Communications in Soil Science and Plant Analysis

ISSN: 0010-3624 (Print) 1532-2416 (Online) Journal homepage: https://www.tandfonline.com/loi/lcss20

Effects of Arbuscular Mycorrhizal Inoculation and Phosphorus Application on Yield and Nutrient Uptake of Yam

M. O. Dare, R. C. Abaidoo, O. Fagbola & R. Asiedu

To cite this article: M. O. Dare, R. C. Abaidoo, O. Fagbola & R. Asiedu (2010) Effects of Arbuscular Mycorrhizal Inoculation and Phosphorus Application on Yield and Nutrient Uptake of Yam, Communications in Soil Science and Plant Analysis, 41:22, 2729-2743, DOI: 10.1080/00103624.2010.518264

To link to this article: https://doi.org/10.1080/00103624.2010.518264

Published online: 25 Nov 2010.

Communications in Soil Science and Plant Analysis, 41:2729–2743, 2010

ISSN: 0010-3624 print / 1532-2416 online
DOI: 10.1080/00103624.2010.518264

Taylor & Francis
Taylor & Francis Group

Effects of Arbuscular Mycorrhizal Inoculation and Phosphorus Application on Yield and Nutrient Uptake of Yam

M. O. DARE,[1,2] R. C. ABAIDOO,[1] O. FAGBOLA,[2] AND R. ASIEDU[1]

[1]International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria
[2]Department of Agronomy, University of Ibadan, Ibadan, Nigeria

*To be sustainable, production in the traditional yam cropping system, faced with declining soil fertility, could benefit from yam–arbuscular mycorrhizal (AM) symbiosis, which can improve nutrient uptake, disease resistance, and drought tolerance in plants. However, only limited information exists about AM colonization of yam. A pot experiment was conducted to collect information on the response of two genotypes (*Dioscorea rotundata *accession TDr 97/00903 and* D. alata *accession TDa 297) to AM inoculation (with and without) and phosphorus (P) (0, 0.05, 0.5, and 5 mg P kg^{-1} soil). Factorial combinations of the treatments were arranged in a completely randomized design with four replicates. The percentage of AM colonization was significantly lowered at 5 mg P kg^{-1} soil rate in mycorrhizal plants of both genotypes. TDr 97/00903 showed more responsiveness to AM inoculation than TDa 297. The greatest AM responsiveness for tuber yield (52%) was obtained at 0.5 mg P kg^{-1} soil rate for TDr 97/00903. Mycorrhizal inoculation significantly increased root dry weight and tuber yield of TDr 97/00903 with the greatest values obtained at the 0.5 mg P kg^{-1} soil rate. Arbuscular mycorrhizal inoculation did not lead to significant ($P < 0.05$) changes in root length and area. Phosphorus application significantly increased the shoot dry weight and root diameter of TDa 297. Uptake of P was greatest at 0.5 mg P kg^{-1} soil in both genotypes and was significantly influenced by AM inoculation. Nitrogen (N) and potassium (K) uptake were greatest in mycorrhizal plants at 0.05 mg P kg^{-1} soil for TDr 97/00903 but at 0.5 mg P kg^{-1} soil of nonmycorrhizal plants of TDa 297. The increased tuber yield and nutrient uptake observed in the mycorrhizal plants indicate the potential for the improvement of nutrient acquisition and tuber yield through AM symbiosis.*

Keywords Arbuscular Mycorrhizal inoculation, nutrient acquisition, yam-based systems

Introduction

Yam (*Dioscorea* spp.) is a major tuber crop in West Africa but is also cultivated in Asia as well as the Pacific and Caribbean islands. The two most cultivated species are *D. rotundata* and *D. alata*. Yam in most traditional yam-based farming systems requires fertile land to perform well because of the high demand for crop nutrients. Therefore, the crop is cultivated first after the natural vegetation has been cleared or after a long period of fallow

Received 20 January 2009; accepted 12 January 2010.
Address correspondence to R. C. Abaidoo, International Institute of Tropical Agriculture (IITA), PMB 5320, Ibadan, Nigeria. E-mail: r.abaidoo@cgiar.org

(Obigbesan 1981; Degras 1993). As a result of the pressure on the land from increased human population, the length of fallow has been drastically reduced to 3 years or less in Nigeria as compared to 6–20 years in the past (Orkwor and Asadu 1998).

As for many other crops, nitrogen (N), phosphorus (P), and potassium (K) are the nutrients most required in yam. Obigbesan and Agboola (1978) observed that 128 kg ha^{-1} N, 17 kg ha^{-1} P, 163 kg ha^{-1} K, 11 kg ha^{-1} magnesium (Mg), and 4 kg ha^{-1} calcium (Ca) were removed by *D. alata* from soil in southwest Nigeria; *D. rotundata* removed 148 kg ha^{-1} N, 17.6 kg ha^{-1} P, 165 kg ha^{-1} K, 11 kg ha^{-1} Mg, and 4.7 kg ha^{-1} Ca in one cropping cycle. To obtain greater yields, especially in areas where the fallow system has been virtually abandoned, nutrient amendments are needed, especially inorganic fertilizers. Although fertilizer improves yam productivity, its limited availability, cost, effect on the environment (Orkwor and Asadu 1998), and reported negative influence on yam tuber quality (Obigbesan 1981) make it unattractive to most yam farmers. As a way of reducing total dependence on fertilizer, a biological approach is desirable which is ecofriendly and less expensive. Mycorrhiza is a symbiotic association between plant roots and specialized soil fungi that helps in the acquisition of immobile nutrients such as P, N, zinc (Zn), and copper (Cu) (Clark and Zeto 2000; Govindarajulu et al. 2005; Padilla and Encina 2005). Cassava's ability to thrive on impoverished soil is connected with its close association with mycorrhizal fungi (Howeler 1990; Sieverding 1991).

It has been established that yam forms a symbiotic association with mycorrhiza (Zaag et al. 1980), but the assessment of the potential benefits from this association has not received enough attention. Zaag et al. (1980) suggested that the low response of yam to phosphate fertilizers might be connected with the high level of mycorrhizal colonization observed on the roots. We hypothesize that if P uptake via mycorrhiza is efficiently utilized in yam, it could indirectly enhance the uptake of N and K in the crop. Mycorrhiza could also directly affect N uptake in plants. Johansen, Jakobsen, and Jensen (1992) proposed that where soil N is present as ammonium (NH_4^+), mycorrhiza might play a significant role in N acquisition. Regarding the soil's critical levels of N, P, and K for yam, it has been emphasized that a response to fertilizer application is likely on soils containing less than 0.1% total N, less than 8 mg kg^{-1} soil-available P, and less than 0.15 $cmol_c$ kg^{-1} K (Obigbesan 1981; Kayode 1985).

Mycorrhiza can be very useful in yam production when the soil P is below the critical level because response to arbuscular mycorrhizal (AM) inoculation has been observed in other plants at a level of soil solution P as low as 0.01 mM (Habte and Manjunath 1991; Azcon, Ambrosano, and Charest 2003). Mycorrhiza can alter the root morphology or root architecture of plants in structural, spatial quantitative, and temporal manners (Atkinson 1992; Padilla and Encina 2005) to enhance the acquisition of nutrients, especially immobile ions such as phosphate. These modifications may depend on the species of host plant and species of colonizing mycorrhiza (Berta, Fusconi, and Trotta 1993; Hooker et al. 1995). Knowledge of the modifications made on the root systems of plants by mycorrhiza might provide better understanding of the process by which nutrient acquisition is improved in yam.

Currently, there are very few reports on the level of colonization and the contribution of mycorrhiza to nutrient uptake, growth, and yield of yam. Zaag et al. (1980) observed colonization of yam roots by indigenous mycorrhizal fungi but provided very little information on the role of AM root colonization in yam nutrition. This study serves as a followup to that of Zaag et al. (1980) to provide additional information on the contribution of yam–AM symbiosis to nutrient uptake and yield. It is conventional to use a pot experiment to understand the role of mycorrhiza in nutrient uptake and the growth of new crops by comparing

mycorrhiza-colonized plants with uncolonized controls. This study reports on a pot experiment conducted with the objective of evaluating the effects of P rates and root colonization by mycorrhiza on the root morphology, nutrient uptake, and yield of yam.

Materials and Methods

Experimental Design

A 2 × 4 factorial experiment in a completely randomized design was carried out to evaluate the effects of two levels of mycorrhiza (with and without) and four P rates (0, 0.05, 0.5, and 5 mg P kg^{-1} soil) on two genotypes of yam, TDa 297 (*D. alata*) and TDr 97/00903 (*D. rotundata*). TDa 297 is a common *D. alata* genotype widely cultivated in Nigeria. TDr 97/00903 is a high-yielding hybrid at the advanced breeding trial stage at the International Institute Tropical Agriculture (IITA). Each genotype was treated separately. Thus, there were eight treatment combinations for each of the genotypes, and each treatment was replicated four times.

Soil Characteristics

Subsoil (30–45 cm) of a Ferric Luvisol (FAO classification) was collected from an experimental plot at IITA, Ibadan, in the derived savannah zone of Nigeria. Subsoil was used to avoid elevated nutrient levels in the topsoil. Selected characteristics of the soil are pH (H_2O) 5.2; carbon (C) 5.5 g kg^{-1}; N 0.57 g kg^{-1}; Olsen P 1.61 mg kg^{-1} soil; Ca 1.28 $cmol_c$ kg^{-1}; Mg 0.38 $cmol_c$ kg^{-1}; K 0.15 $cmol_c$ kg^{-1}; Zn 3.82 $cmol_c$ kg^{-1}; sand 800 g kg^{-1}; clay 80 g kg^{-1}; and silt 120 g kg^{-1}. The soil was sieved using a 2-mm sieve and mixed with acid-washed beach sand (1:2 w/w). The soil–sand mixture was steam sterilized (121 °C for 1 h each day on three consecutive days), allowed to cool, and poured into 144 pots at 6 kg pot^{-1}.

Planting Materials and Mycorrhizal Inoculation

Tubers from each yam genotype were surface sterilized in 0.06% of sodium hypochlorite for 10 min, washed with distilled water, and allowed to air dry before they were cut with a presterilized kitchen knife into sets weighing 45–50 g. The sets were buried in a sterile growth medium (carbonized rice husks) for 3 weeks before being transplanted into pots. Sprouted sets with uniform height and vigor of shoots were selected and transplanted at one per pot. Each pot for mycorrhizal inoculation treatment was inoculated with 10 g of mycorrhizal inoculum (soil–root mixture) added just at the base of the transplanted sets. The AM inoculum was obtained from IITA and contained propagules of *Glomus mosseae*, *Glomus deserticola*, and *Acaulospora laevis*.

Growth Conditions

Plants were grown in a greenhouse for 16 weeks. Each plant was staked with a surface-sterilized PVC pipe. Watering was done daily by adding 400–500 mL of distilled water (70–80% of water-holding capacity) to each pot, depending on the weight of pot. Modified Hoagland's solution with monopotassium phosphate (KH_2PO_4) levels of 0.05, 0.5, and 5 mg P kg^{-1} soil was applied. These treatments were designated as low, medium, and high P rates based on the P requirement (10 kg ha^{-1}) of yam (Obigbesan 1981). The control

treatment received no addition of KH_2PO_4. The P treatments were applied by adding 50 mL per pot of Hoagland's solution prepared for each concentration of P at 6-day intervals to attain the desired P rates. The Hoagland's solution contained the following other nutrients (mg l^{-1}): N 42; K 39; Mg 24; Ca 40; boron (B) 0.46; manganese (Mn) 0.5; Zn 0.05; molybdenum (Mo), 0.04; copper (Cu) 0.023; iron (Fe) 0.14; sodium (Na) 0.005; and ethylenediaminetetraacetic acid (EDTA) 1.5. Each treatment was replicated four times.

Harvesting

Before harvesting at 16 weeks after transplanting, six young fully mature leaves (recently expanded) with petioles were sampled per plant between the hours of 0800 and 1000 for the determination of leaf N, P, and K contents. Soil was carefully removed by immersion of the root system in water with gentle agitation, after which roots were retrieved. Roots were subsampled for assessment of AM colonization and other root characteristics. All shoots and the remaining roots were oven dried for 5 days at a temperature of 80 °C to a constant weight, and the dry weights were recorded.

Plant Analysis

Leaf N and P were determined by digesting ground dried leaf samples in hot sulfuric acid solution with selenium dioxide (SeO_2) catalyst (Novozamsky et al. 1983). The digest solutions were then read colorimetrically in an autoanalyzer for the simultaneous determination of N and P. Nitrogen content was determined using the Berthalot or indophenol reaction method (Searle 1984). The ascorbic acid method (Murphy and Riley 1962) was used for P analysis, and the dry ash digestion method (Jones and Case 1990) was used for K determination.

Colonization with AM Fungi

The percentage mycorrhizal colonization of roots was determined by the gridline-intersect method (Giovanetti and Mosse 1980) after the sampled roots were cut into approximately 1-cm segments, cleared with 10% potassium hydroxide (KOH) in a water bath (80 °C) for 40 min, and rinsed in water. Roots were then bleached in 5% hydrogen peroxide (H_2O_2) for 10 min and stained with Chlorazol black E (Brundrett, Piche, and Peterson 1984). Yam responsiveness to AM (MR) was calculated at each of the P rates for tuber yield as described by Baon, Smith and Alston (1993):

$$\mathrm{MR} = 100 \times (\mathrm{M} - \mathrm{NC})/\mathrm{NC}$$

where M represents tuber yield of inoculated plants and NC represents tuber yield of noninoculated plants. Yam response to AM in this study reflects the proportional growth improvement in the tuber yield attributable to AM.

Root Morphology

Cleaned fresh subsampled roots were arranged with minimum overlap in an A4-sized Perspex tray and scanned in black and white color [400 dpi, tagged image format (TIF), white background] using Delta T-Scan software (Delta Devices Ltd., England). After

scanning, the root samples were oven dried to constant weight. The total and scanned root dry weights were used to estimate total root length, root area, and root diameter. Standardization of the root length measurement was done using Delta T generic defined standardization.

Statistical Analysis

Percentage AM colonization was arc-sine transformed (Gomez and Gomez 1984) for statistical analysis to ensure normal distribution of the data. Data were subjected to analysis of variance using PROC GLM and correlation analysis using PROC CORR of Statistical Analysis System (SAS 2003). Treatment differences were evaluated using least significant difference (LSD) at $P < 0.05$.

Results

The application of P and mycorrhizal inoculation did not significantly ($P \leq 0.05$) affect the shoot dry weight, root length, and root area in the *D. rotundata* genotype (Table 1). Root dry weights of *D. rotundata* genotype were significantly ($P \leq 0.05$) influenced by mycorrhizal inoculation. In general, inoculated plants without P had significantly greater root weight than the noninoculated P control (Table 1). At the 5 mg P kg^{-1} soil rate, there was a reduction in root dry weight of mycorrhizal plant when compared to the other mycorrhizal-inoculated P treatments. No significant difference was observed in nonmycorrhizal plants. Roots of noninoculated plants were not colonized by mycorrhiza; high P rates significantly lowered root colonization in inoculated plants. The thickest root diameter was obtained at 0.5 mg P/kg soil; the thinnest was obtained on mycorrhizal plants in the 5 mg P/kg soil. Mycorrhizal inoculation significantly ($P \leq 0.05$) increased tuber yields of TDr 97/00903 at 0.05 and 0.5 mg P kg^{-1} soil compared to their nonmycorrhizal counterparts (Table 1). The greatest yields were obtained with 0.5 mg P kg^{-1} soil in mycorrhizal plants and at 5 mg P kg^{-1} soil in nonmycorrhizal plants. Application of P at greater rates (0.5 and 5 mg P kg^{-1} soil) also significantly increased the tuber yield of TDr 97/00903 when compared with 0 and 0.5 mg P kg^{-1} soil.

In TDa 297, mycorrhizal application had no significant effect on the parameters measured (Table 2). Increasing P application rates, however, significantly decreased the percentage of root colonization and root diameter. At 5 mg P kg^{-1} soil rate, AM colonization was significantly lower in inoculated plants than at the other levels of P. The root diameter of TDa 297 was significantly thicker at the control P rate than those of other P rates in nonmycorrhizal plants. Application of P significantly influenced the tuber yield of TDa 297. A significant ($P \leq 0.05$) increase in tuber yield was obtained at the 0.5 mg P/kg soil application rate when compared to P treatments (Table 2).

Yam responsiveness to AM inoculation was observed in tuber yield of TDr 97/00903 (Table 3). This was most pronounced (51.7%) at 0.5 mg P kg^{-1} soil followed by that of 0.05 mg P kg^{-1} soil (49.5%) (Table 3). Uptake of N (mg/plant) by mycorrhizal plants of TDr 97/00903 was significantly greater at the 0.05 mg P kg^{-1} soil rate than that of nonmycorrhizal plants (Figure 1a). Mycorrhizal inoculation tended to raise P uptake of TDr 97/00903 (Figure 1b). Significant increase in P uptake was observed at 0.05 mg P kg^{-1} soil. The K uptake of AM-inoculated TDr 97/00903 was greater by 42% at 0 mg P kg^{-1} soil rate and by 35% at 0.05 mg P kg^{-1} than those of the uninoculated plants (Figure 1c).

Table 1
Effect of mycorrhizal inoculation and phosphorus application on the biomass yield, root colonization, root morphology, and tuber yield of *Dioscorea rotundata* genotype TDr 97/00903

Mycorrhizal inoculation (MI)	P rates (mg/kg soil)	Shoot dry weight (g)	Root dry weight (g)	Root length (m/plant)	Root area (m^2/plant)	Root diameter (mm/plant)	AM colonization (%)	Tuber yield (g/plant)
Mycorrhizal inoculated	0 (control)	14.2	12.8	271	0.253	0.90 bc	36.0 a	112.35 bcd
	0.05	16.2	11.8	214	0.211	1.01 abc	23.4 b	125.79 bc
	0.5	14.4	12.3	206	0.240	1.15 a	15.9 b	153.30 a
	5.0	11.1	7.7	171	0.166	0.88 c	5.2 c	134.09 ab
	Means	14.0	11.2	215.5	0.218	0.99	20.1	131.38
Mycorrhizal uninoculated	0 (control)	11.1	8.5	167	0.190	1.06 ab	0 c	97.10 d
	0.05	12.0	10.5	146	0.181	0.99 bc	0 c	84.15 e
	0.5	14.1	10.1	209	0.206	0.94 bc	0 c	101.03 c
	5.0	12.7	10.0	194	0.189	0.95 bc	0 c	120.82 bcd
	Means	12.5	9.8	179	0.192	0.98	0	100.78
MI		ns	*	ns	ns	ns	***	***
P rate		ns	ns	ns	ns	ns	***	*
MI × P		ns	ns	ns	ns	*	***	**

Note. ns denotes not significant.
*, **, and *** denote significance at 5%, 1%, and 0.1% levels of significance, respectively.

Table 2
Effects of mycorrhizal inoculation and phosphorus application on the biomass yield, root colonization, root morphology, and tuber yield of *Dioscorea alata* genotype TDa 297

Mycorrhizal inoculation (MI)	P rate (mg/kg soil)	Shoot dry weight (g)	Root dry weight (g)	Root length (m/ plant)	Root area (m^2/plant)	Root diameter (mm/plant)	AM colonization (%)	Tuber yield (g/plant)
	0 (control)	9.7	5.4	116	0.122	0.972	33.3 a	70.06
Mycorrhizal	0.05	9.3	4.7	77	0.083	0.997	25.5 a	71.79
inoculated	0.5	11.5	6.6	116	0.108	0.868	32.3 a	97.71
	5.0	9.9	4.6	80	0.084	0.892	13.4 b	90.66
	Means	10.1	5.3	97.3	0.099	0.932	26.1	82.56
	0 (control)	8.6	4.9	91	0.102	1.025	0 c	57.11
Mycorrhizal	0.05	9.7	5.8	126	0.118	0.874	0 c	69.00
uninoculated	0.5	11.3	6.2	129	0.120	0.865	0 c	108.03
	5.0	8.2	3.8	71	0.067	0.881	0 c	89.38
	Means	9.5	5.2	104.3	0.102	0.911	0	80.88
MI		ns	ns	ns	ns	ns	***	ns
P rate		ns	ns	ns	ns	*	*	*
MI × P		ns	ns	ns	ns	ns	*	ns

Note. ns denotes not significant.
*,**, and *** denote significance at 5%, 1%, and 0.1% levels of significance, respectively.

Table 3
Responsiveness of TDr 97/00903 to mycorrhizal inoculation based on tuber yield in relation to phosphorus concentrations

P rate (mg/kg soil)	Responsiveness (%)
0 (control)	15.7
0.05	49.5
0.5	51.7
5.0	11.0

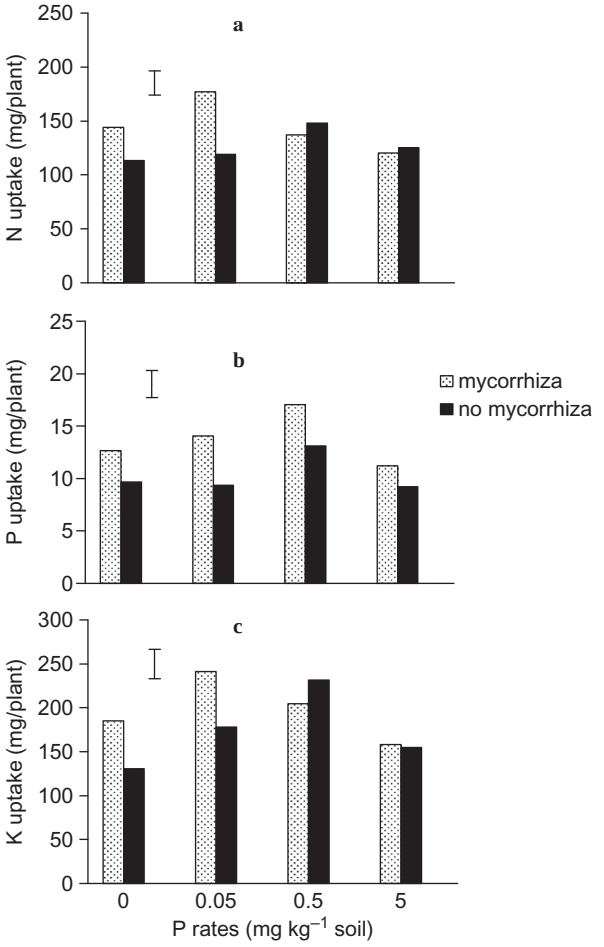

Figure 1. Nitrogen, phosphorus, and potassium uptakes of TDr 97/00903 in response to AM application and P concentration. Bars represent $LSD_{(P \leq 0.05)}$.

No significant effects of mycorrhizal inoculation and P application were found on N uptake in TDa 297 (Figure 2a). In the nonmycorrhizal plants of TDa 297, application of P significantly ($P \leq 0.05$) enhanced P uptake (Figure 2b). At 0.5 mg P/kg soil rate, P uptake was significantly ($P \leq 0.05$) greater than at the other P rates. In TDa 297 plants without P

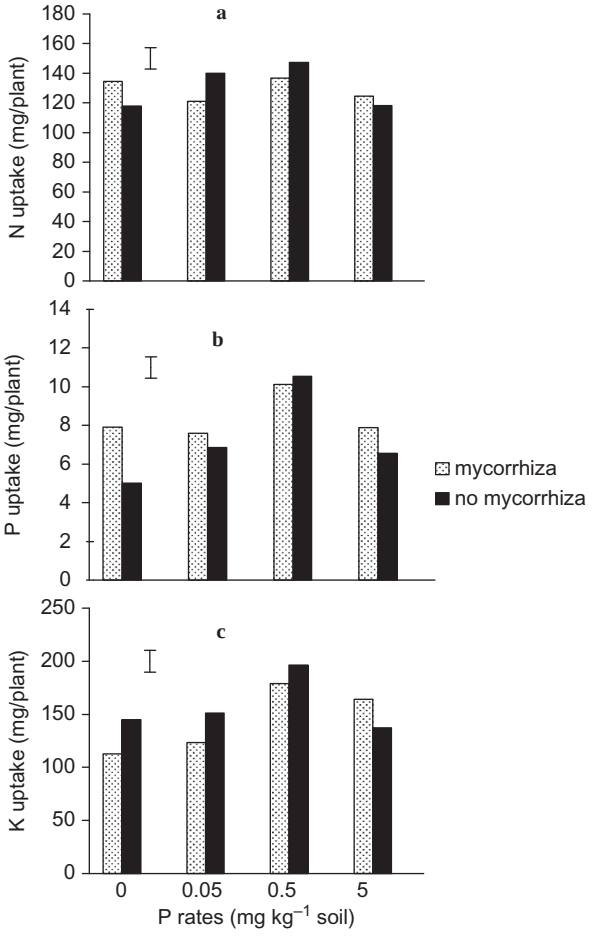

Figure 2. Nitrogen, phosphorus, and potassium uptakes of TDa 297 in response to AM application and P concentration. Bars represent $LSD_{(P \leq 0.05)}$.

application, mycorrhizal plants significantly absorbed more P than nonmycorrhizal plants. The P uptakes at 0.05 and 0.5 mg P/kg soil were significantly greater than those of 0 and 5 mg P kg^{-1} soil (Figure 2c). There was no significant influence of mycorrhizal inoculation on the uptake of K.

There were strong positive correlations ($P \leq 0.05$) in TDr 97/00903 between shoot dry weight and uptake of N, P, and K (Table 4). The uptake of these nutrients also showed a slightly strong correlation with root dry weight. Positive correlations ($P \leq 0.05$) were found between percentage mycorrhizal colonization and root dry weight, shoot dry weight, root length, root area, and uptake of N, P, and K. Root diameter was negatively correlated with root length, but no significant correlation was shown among the other variables.

In TDa 297, strong correlations ($P \leq 0.05$) were also observed among the shoot dry weight, root dry weight, root length, root area, and uptake of N, P, and K (Table 5). Tuber weight showed positive correlation with root and shoot dry weights, root length, root area, and the uptake N, P, and K. However, percentage mycorrhizal colonization was not significantly correlated with the other parameters.

Table 4
Correlation coefficients of the measured parameters in TDr 97/00903

	Shoot dry weight	Root dry weight	Tuber weight	AM colonization (%)	Root length	Root area	Root diameter	N uptake	P uptake	K uptake
Shoot dry weight	—									
Root dry weight	0.69***	—								
Tuber weight	0.005	0.23	—							
AM colonization (%)	0.41*	0.58***	0.34	—						
Root length	0.33	0.74***	0.15	0.42*	—					
Root area	0.40*	0.83***	0.22	0.47**	0.94***	—				
Root diameter	0.13	−0.005	0.20	0.01	−0.48**	−0.17	—			
N uptake	0.92***	0.54***	−0.49	0.39*	0.19	0.25	0.15	—		
P uptake	0.80***	0.58***	0.15	0.44**	0.23	0.36*	0.32	0.74***	—	
K uptake	0.85***	0.51***	0.08	0.38*	0.26	0.28	0.06	0.82***	0.80***	—

***,**, and * denote significance at $P = 0.0001$, 0.01, and 0.05 levels, respectively.

Table 5
Correlation coefficients of the measured parameters in TDa 297

	Shoot dry weight	Root dry weight	Tuber weight	AM colonization (%)	Root length	Root area	Root diameter	N uptake	P uptake	K uptake
Shoot dry weight	—									
Root dry weight	0.74***	—								
Tuber weight	0.59***	0.53***	—							
AM colonization (%)	0.26	0.23	0.020	—						
Root length	0.63***	0.87***	0.48**	0.14	—					
Root area	0.64***	0.89***	0.44**	0.18	0.97***	—				
Root diameter	0.014	0.04	−0.07	0.13	−0.07	0.15	—			
N uptake	0.80***	0.51***	0.43**	0.18	0.38*	0.44**	0.15	—		
P uptake	0.69***	0.62***	0.57***	0.25	0.56***	0.53***	−0.19	0.62***	—	
K uptake	0.64***	0.53***	0.55***	−0.23	0.43*	0.44**	−0.12	0.56***	0.67***	—

***, **, and * denote significance at $P = 0.0001$, 0.01, and 0.05 levels, respectively.

Discussion

The contribution of mycorrhiza to the nutrient uptake and growth of crops is largely determined by the P status of soil. With increasing level of P, the responses of the two genotypes of yam to mycorrhizal inoculation varied, especially in tuber yield, root biomass, and uptake of N, P, and K. TDr 97/00903 showed a greater degree of responsiveness to mycorrhiza than TDa 297. Variations in response to mycorrhizal inoculation have been reported in different species and genotypes of other crops (Krishna et al. 1985; Schoeneberger, Volk, and Davey 1989).

The differential response of TDr 97/00903 and TDa 297 to AM could be due to host plant AM preferences and/or different physiological and biochemical processes occurring in the two genotypes. The species of AM fungi used in the study seemed to interact more positively with TDr 97/00903 than with TDa 297. Monzon and Azcon (1996) reported that a specific compatibility exists between AM fungal species and host plants. Root morphology can affect mycorrhizal dependence or responsiveness via P uptake and acid phosphatase activities in low-P soils (Khalil, Loynachan, and Tabatabai 1994, 1999). Change in photosynthate availability in the plant may also affect the relationship of AM with the plant (Klironomos, McCune, and Moutoglis 2004). The photosynthate availability of TDa 297 is likely to differ from that of TDr 97/00903 because of the difference in the leaf and vine structure of the two species (Asiedu et al. 1998). This may account in part to the differential responsiveness of the two genotypes.

The greater responsiveness to AM inoculation obtained in tuber yield compared to shoot dry weight is probably due to the period of harvest as this coincided with the period of tuber bulking (Orkwor and Ekanayake 1998). At this growth stage (14–19 weeks after planting), translocation of assimilates and photosynthates is totally directed to tubers (Orkwor and Ekanayake 1998). It is advantageous to have greater responsiveness to AM obtained in tuber yield because yams are cultivated for their tubers. The relatively low responsiveness to AM in this study was likely to have been the result of the shorter duration of the experiment and the set size used. Yam plantlets depend on the stored food in the planted sets until they are fully autotrophic (Orkwor and Asadu 1998), which could be up to the 13th week after sprouting (Orkwor and Ekanayake 1998). Longer duration of growth and smaller set sizes would probably give a greater responsiveness to AM in pot experiments. Despite the low responsiveness that was generally exhibited, the potential exists for improving yields through yam–mycorrhizal symbiosis. However, this will likely be influenced by the genotype of yam, soil P availability, indigenous mycorrhizal fungi species population, and other biotic factors.

Yam requires P in smaller quantities than N and K (Obigbesan and Agboola 1978; Zaag et al. 1980; Shiwachi, Okonkwo, and Asiedu 2004). Our results showed that P uptake in both mycorrhizal and nonmycorrhizal plants of the two genotypes peaked at 0.5 mg P kg^{-1} soil, suggesting this is the optimum level of P for both genotypes under greenhouse conditions. For both genotypes, N and K uptakes were also greatest at 0.5 mg P kg^{-1} soil with the exception of mycorrhizal plants of TDr 97/00903, where it peaked at 0.05 mg P kg^{-1} soil rate. Contradictory results of the yam response to P application (Koli 1973; Zaag et al. 1980; Obigbesan 1981) obtained in the past have made the needs of yam for P less understood or ill defined. It can be inferred, however, from our results that N, P, and K uptake in yam could be increased in low-P soil by mycorrhiza and well-targeted application of P fertilizer. With the strong positive correlations among the uptake of the three nutrients in both genotypes, P application and uptake may indirectly influence the uptake of N and K.

Mycorrhizal inoculation and P application significantly influenced the root morphology of the two species. The relatively shorter root length and smaller root area in TDa 297 than in TDr 97/00903 may be due to species differences. The root dry weight, root length, and area were remarkably increased by mycorrhizal inoculation in the control plants of both genotypes. This suggests that mycorrhizal association can induce better root growth in yam under low-P conditions and result in improved nutrient uptake and tuber yield. Variations in the modifications of root morphology by mycorrhizal association may depend on fungus, plant type and species, and environmental conditions. (Hetrick, Wilson and Todd 1992; Gao, Delp, and Smith 2001). The smaller root diameter obtained (about 1 mm), contrary to the diameter of about 3 mm reported under field conditions (Orkwor and Ekanayake 1998; Bai and Ekanayake 1998), may be due to confinement inside pots and possibly reduced root exploration.

Conclusions

The current study has shown that TDr 97/00903 was more responsive to mycorrhizal inoculation than TDa 297 but that the response was greatly influenced by soil P availability. There are potential benefits derivable from mycorrhizal colonization of yam genotypes, but this needs to be confirmed with further studies using more yam genotypes grown for longer growth periods in bigger pots.

References

Asiedu, R., S. Y. C. Ng, K. V. Bai, I. J. Ekanayake, and N. M. W. Wanyera. 1998. Genetic improvement. In *Food yams: Advances in research*, ed. G. C. Orkwor, R. Asiedu, and I. J. Ekanayake, 63–104. Ibadan, Nigeria: International Institute of Tropical Agriculture (IITA) and National Root Crops Research Institute (NRCRI).

Atkinson, D. 1992. Tree root development: The role of models in understanding the consequences of arbuscular endomycorrhizal infection. *Agronomie* 12:817–820.

Azcon, R., E. Ambrosano, and C. Charest. 2003. Nutrient acquisition in mycorrhizal lettuce plants under different phosphorus and nitrogen concentrations. *Plant Science* 165:1137–1144.

Bai, K. V., and I. J. Ekanayake. 1998. Taxonomy, morphology, and floral biology. In *Food yams: Advances in research*, ed. G. C Orkwor, R. Asiedu, and I. J. Ekanayake, 13–37. Ibadan, Nigeria: IITA and NRCRI.

Baon, J. B., S. E. Smith, and A. M. Alston. 1993. Mycorrhizal responses of barley cultivars differing in P efficiency. *Plant and Soil* 157:97–105.

Berta, G., A. Fusconi, and A. Trotta. 1993. Vesicular–arbuscular mycorrhizal infection and the morphology and function of the root systems. *Environment and Experimental Botany* 33:159–173.

Brundrett, M., Y. Piche, and R. L. Peterson. 1984. A new method for observing the morphology of vesicular arbuscular mycorrhiza. *Canadian Journal of Botany* 62:2118–2134.

Clark, R. B., and S. K. Zeto. 2000. Mineral acquisition by arbuscular mycorrhizal plants. *Journal of Plant Nutrition* 23 (7): 867–902.

Degras, L. 1993. *The yam: A tropical root crop*. London: MacMillan Press.

Gao, L. L., G. Delp, and S. E. Smith. 2001. Colonization patterns in a mycorrhiza-defective mutant tomato vary with different arbuscular-mycorrhizal fungi. *New Phytologist* 138:275–285.

Giovanetti, M., and B. Mosse. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. *New Phytologist* 84:489–500.

Gomez, K. A., and A. A. Gomez. 1984. *Statistical procedures for agricultural research*. 2nd ed. New York: John Wiley & Sons.

Govindarajulu, M., P. E. Pfeffer, H. R. Jin, J. Abubaker, D. D. Douds, J. W. Allen, H. Bucking, P. J. Lammers, and Y. Shachar-Hill. 2005. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. *Nature* 435:819–823.

Habte, M., and A. Manjunath. 1991. Categories of vesicular–arbuscular mycorrhizal dependency of host species. *Mycorrhiza* 1:3–12.

Hetrick, B. A. D., G. W. T. Wilson, and T. C. Todd. 1992. Relationship of mycorrhizal symbiosis, rooting strategy, and phenology among tall grass prairie forbs. *Canadian Journal of Botany* 70:1521–1428.

Hooker, J. E., K. E. Black, R. L. Perry, and D. Atkinson. 1995. Arbuscular mycorrhizal–induced alteration to root longevity of poplar. *Plant and Soil* 172:327–329.

Howeler, R. H. 1990. Phosphorus requirements and management of tropical root and tuber crops. In *Phosphorus requirement for sustainable agriculture in Asia and Oceania*, 427–444. Los Baños, Philippines: International Rice Research Institute Publication.

Johansen, A., I. Jakobsen, and E. S. Jensen. 1992. Hyphal transport of ^{15}N-labelled nitrogen by a vesicular–arbuscular mycorrhizal fungus and its effect on depletion of inorganic soil N. *New Phytologist* 122:281–288.

Jones, J. B. Jr., and V. W. Case. 1990. Sampling, handling, and analyzing plant tissue samples. In *Soil testing and plant analysis*, 3rd ed., ed. R.L. Westerman. Madison, Wisc.: SSSA.

Kayode, G. O. 1985. Effects of NPK fertilizers on tuber yield, starch content, and dry matter accumulation of white guinea yam (*Dioscorea rotundata*) in a forest Alfisol of southwestern Nigeria. *Experimental Agriculture* 21 (4): 389–393.

Khalil, S., T. E. Loynachan, and M. A. Tabatabai. 1994. Mycorrhizal responsiveness and nutrient uptake by improved and unimproved corn and soybean cultivars. *Agronomy Journal* 86: 949–958.

Khalil, S., T. E. Loynachan, and M. A. Tabatabai. 1999. Plant determinants of mycorrhizal responsiveness in soybean. *Agronomy Journal* 91:135–141.

Klironomos, J. N., J. McCune, and P. Moutoglis. 2004. Species of arbuscular mycorrhizal fungi affect mycorrhizal response to simulated herbivory. *Applied Soil Ecology* 26:133–141.

Koli, S. E. 1973. The response of yam (*Dioscorea rotundata*) to fertilizer application in northern Ghana. *Journal of Agricultural Science* 80:245–249.

Krishna, K. R., K. G. Shetty, P. J. Dart, and D. J. Andrews. 1985. Genotype-dependent variation in mycorrhizal colonization and response to inoculation of pearl millet. *Plant and Soil* 86:113–125.

Monzon, A., and R. Azcon. 1996. Relevance of mycorrhizal fungal origin and host plant genotype to inducing growth and nutrient uptake in *Medicago* species. *Agriculture, Ecosystem, and Environments* 60:9–15.

Murphy, J., and J. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytical Chimica Acta* 27:31–36.

Novozamsky, I., V. J. G. Houba, R. van Eck, and W. van Vark. 1983. A novel digestion technique for multi-element plant analysis. *Communications in Soil Science and Plant Analysis* 14:239–248.

Obigbesan, G. O. 1981. Nutrient requirements of yams (*Dioscorea* spp.). *University of Ibadan, Nigeria, Agricultural Research Bulletin* 2 (1): 20.

Obigbesan, G. O., and A. A. Agboola. 1978. Uptake and distribution of nutrients by yams (*Dioscorea* spp.) in western Nigeria. *Experimental Agriculture* 14:349–355.

Orkwor, G. C., and I. J. Ekanayake 1998. Growth and development. In *Food yams: Advances in research*, ed. G. C. Orkwor, R. Asiedu, and I. J. Ekanayake, 39–62. Ibadan, Nigeria: IITA and NRCRI.

Orkwor, G. C., and C. L. A. Asadu. 1998. Agronomy. In *Food yams: Advances in research*, ed. G. C. Orkwor, R. Asiedu, and I. J. Ekanayake, 105–141. Ibadan, Nigeria: IITA and NRCRI.

Padilla, I. M. G., and C. L. Encina. 2005. Changes in root morphology accompanying mycorrhizal alleviation of phosphorus deficiency in micropropagated *Annona cherimola* Mill. plants. *Scientia Horticulturae* 106 (3): 360–369.

SAS. 2003. *SAS/STAT guide for personal computers, version 9.1*. Cary, N.C.: SAS Institute Inc.

Schoeneberger, M. M., R. J. Volk, and C. B. Davey. 1989. Factors influencing early performance of leguminous plants in forest soils. *Soil Science Society of America Journal* 53:1429–1434.

Searle, P. L. 1984. The Berthalot or indophenol reaction and its use in analytical chemistry of nitrogen. *Analyst* 109:549–568.

Shiwachi, H., C. C. Okonkwo, and R. Asiedu. 2004. Nutrient deficiency symptoms in yams (*Dioscorea* spp.). *Tropical Science* 44:155–162.

Sieverding, E. 1991. *Vesicular–arbuscular management in the agroecosystem*. Essenborn, Germany: GTZ GmbH.

Zaag, P., R. L. Fox, P. K. Kwakye, and G. O. Obigbesan. 1980. The phosphorus requirements of yam (*Dioscorea* spp.). *Tropical Agriculture (Trinidad)* 57:97–106.