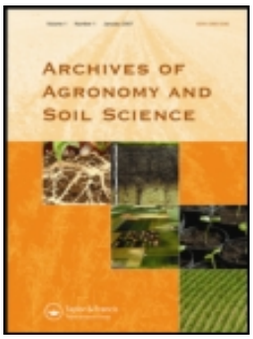

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Diversity of arbuscular mycorrhizal fungi in soils of yam (*Dioscorea* spp.) cropping systems in four agroecologies of Nigeria

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The diversity of arbuscular mycorrhizal (AM) fungi in soils under a yam cropping system in four agroecologies of Nigeria was investigated. Soil samples were collected from yam fields at Onne (humid forest, high rainfall area), Ibadan (derived savanna), Abuja (Guinea savanna) and Ubiaja (humid forest, medium rainfall area). Soil characteristics, AM fungi species, spore abundance, Shannon diversity index, species richness and evenness were determined. A total of 31 AM fungi species was isolated from the four agroecologies with a range of 14–20 species found in a single location. *Glomus* species were the most abundant among AM fungi species with *G. geosporum*, *G. intraradices* and *G. mosseae* occurring in large populations in all locations. Ubiaja, which had a cassava/natural vegetation sequence before yam, had significantly higher spore abundance and species richness than the other locations, which had a yam/legumes or a maize/legume sequence before yam. However, diversity was significantly higher at Abuja, which had a maize/legume sequence with yam, than Ibadan, which had only a yam/legume sequence. The study revealed significant diversity in AM fungal species across agroecologies in yam-growing regions. Further research on the functional consequences of changing composition of AM fungi species across the region is recommended.

Keywords: arbuscular mycorrhizal fungi; biodiversity; environment; soil; land use; yam

Introduction

Arbuscular mycorrhizal fungi (AMF) are an integral part of plant terrestrial communities, forming symbiotic associations with roots in the majority of plants. This association evidently improves the uptake of mineral nutrients such as P, N, Zn and Cu in plants (Allen et al. 2003; Smith and Read 2008; Dare et al. 2010), suppresses plant diseases (Borowicz 2001; Abdel-Fattah and Shabanam 2002), improves plant tolerance to drought and water stress (Fagbola et al. 2001; Augé 2004) and stabilizes soil structure (Rillig and Mummey 2006). The occurrence of AMF in soils varies in population and diversity across ecologies and is affected by various factors including soil and environmental conditions, host plant and agricultural practices such as crop

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rotation, fertilizer application and tillage (Miller and Jackson 1998; Jansa et al. 2002; Oehl et al. 2003; Mathimaran et al. 2007). Many of these factors affect the AMF propagule composition and root colonization and may consequently affect the benefits derivable from mycorrhizal association with the plant.

Yam is a tuber crop widely cultivated in West and Central Africa, Asia and the Caribbean (Onwueme and Charles 1994; Suja et al. 2003; FAO 2007). It is one of the most important tuber crops cultivated in Nigeria, the world largest producer with >70% of world production (Orkwor and Asadu 1998). Yam accounts for >70% of the daily calories of the people of Nigeria. The yam-growing regions of Nigeria have many climatic conditions and soil types, resulting in a wide range of ecosystems and vegetation structure. The yam belt of Nigeria covers ~9000 km^2, ranging from the northern Guinea savanna in the north to the humid forest zone in the south. In spite of the importance of yam in Nigeria, declining soil fertility has been an impediment to attain optimum yields and even to maintain current yields.

In a bid to solve the problem of yam productivity, which stemmed from dwindling fertile land areas and reduced length of fallow, AM association can play a significant role especially under integrated fertility management approach. AM colonization has been reported to increase the yield of yam in Nigeria (Oyetunji and Afolayan 2007; Tchabi et al. 2010) and breeding of yam genotypes with efficient AM colonization may be possible because AM root colonization in yam is both host dependent and influenced by the environment (Dare et al. 2008). Yam is mostly produced under low-input agriculture and the enhancement of nutrient uptake through symbiosis with indigenous AM population may become useful, especially under stress conditions. This may be achieved by adopting cultural practices that promote the growth of functionally compatible indigenous AM species in yam production systems. Previous studies have suggested that an AMF population could be managed for increased crop production (Sieverding 1991). A survey of AMF diversity in the yam cropping systems thus becomes imperative for knowledge and understanding of the potential contribution of symbiosis to yam production. Information about species composition of the AMF community is important for understanding mycorrhizal function in agroecosystems (Johnson et al. 1992). Knowledge of the AM community structure in yam cropping systems could provide a basis for managing the biological component of soil to achieve higher yield. The aim of this study is to determine the AMF population and diversity under yam cropping systems in different agroecologies of Nigeria.

Materials and methods

Study area and sites

Yam-based cropping sites were selected in four agroecological zones of Nigeria. These were Ibadan (3°45′E, 7°30′N; rainfall, 1119.55 mm; mean solar radiation [MSR], 13.55 MJ m^{-2} day^{-1}) in the derived savanna; Onne (7°E, 4°48′N; rainfall, 2356.80 mm; MSR, 6.10 MJ m^{-2} day^{-1}) in the humid forest (high rainfall area); Ubiaja (6°25′E, 6°40′N; rainfall, 1534.56 mm; MSR, 13.05 MJ m^{-2} day^{-1}) in the humid forest (medium rainfall area); and Abuja (7°20′E, 9°16′N; rainfall, 1302.38 mm; MSR, 13.75 MJ m^{-2} day^{-1}) in the Guinea savanna. The minimum and maximum temperatures were 22 and 33°C at Abuja, 21 and 31°C at Ibadan, 23 and 31°C at Onne and 21 and 33°C at Ubiaja. Soil at Ibadan and Abuja was Ferric Luvisols; at Ubiaja it was Dystric Nitosols; and at Onne, it was Thionic Fluvisol (Jagtap 1995).

The selected sites in each location were International Institute of Tropical Agriculture (IITA) yam breeding trial plots for *Dioscorea rotundata* and *D. alata* genotypes and had different crop sequence. The sites at Abuja, Ibadan and Ubiaja were cultivated with maize, yam and cassava in 2000, respectively, and fallowed for three years. Cover crops (*Pueraria*) were grown from 2001 to 2003 at Abuja and Ibadan sites, while the site at Ubiaja was grown with natural vegetation, which consists of grass and broad leaved plant species. At Onne, the site was planted with tree legumes (*Dactyladenia barteri*) from 1985 to 1997 as an experimental site for alley cropping system studies. Five cowpea varieties were later planted on the alley between 1998 and 2001 and thereafter it was left for natural vegetation between 2001 and 2003. Yam genotypes of *D. rotundata* and *D. alata* were planted at each site in 2005 and 2006.

Soil sampling and analysis

Soils were sampled in June 2006 when the yams were about four months old, at a depth of 0–20 cm, using a soil auger. At each sampling site, three replicate quadrant plots (200 m^2) were selected and six points were sampled per quadrant plot and bulked together as one composite sample representing a replicate. Three replicates were, therefore, used for each site. Samples were air dried for 72 h, kept in bags and refrigerated at 4°C before analysis. Samples were divided into three portions for physico-chemical analysis, trap culture and isolation of fungi.

For physico-chemical properties, soil pH was obtained in a 1:1 soil/water ratio and 2:1 soil/KCl ratio (IITA 1982); total N by the macro-Kjedahl method (Bremner and Mulvaney 1982); organic carbon by chromic acid digestion (Heanes 1984); phosphorus and exchangeable cations were studied using Mehlich 3 extraction (Mehlich 1984). Phosphorus was determined colorimetrically using the Technicon AAII Auto-analyser, while the cations were determined using an atomic absorption spectrophotometer (Model Buck 200A). Particle size analysis was carried out according to the Bouyoucos (1951) hydrometer method using sodium hexametaphosphate as the dispersant. The summary of the physico-chemical properties of the soils is presented in Table 1.

Table 1. Soil properties of the sampled plots in each location.

Soil properties	Abuja	Ibadan	Onne	Ubiaja
pH (H_2O)	4.7	6.1	3.6	5.7
pH (KCl)	3.9	5.5	3.2	4.8
Organic matter (%)	0.98	1.62	2.38	1.64
N (g kg^{-1})	0.03	0.11	0.10	0.09
P (mg kg^{-1} soil)	2.68	20.28	20.76	2.13
Ca (cmol kg^{-1})	0.65	2.25	0.46	1.44
Mg (cmol kg^{-1})	0.13	0.56	0.10	0.60
K (cmol kg^{-1})	0.10	0.24	0.06	0.08
Zn (mg kg^{-1} soil)	2.13	5.58	2.96	2.16
Cu (mg kg^{-1} soil)	1.39	2.23	1.15	0.94
Mn (mg kg^{-1} soil)	35.29	63.81	2.88	41.85
Fe (mg kg^{-1} soil)	36.69	62.42	143.74	27.27
Sand (g kg^{-1})	780	820	720	800
Clay (g kg^{-1})	100	80	80	60
Silt (g kg^{-1})	120	100	200	140

Trap culture

A trap culture was established in a growth chamber (photoperiod 12 h, relative aerial humidity 65 ± 5 and 28 : 21°C max/min temperature) for five months using sorghum and soyabean as trap plants. Six trap culture pots (5 L size) were used for each site. A sample of a plot replicate was used as inoculum in two pots, one planted with sorghum and the other with soyabean. A total of 24 pots were planted for the four sites. Each pot was filled with 3 kg sterilized substrate (soil–sand mixture), which had the following chemical characteristics: pH (H_2O), 5.2; organic C, 5.5 g kg^{-1}; total N, 0.57 g kg^{-1}; Olsen-P, 1.61 mg kg^{-1}. The substrate was prepared using 2-mm-sieved unsterilized soil mixed with acid-washed beach sand (2:1 w/w) and autoclaved at 121°C for 1 h each day for three consecutive days. At planting, 50 g of inoculum was applied to the upper three quarters of the substrate in the pot, covered by the substrate and planted with the seeds of trap plants. Sorghum was grown for five months. Because soybean has a growth cycle of three months, the shoots were removed and the pots (with the substrate left undisturbed) were replanted with the same plant species. Trap pots were watered with distilled water and fertilized once every two weeks with 50 mL of Hoagland nutrient solution (Dare et al. 2010). At five months after planting, plant shoots were removed from each pot and the substrate inside each pot was thoroughly mixed. Samples of the substrates were collected for AMF spore isolation and identification.

Spore count, identification and isolation

A modified wet-sieving method of Gerdamann and Nicholson (1963) was used to estimate AM spore populations. Soil (100 g) was suspended in water for sedimentation after which the suspension was mixed vigorously. The suspension was allowed to settle for 30 s and the supernatant was decanted through sieves of 506, 250, 100 and 35-μm mesh sizes arranged in that order. This procedure was repeated three times for each sample. The contents of the 100 and 35-μm sieve sizes were collected and centrifuged (2000 rpm for 4 min). The sediment was resuspended in 40% sucrose solution and centrifuged (2000 rpm for 2.5 min) again to allow floatation of spores. The spores in suspension were filtered and counted using a stereomicroscope at a magnification $\times 40$. The spores were separated into groups according to general morphological similarities and mounted in polyvinyl alcohol/lactic acid/glycerol (PVLG) and PVLG mixed 1:1 (v/v) with Melzer's reagent for identification as proposed by Brundrett et al. (1994). Spores were cracked open under a cover slip to allow for observation of spore wall and inner wall characteristics under a compound microscope at a magnification of $\times 400$. Identification and classification were based on size, shape, color, surface structure, and general nature of the contents, hyphal attachments and wall details of spores. The species descriptions and identification manuals (Schenck and Pérez 1990), Schuessler lab webpage (http://www.lrz.de/~schuessler/amphylo/amphylogeny.html) and INVAM collections (http://invam.caf.wvu.edu) served as guides for species identification.

Calculations and statistical analysis

Spore abundance or population was expressed as the number of AM fungal spores in 100 g os soil and species richness as the number of AM fungal species taxa found in

100 g of soil. Shannon diversity index (SDI) and evenness (E) (Krebs 1989) were calculated as follows:

$$SDI = -\sum^{ni=1} Pi \ln Pi$$

$$E = \mathrm{SDI}/\ln X$$

where Pi is the proportion of individuals in a species, ni is the number of each individual species, N is the total number of individuals and X is the number of species recorded. All data were analysed using PROC GLM of Statistical Analytical System (SAS 2003). Significant differences between field sites were tested using Fisher's least significant difference (LSD) at $p < 0.05$. Data on spore abundance were $\log(x + 1)$ in conformity with ANOVA assumptions.

Results

Mycorrhizal diversity in the yam-growing region of Nigeria

A total of 31 species of AMF were isolated from the soils of the four locations used in this study (Table 2). A *Glomus* species and one *Scutellospora* species found at Ubiaja and Ibadan, respectively, could not be recognized beyond the genera level (Table 2). All the species isolated belonged to *Glomus, Gigaspora, Scutellospora, Paraglomus* and *Acaulospora*, and were found in all the locations except Ibadan where *Paraglomus* was not isolated (Table 2). The majority of the isolated species were identified as members of Glomaceae, comprising 13 *Glomus*, 7 *Acaulospora* and 1 *Paraglomus* species. Nine species belonged to the family Gigasporaceae, with six in the genus *Scutellospora* and three in *Gigaspora*. *Glomus geosporum, G. mosseae, G. intraradices, Gigaspora decipiens* and *Scutellospora calospora* were found in all locations (Table 2). *Acaulospora denticulata*, *G. claroideum*, *G. aggregatum*, *G. versiforme*, *G. luteum*, *Gigaspora gigantean*, *S. aurigloba* and the two species not identified beyond the genera level were each found in just one of the locations (Table 2). The three *Gigaspora* species isolated in this study were found at Ubiaja while one species was found at Abuja and Onne.

Spore abundance, diversity and species richness of AMF in the yam-growing regions were significantly ($p < 0.05$) different among locations (Table 3). Total spore abundance was significantly higher at Ubiaja than those of other locations, whereas total spore abundance at Ibadan and Abuja were significantly lower than that of Onne. The total spore abundance at Ubiaja was $\sim$280% higher than that of Ibadan, which had the lowest total spore abundance (Table 3). The species richness of AMF ranged from 14 to 20 species in the four locations. The highest species richness was observed at Ubiaja and the lowest at Ibadan (Table 3). The species richness at Ubiaja was significantly higher than those of other locations. However, the species richness at Abuja and Onne was not significantly different. The SDI for AM species was significantly higher at Abuja than at Ibadan, but the differences between SDI recorded at Ibadan, Ubiaja and Onne were not significant. Species evenness was comparable in all locations (Table 3).

Glomus species had the highest spore abundance in all the locations studied in the yam-growing regions of Nigeria (Figure 1). Spore abundance of *Glomus* species was $>$50% higher than *Acaulospora* species. *Gigaspora* species had the least spore abundance of $<$50 spores 100 g^{-1} across the location. The abundance of *Gigaspora*

Table 2. Arbuscular mycorrhizal fungi species isolated at four locations in the yam growing area of Nigeria.

Species	Location			
	Abuja	Ibadan	Onne	Ubiaja
Acaulospora scorobiculata	+	−	+	−
A. mellea	−	+	−	+
A. denticulata	−	−	+	−
A. elegans	+	−	+	−
A. rugosa	−	+	−	+
A. tuberculata	+	−	+	+
A. leavis	+	−	+	+
Glomus caledonium	−	−	−	+
G. claroideum	−	+	−	−
G. aggregatum	−	−	−	+
G. clarum	+	+	−	−
G. fasciculatum	−	+	−	+
G. etunicatum	−	−	+	+
G. geosporum	+	+	+	+
G. intraradices	+	+	+	+
G. mosseae	+	+	+	+
G. versiforme	−	−	−	+
G. deserticola	+	+	−	−
G. constrictum	+	−	+	−
G. luteum	+	−	−	−
Glomus sp.[a]	−	−	−	+
Gigaspora decipiens	+	+	+	+
Gigaspora margarita	−	+	−	+
Gigaspora gigantea	−	−	−	+
Paraglomus occultum	+	−	+	+
Scutellospora nigra	+	−	+	+
S pellucida	+	−	+	+
S. aurigloba	−	−	+	−
S. calospora	+	+	+	+
S. heterogama	−	+	+	−
Scutellospora sp.[a]	−	+	−	−

Note: [a]Not identified beyond the genera level.

Table 3. Diversity of AM fungi in four locations in the yam growing area of Nigeria.

Location	Spore abundance (100 g^{-1} soil)	Shannon diversity index	Species evenness	Species richness
Abuja	231	2.63	0.93	16
Ibadan	189	2.23	0.84	14
Onne	358	2.44	0.89	17
Ubiaja	529	2.45	0.87	20
LSD ($p < 0.005$)	45.61	0.304	ns	1.48
*F-value	<0.0001	<0.0001	0.2853	<0.0001

Note: *Statistical significance. ns, not significant.

and *Glomus* species were significantly higher at Ubiaja than other locations. Whereas >25 spores of *Gigaspora* per 100 g of soil were observed at Ubiaja, population sizes recorded for the other locations were <10 (Figure 2a). The same trend was observed

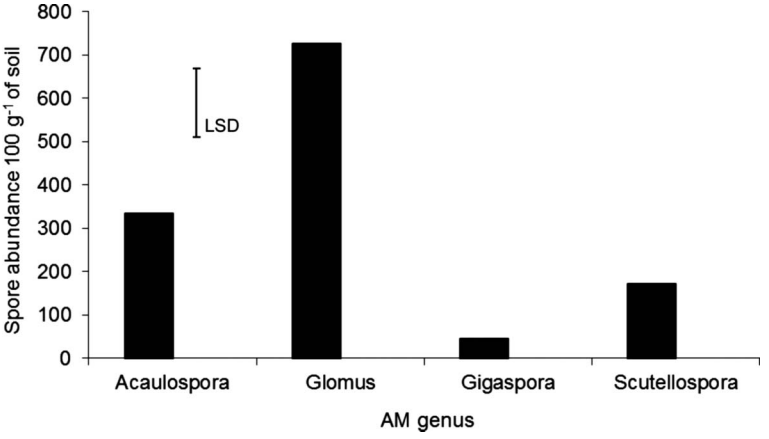

Figure 1. Total spore abundance of AM genera isolated in yam cropping systems of Nigeria.

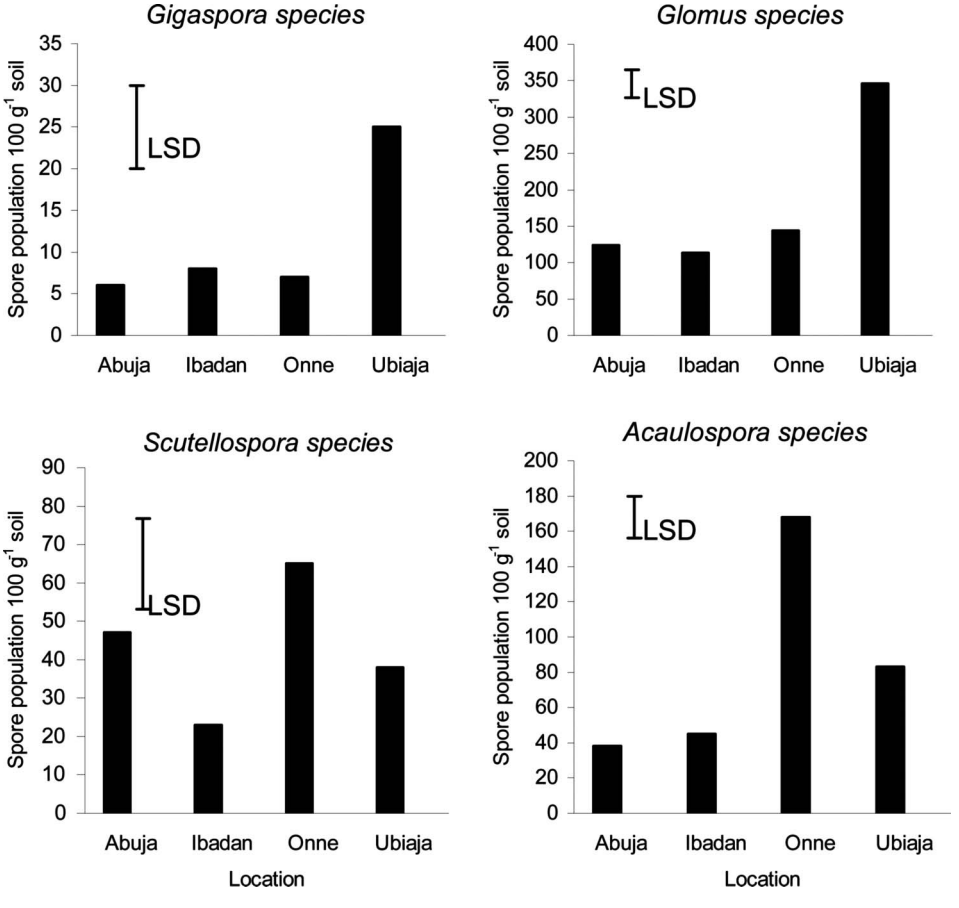

Figure 2. Spore abundance of four genera (*Gigaspora*, *Glomus*, *Scutellospora* and *Acaulospora*) of AM fungi as distributed in four yam growing areas of Nigeria.

for *Glomus* species with ~350 spores per 100 g of soil at Ubiaja compared with <150 spores per 100 g of soil recorded for other locations (Figure 2b). The abundance of *Scutellospora* species at Onne was significantly higher than Ibadan and Ubiaja (Figure 2c). Similarly, Onne also had significantly higher spores of *Acaulospora* species than those of other locations (Figure 2d).

Discussion

The five genera of AMF observed in our investigation were not evenly distributed in the study sites. Of the 31 species isolated from the locations, *Glomus* species were the most abundant followed by *Acaulospora* species. The abundance of *Glomus* species in this study corroborated previous results on AMF abundance in Nigeria (Redhead 1977). Several studies have reported *Glomus* dominance in many ecosystems. *Glomus* are reported to dominate temperate, subtropical and tropical parts of China (Gai et al. 2006a), and arid and semi-arid zones in India (Pande and Tarafdar 2004). Association of AM with a wide range of hosts has contributed to their dominance in many ecosystems.

An important observation in this study is the abundance of AM spores in Onne despite the high acidity, rainfall and soil available P in the site. AMF are adapted to varied temperature conditions and able to survive in acidic as well as alkaline soils (Ho 1987; Al-Raddad 1993; Tarafdar and Praveen-Kumar 1996). The dominance of *Scutellospora* at Onne revealed that this genus may survive well under acidic conditions. It was found in China that *Scutellospora* are mostly found in the coastal areas or in areas near the sea (Gai et al. 2006b). The dominance of *Glomus* species in Ibadan was contrary to result of Sanni (1976) that *Gigaspora* were the commonest AM species in the soils of Ibadan. This difference could have resulted from the sieve size used in this study for the collection of spores (100 and 35 μm) and the one (100 μm) used by Sanni (1976), which invariably allow smaller spores to escape. In general, *Glomus* spores tend to be smaller than *Gigaspora* spores, thus lower number of *Glomus* was obtained compared to *Gigaspora*.

The range of AMF species (14–20) found in each of the locations are far less than the ~44 species detected by Redhead (1968) in the tropical rainforest of Nigeria. It is, however, important to state that the Redhead study was conducted under a forest tree ecosystem where there was likelihood of higher AM spore diversity. Helgason et al. (1998) reported a higher AMF diversity and very different community in deciduous woodland compared with adjacent agricultural land. The present study was conducted under a yam cropping system and covered agroecological regions other than forest ecosystem. The number of species observed in this study, however, compares favourably with numbers reported for many agricultural soils (Douds and Millner 1999).

One of the common factors that affect AM species diversity in an environment is the cropping management history (Johnson and Pfleger 1992; Kurle and Pfleger 1996; Lekberg and Koide 2005). The heterogeneity of the crops preceding yam and the history of rotation probably influenced the AMF species diversity and richness. High plant diversity in the natural vegetation and highly mycorrhizal cassava crop (Howeler 1985) preceding yam cultivation likely contributed to the higher spore abundance and species richness at Ubiaja than the other locations. Uncontrolled weeds may be effective in increasing AM population and infectivity (Plenchette et al. 2005). According to Plenchette et al. (2005), cropping systems that include highly

mycorrhizal-dependent plants can increase mycorrhizae in soil and consequently increase AMF population. Therefore, mycorrhizal development in the field is largely dependent on cropping systems, and in particular, the cropping sequence of plants that exhibit a range of mycorrhizal dependency. It has also been stated that the composition of the mycorrhizal fungal community can be potentially influenced by plant community composition. Douds et al. (1997) reported consistently lower spore numbers in soil following weakly colonized spinach (*Spinacea oleraceae*) or pepper (*Capsicum annuum*), compared with more strongly colonized maize, wheat or oats (*Avena sativa*). In a Kenyan soil, maize–crotolaria rotation significantly increased the abundance of *Acaulospora scorobiculata* and *Scutellospora verrucosa* when compared with a maize–maize rotation (Mathimaran et al. 2007). Interactions of mycorrhizal fungal community and plant community clearly have relevance to agroecosystems, particularly where crop rotations or intercropping are involved (Koide and Mosse 2004). The lower diversity at Ibadan could have resulted from the plant communities that have been dominated by two plant species, pueraria and yam, in the last six years, since the diversity of AMF reduces as cropping systems tend to monocropping (An et al. 1993).

Conclusion

In conclusion, the mycorrhizal fungal diversity under yam cropping system varied across agroecologies and to a large extent was influenced by the cropping sequence and fallow history. To maintain or increase the AMF diversity and function in yam cropping systems, we suggest that fallow practices should consider introduction of high plant diversity that are mycorrhizal dependent, and reduction of excessive and continuous cropping of land. Because large-scale inoculation of AMF on farms may not be feasible in yam production, indigenous AMF species could be positively exploited through biopropagation and adoption of soil management and agronomic practices that enhance survival of plant-growth-promoting AM propagules.

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