were subject to analysis of variance with GENSTAT Release 3·2 (Lawes Agricultural Trust 1993).

RESULTS

In the field experiments, the root systems of pearl millet plants grown at different sites in Niger were always well colonized with VAM fungi (Table 2). Similar results were obtained with sorghum and cowpea. In the pot experiment, irrespective of the species, plants in control pots showed visual symptoms of P deficiency by the end of the second week leading to very poor plant growth without P thereafter.

Pearl millet

Dry matter

Phosphorus application increased root dry matter (DM) 18-fold, root length density 17-fold and shoot DM 24-fold (Fig. 1; Table 3). VAM inoculation resulted in a significant increase in shoot DM (Fig. 1; Table 4) and also led to a small but non-significant increase in root length density (Table 3). Millet had a much larger root length density than sorghum and particularly cowpea which translated to specific root length densities in −VAM plants with P application of 11 m/g root dry weight for millet, 7 m/g for cowpea and 6 m/g for sorghum. Shoot to root ratio was significantly higher with P fertilization compared with the unfertilized control ($P < 0{\cdot}001$), but it was similar for both VAM treatments (data not shown).

VAM infection

Phosphorus application did not reduce the VAM infection rate (Fig. 1). Although the difference was not significant, roots of plants with P application tended to have higher VAM infection compared with the unfertilized control. No infection was recorded for the control, indicating that there had been no contamination during the course of the experiment.

Nutrient uptake

Phosphorus application led to higher P concentrations and total P uptake, but lower K, Ca, Mg and Zn concentrations (Tables 5 and 6, Fig. 2). Total uptake of K, Ca, Mg and Zn, however, was significantly higher with P than without P (Fig. 2). The effect of VAM inoculation on the concentrations of K, Ca, Mg, and Zn generally depended on P application (Table 6). Without P, VAM inoculation resulted in higher P, K and Zn but lower Ca concentrations compared with uninoculated plants, whereas with the application of 10 mg P/kg soil, the concentrations of K, Mg and Zn were lower in VAM treated plants (Table 6). Without P, total nutrient uptake was five-fold higher for K and ten-fold higher for Zn in +VAM versus −VAM plants. Also, for P, Ca and Mg total uptake was higher in +VAM plants in absolute values, but differences were not statistically significant (Fig. 2). However, with P application VAM inoculation reduced K and Zn uptake. The

Table 2. *Effects of cropping systems on pearl millet root infection by vesicular arbuscular mycorrhizae (VAM) in a field experiment at the sites of Gobery and Gaya (Niger). Roots were sampled at maturity in 1996 and 45, 50 and 75 days after sowing (DAS) in 1997*

	1996		1997		
	Gobery	Gaya	Gobery		Gaya
	120 DAS*		45 DAS	75 DAS	50 DAS
Cropping systems	VAM infection (% of roots)				
Continuous millet	35	31	27	48	11
Millet after cowpea	39	33	48	64	31
S.E.D.†	7	3	3	4	4

* DAS, days after sowing.
† Standard error of the difference.

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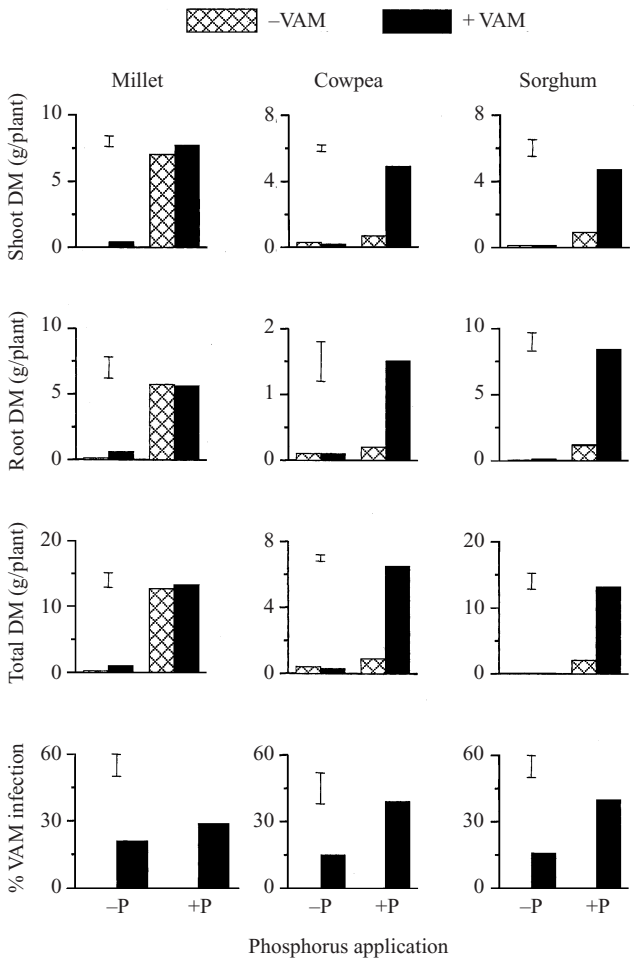

Fig. 1. Shoot, root and total dry matter (DM) of millet, cowpea and sorghum as affected by AM inoculation with *Glomus mosseae* and phosphorus (P) application. Phosphorus was applied as powdery KH_2PO_4 at the rate of 10 mg P/kg soil and mixed with the soil before planting. Vertical lines next to the bars are one standard error of the difference (S.E.D.).

Table 3. *Effects of mycorrhizae* (*VAM*) *and phosphorus* (*P*) *application on root length density of millet, cowpea and sorghum in a pot trial*

	Millet	Cowpea	Sorghum
Treatments		m/pot	
−P−VAM	4	2	1
−P+VAM	21	2	1
+P−VAM	188	4	21
+P+VAM	234	56	225
*P**	0·271	< 0·001	0·007
S.E.D.†	38	2	42

* Probability of a treatment effect (significance level).
† Standard error of the difference.

same tendencies were observed for the uptake of P and Mg.

Cowpea

Dry matter

Mycorrhizal effects on shoot and root DM strongly depended on the level of P application (Fig. 1; Table 4). Without P, VAM inoculation did not increase the total DM, but with P application shoot and root DM increased seven- to eight-fold in +VAM plants compared with −VAM plants that were fertilized with P. Without P application, the total root length density was similar in +VAM and −VAM plants. However, when P fertilizer was applied, total root length density was increased 16-fold (Table 3). In contrast to millet, there was no treatment effect on the shoot to root ratio (data not shown).

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Table 4. *Effects of mycorrhizae (VAM) and phosphorus (P) application on shoot, root and total dry matter of millet, cowpea and sorghum in a pot trial*

		Millet			Cowpea			Sorghum		
Factors	D.F.	Shoot	Root	TDM	Shoot	Root	TDM	Shoot	Root	TDM
						P				
P fertilizer	1	0·134	< 0·001	< 0·001	< 0·001	0·009	< 0·001	< 0·001	< 0·001	< 0·001
VAM	1	< 0·001	0·116	0·773	< 0·001	0·014	< 0·001	< 0·001	< 0·001	< 0·001
P × VAM	1	0·134	0·519	0·619	< 0·001	0·016	< 0·001	< 0·001	< 0·001	< 0·001
CV (%)		37	15	39	23	97	12	49	44	43

TDM, total dry matter; *P*, probability of a treatment effect (significance level); CV, coefficient of variation.

Table 5. *Effects of mycorrhizae (VAM) and phosphorus (P) application on total nutrient uptake of millet, cowpea and sorghum in a pot trial*

Factors	D.F.	P	K	Ca	Mg	Zn
				P		
Millet						
P fertilizer	1	< 0·001	< 0·001	< 0·001	< 0·001	< 0·001
VAM	1	0·924	0·730	0·432	0·655	0·761
P × VAM	1	0·771	0·008	0·595	0·283	0·011
CV (%)		32	15	63	31	38
Cowpea						
P fertilizer	1	< 0·001	< 0·001	< 0·001	< 0·001	0·023
VAM	1	< 0·001	< 0·001	< 0·001	< 0·001	0·303
P × VAM	1	< 0·001	< 0·001	< 0·001	< 0·001	0·012
CV (%)		32	33	16	22	63
Sorghum						
P fertilizer	1	< 0·001	< 0·001	< 0·001	< 0·001	< 0·001
VAM	1	< 0·001	0·008	0·009	< 0·001	0·007
P × VAM	1	< 0·001	0·009	0·008	< 0·001	0·009
CV (%)		34	47	63	39	43

P, probability of a treatment effect (significance level); CV, coefficient of variation.

Table 6. *Effects of mycorrhizae (VAM) and phosphorus (P) application on the nutrient concentrations of millet shoots in the pot trial*

Treatments	P	K	Ca	Mg	Zn
	mg/g*				μg/g
−P−VAM	0·7	45·0	17·0	8·2	203
−P+VAM	1·0	48·3	7·4	6·0	392
+P−VAM	2·7	15·3	3·4	4·1	75
+P+VAM	2·4	12·2	3·8	3·2	45
S.E.D.	0·2	1·7	1·3	0·7	18
			P		
P	< 0·001	< 0·001	< 0·001	< 0·001	< 0·001
VAM	0·794	0·941	< 0·001	0·150	< 0·001
P × VAM	0·133	0·025	< 0·001	0·219	< 0·001
CV (%)	19	8	23	19	14

* Dry matter.
S.E.D., standard error of the difference; *P*, probability of a treatment effect (significance level); CV, coefficient of variation.

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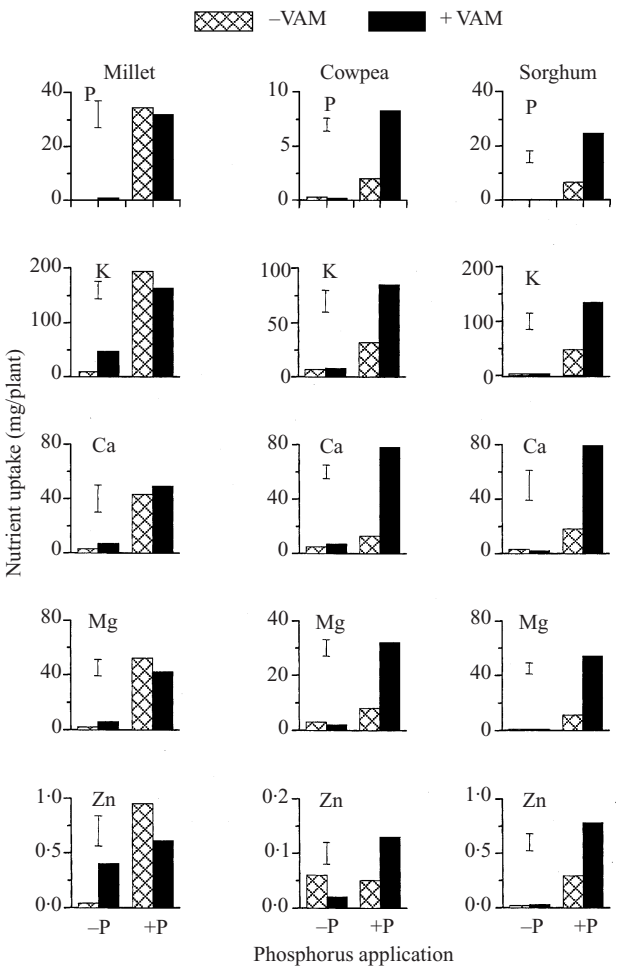

Fig. 2. Nutrient uptake by millet, cowpea and sorghum as affected by *Glomus mosseae* and phosphorus (P) application in a pot experiment. Phosphorus was applied as powdery KH_2PO_4 at the rate of 10 mg P/kg soil and mixed with the soil before planting. Vertical lines next to the bars are one standard error of the difference (S.E.D.).

VAM infection

Root colonization by VAM was significantly higher ($P = 0{\cdot}037$) with P application compared to those without P (Fig. 1). No infection was recorded for roots of non-inoculated plants.

Nutrient uptake

Phosphorus application increased P concentration in the shoots by 170%, but decreased the concentration of Ca by 22%, Mg by 10% and Zn by 64% (Table 7). Across P treatments, VAM inoculation resulted in a decrease in P, K, Mg and Zn concentrations but in an increase in Ca concentration. As a reflection of differences in DM, total nutrient uptake per plant increased with both P and VAM inoculation (Fig. 2). However, the magnitude of these increments was largely influenced by the interaction between VAM and P levels. Without P there were no clear differences in nutrient uptake due to VAM inoculation for any element except Zn. In contrast with P application, the total nutrient uptake of plants with VAM inoculation was significantly higher than of those without VAM.

Sorghum

Dry matter

As for cowpea, VAM effects on shoot and root growth depended on P application. Without P, no VAM effects were observed, but with P application shoot DM increased five- and root DM seven-fold due to mycorrhizal colonization (Fig. 1). As for cowpea, without P the total root length density was

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Table 7. *Effects of mycorrhizae (VAM) and phosphorus (P) application on the nutrient concentrations of cowpea shoots in the pot trial*

Treatments	P	K	Ca	Mg	Zn
		mg/g*			μg/g
−P−VAM	0·7	25·4	13·1	7·8	156
−P+VAM	0·6	25·3	21·0	7·0	51
+P−VAM	2·2	36·4	14·6	8·4	54
+P+VAM	1·3	13·0	12·0	4·9	20
S.E.D.	0·1	13·0	2·4	1·2	8·6
			P		
P	< 0·001	0·755	0·059	0·417	< 0·001
VAM	< 0·001	< 0·001	0·154	0·035	< 0·001
P × VAM	< 0·001	< 0·001	0·013	0·149	< 0·001
CV (%)	16	17	23	25	21

* Dry matter.
S.E.D., standard error of the difference; *P*, probability of a treatment effect (significance level); CV, coefficient of variation.

Table 8. *Effects of mycorrhizae (VAM) and phosphorus (P) application on the nutrient concentrations of sorghum shoots in the pot trial*

Treatments	P	K	Ca	Mg	Zn
		mg/g*			μg/g
−P−VAM	0·7	28·1	25·9	11·1	215
−P+VAM	0·6	26·8	17·2	7·0	210
+P−VAM	3·6	23·2	9·1	5·5	155
+P+VAM	1·9	10·2	6·4	4·2	64
S.E.D.	0·4	1·5	2·0	0·6	24
			P		
P	< 0·001	< 0·001	< 0·001	< 0·001	< 0·001
VAM	0·019	< 0·001	0·003	< 0·001	0·018
P × VAM	0·030	< 0·001	0·064	0·010	0·030
CV (%)	37	9	20	12	21

* Dry matter.
S.E.D., standard error of the difference; *P*, probability of a treatment effect (significance level); CV, coefficient of variation.

similar for +VAM and −VAM plants but increased more than ten-fold with P fertilizer (Table 3). Also, shoot to root ratio was not significantly affected by treatments (data not shown).

VAM infection

As for millet and cowpea, no VAM infection was observed at roots from the uninoculated pots. Also, VAM infection was higher ($P = 0{\cdot}009$) with P application compared with the control (Fig. 1).

Nutrient uptake

Phosphorus fertilization increased the concentration of P but decreased concentrations of K, Ca, Mg and Zn (Table 8). VAM inoculation reduced the concentration of all nutrients to an even larger degree when P fertilizer was applied. Without P, total nutrient uptake by VAM inoculated plants did not significantly differ from that of uninoculated plants, but with P nutrient uptake in +VAM plants was three- to four-fold higher than in −VAM plants (Fig. 2).

DISCUSSION

Plant growth and dry matter

In P deficient soils, root colonization by VAM can significantly improve P uptake per unit root length due to the enhancement of the total root surface by hyphal growth (Li *et al*. 1991). The present data show that total root length density of millet was highly correlated with P-uptake in the shoot indicating the effects of root development on P nutrition in this plant species (Fig. 3). The results of the pot experiment indicate that under controlled growth conditions P availability governed dry matter and root colonization by VAM in millet, cowpea and sorghum. During the first 2 weeks, plant growth may have been sustained

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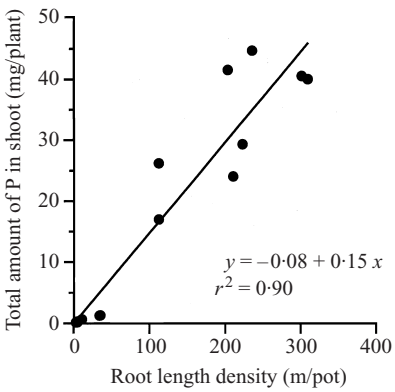

Fig. 3. Relationship between millet root length density and the amount of phosphorus (P) accumulated in the shoot.

by P reserves in the seeds after which the first visual symptoms of P deficiency appeared. The fact that P application increased VAM infection compared to plants without P indicates that early shoot and subsequent root development is an important prerequisite for early VAM colonization. A similar beneficial effect of a moderate P-fertilization on the mycorrhizal contribution to plant growth on P deficient soils was also shown by Siqueira *et al.* (1998). It is well known that the establishment and maintenance of mycorrhizal symbiosis is linked to a flow of carbon from the host plant to the fungus (Todd *et al.* 1984). The overall much lower effects of VAM inoculation on millet root and shoot DM compared with cowpea and sorghum may be explained by differences in the rooting system of these crops. Pearl millet with its much larger root length density even without VAM colonization (Table 3) appears to have a better spatial access to nutrients in soil than cowpea and sorghum. This suggests a larger relative benefit of VAM-induced increases in the total rooting system for sorghum and cowpea than for millet.

Nutrient uptake

Millet

The decrease in K, Ca, Mg and Zn concentrations with P application was clearly related to increases in dry matter and thus reflected dilution effects. In this study, without P, VAM contributed to an only minor increase in the nutrient uptake of millet which is in agreement with Hafner (1992) and support the hypothesis that the high root length density of millet may reduce the benefits from VAM inoculation.

Cowpea and sorghum

Compared with millet, cowpea and sorghum may benefit much more from VAM inoculation because of their coarser rooting systems. In this experiment, nutrient concentrations and accumulation by cowpea were significantly influenced by P application and VAM inoculation. The higher P and lower Ca and Zn concentrations with P are certainly due to dilution effects given the much larger dry matter with P application. Unlike in millet, nutrient uptake in cowpea and sorghum was maximized by the combined effect of VAM inoculation and P application. In the field, mycorrhizal contribution to plant growth is likely to be larger than in the small pots used in this study because the root-to-root distances are larger which will increase the role of mycorrhizal hyphae for nutrient uptake from root-distant soil. In addition, mycorrhizal colonization may help the plant to withstand temporary drought stress (Subramanian *et al.* 1997) often occurring under field conditions on sandy Sahelian soils.

CONCLUSIONS

For the sandy and severely P deficient West African soil used in this experiment the results show the effects of a small dose of P fertilizer to enhance root growth which appears to be a prerequisite for early mycorrhizal infection and a subsequent significant contribution of VAM to plant growth and nutrient uptake. In general all three tested crops derived some benefit from VAM inoculation, but given the differences in root morphology of the crops, VAM effects on plant growth and nutrient uptake were more important for sorghum and cowpea than for pearl millet.

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