

# Distribution of arbuscular mycorrhizal fungi spores in soils of smallholder agroforestry and monocultural coffee systems in southwestern Ethiopia

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**Abstract** Arbuscular mycorrhizal fungi (AMF) are associated with the root system of coffee (*Coffea arabica* L.) plants, but their distribution in smallholder agroforestry and monocultural coffee systems is not well known. This study investigates the spatial distribution of AMF spores in a field study in southwestern Ethiopia. Soil samples from different depths (0–50 cm) were collected under the tree canopies of *Acacia abyssinica*, *Albizia gummifera*, *Ficus sur*, *Ficus vasta* and randomly selected unshaded coffee plants at different sampling points (canopy base, radius, edge and outside canopy). Significantly higher AMF spore densities were recorded at canopy bases and at 0–30 cm soil depth. Spore populations were found to belong to five genera: *Acaulospora*, *Entrophospora*, *Glomus*, *Gigaspora* and *Scutellospora*, with *Glomus* and *Acaulospora* dominating. Sampling points, sites and depths, shade tree species and shade tree/coffee plant age affected AMF spore density. Agroforestry practices including the use of leguminous shade trees effectively maintained AMF numbers in soils even at depth compared with unshaded coffee plants (monocultures).

**Keywords** AMF distribution · *Coffea arabica* · Glomeromycota · Shaded/unshaded coffee plants · Tree legumes

## Introduction

The agriculture-based Ethiopian economy is highly dependent on *Coffea arabica* L., which contributes more than 60% of the country's foreign currency (Gole et al. 2002). Traditional shaded coffee is cultivated principally by small-scale growers and is the main livelihood for more than 60% of the local population in the coffee-growing montane rainforest areas of southwestern Ethiopia (Tafesse 1996).

Cultivation involves planting young coffee plants in the understorey of a remnant native tree cover that includes *Albizia gummifera* (Gmel) C.A.Sm, *Acacia abyssinica* Hochst. ex Benth., *Millettia ferruginea* (Hochst.) Baker, *Ficus sur* Forssk., *Ficus vasta* Forssk., *Cordia africana* Lam., *Croton macrostachyus* Del. and others (Taye 2001). Coffee crops in Ethiopia are managed with low-input technology (no agrochemicals), which means that much of Ethiopia's coffee production can be considered organic, although little certification has taken place as yet. The present investigation placed special emphasis on this type of production system, which protects the environment and maintains biodiversity because of various shade tree species.

Studies have revealed that agroforestry coffee systems are effective in soil conservation compared with conventional monocultural (unshaded) coffee systems (Cardoso et al. 2003). To improve the efficiency of nutrient recycling in these agroforestry systems, however, a better understanding of the underlying biological processes is needed. In this regard, studies on the distribution of beneficial soil microorganisms such as arbuscular mycorrhizal fungi (AMF) are vital because there is growing evidence that agroforestry practices may be important in maintaining the mycorrhizal inoculum potential in soils (Cardoso et al. 2003). The ability of AMF to enhance tropical crop (host plant) uptake of relatively immobile nutrients, in particular P and Zn, in

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nutrient-poor soils is well recognised (Thompson 1987). Furthermore, Graham (2001) has indicated that arbuscular mycorrhiza colonisation may also protect host roots from certain pathogens and improve moisture status, especially under nutrient-limited conditions.

Coffee is highly dependent on arbuscular mycorrhizal association (Habe and Bittenbender 1999). Monoculture may reduce the spectrum of AMF species found in the soil after several years of continuous cultivation (Sieverding 1991). Coffee monoculture is a common practice in southwestern Ethiopia, where the current study was carried out.

In Ethiopia, propagules of indigenous AMF have been encountered in natural coffee forests (Muleta et al. 2007), in traditional agroforestry land (Asfaw 2003) and in dry afro-montane forests (Wubet et al. 2003, 2004). However, information on the spatial distribution of indigenous AMF populations in smallholder agroforestry and monocultural coffee systems in the country is very scarce. Studies in Bonga and Yayu natural coffee forests have revealed significant variations in AMF spore density with soil depths (Muleta et al. unpublished). A decrease is often found already at 15–25 cm soil depth in the percentage of roots colonised by AMF, the number of infective propagules, the amount of extra-radical AMF hyphae and species numbers (Oehl et al. 2004). In addition, He et al. (2004) reported significantly higher spore density at the stem base of a tree legume compared with that in the canopy radius.

Thus, the aim of this work was to study the spatial distribution of AMF spores associated with smallholder agroforestry and monocultural (unshaded) coffee systems in southwestern Ethiopia. The specific objective was to measure the spatial variation in AMF spore density and genus with respect to coffee production practices, type of shade trees, age of shade trees/understorey coffee bushes, sampling points, soil depth profiles and sites.

## Materials and methods

### Description of the study areas

The sample sites included Yayu (Illubabor zone), Agaro, Yabba, Melko and Shabe areas (Jimma zone), all in Oromia regional state, Ethiopia (07°28′–08°28′N, 35°50′–36°45′E). The altitude ranges from 1,376 to 1,890 m above sea level. The mean annual rainfall is about 1,600 mm, the majority of which falls in the period June to August. Rainfall distribution in the study areas is bi-modal, and temperatures range between 15 and 25°C.

The soil in southwestern Ethiopia is of volcanic origin, with a high nutrient-holding capacity by clay minerals (Dubale and Mikru 1994), and the soil composition is clay (13%), loamy clay (29%), silty clay (29%) and sandy clay

(22%) in relative proportions, with a pH ranging mostly from 5 to 6.8 (water extract; Höfner 1987). The topsoil is commonly dark brown or brownish in colour. There are four types of coffee production systems in Ethiopia: forest coffee, semi-forest coffee, smallholder coffee and plantation coffee (Aga et al. 2003). Small-scale coffee farmers are the major producers of coffee in the country and were the focus of the present investigation. Under such a production system, coffee plants are grown at low density beneath the canopy of suitable shade tree species, ranging from 500 to 1,800 trees per hectare (Dubale and Mikru 1994). They are fertilised with organic wastes and rarely intercropped. There is little pruning, field hygiene or stumping. Unshaded coffee plants are generally grown in the vicinity of farmers' dwellings but sometimes in fields on farmland. The size of the monocultural coffee sites investigated here ranged from 0.13 to 0.25 ha. Coffee plants were generally hoed and cleared at least once annually.

### Sampling design

All the 13 study sites chosen according to a reconnaissance survey were located in the same climate and class of soil and occupied similar positions in the landscape. Only sites with more than 300 coffee stems/site were included. Patchy on-farm/field shade tree species and monocultures were checked and identified. Farmers were interviewed about the age of shade trees and coffee plants and their coffee management practices. During this survey, the study team identified the major shade tree species at all sites to be *A. abyssinica* and *A. gummifera* (Leguminosae). *F. sur* and *F. vasta* (Moraceae) were the other shade tree species identified. *C. africana* (Boraginaceae) was rarely encountered and is not included in this study. The southwestern part of the country was once fully covered with forests, and these trees are remnant forest species.

Ten different shaded and three unshaded (monoculture) coffee sites were investigated (Table 1). The patchy on-farm/field shade tree species and monoculture coffee plants were scattered along the specified altitude range at five major sites, including Agaro (one sampling site), Melko (two sub-sites), Shabe (two sub-sites), Yabba (three sub-sites) and Yayu (five sub-sites). The distance between the five main sites was 20–130 km, while the distance between sub-sites was 2–3 km. Soil samples for AMF spore counts were collected from root zones of coffee bushes that were under the canopy of shade tree species at four sampling points (canopy base [CB], canopy radius [CR], canopy edge [CE] and outside the canopy [OC, approx. 3 m away from the CE]) at ten different sub-sites and from unshaded coffee systems at three different sites. Soil samples were collected using a soil auger of 5 cm diameter at four places at each sampling point and mixed to obtain representative

**Table 1** General description of the smallholder agroforestry based/monocultural coffee systems studied in southwestern Ethiopia

Number	Site	Shade trees/ monoculture	Age of shade trees (years)	DBH (m)	Canopy diameter (m)	Age of coffee plants (years)
1	Yabbu3	<i>Albizia gummifera</i>	100	3.60	16.00	26
2	Shabe1	<i>Ficus sur</i>	45	7.30	17.40	24
3	Yayu2	<i>Ficus vasta</i>	40	8.09	19.00	25
4	Yabbu1	<i>Acacia abyssinica</i>	35	2.85	11.00	23
5	Yayu1	<i>Acacia abyssinica</i>	30	3.50	8.70	10
6	Melko1	<i>Acacia abyssinica</i>	26	3.15	13.00	9
7	Agaro	<i>Albizia gummifera</i>	25	6.70	20.00	15
8	Yayu4	<i>Acacia abyssinica</i>	20	2.76	12.00	10
9	Yayu3	<i>Albizia gummifera</i>	17	2.98	8.00	17
10	Yabbu2	<i>Acacia abyssinica</i>	15	1.65	10.00	6
11	Shabe2	Unshaded coffee	NA	ND	0.43	12
12	Yayu5	Unshaded coffee	NA	ND	1.00	25
13	Melko2	Unshaded coffee	NA	ND	0.89	17

NA Not applicable, ND not determined

samples for the soil depths studied (0–10, 10–20, 20–30, 30–40 and 40–50 cm). The rhizospheres of coffee plants were not specifically targeted for soil sampling in the case of OC (shade trees) because the distribution of coffee bushes was restricted to CB–CE. The same implies for CR, CE and OC in monocultures because coffee plants were not uniformly encountered at these particular sampling points. In all cases, triplicate composite soil samples (about 1 kg), a total of 780 (4×5×3×13) samples, were collected from the study sites and transported to the laboratory within 3 to 4 days in an insulated container and stored at 4°C before processing.

#### AMF spore extraction and enumeration

Spore isolation and characterisation were carried out according to Brundrett et al. (1996). Spores were extracted from 50-g triplicate sub-samples of soil by the wet sieving method and sucrose density centrifugation. The centrifuged samples were observed under a stereomicroscope at ×40 magnification for quantification and characterisation. In addition, a compound microscope was used to identify the quantified spores to their respective genera based on spore size, colour, surface ornamentation, wall structure and presence/absence of subtending hyphae.

#### Statistical analysis

The significance of differences in spore density at different sites, sampling points, depth profiles and production systems was tested using Tukey's Honestly Significantly Different post-hoc test at  $p < 0.05$  after a one-way analysis of variance using SPSS version 10. Pearson correlation analysis was used to explore the relationship between shade tree and coffee plant parameters and altitude and AMF spore density.

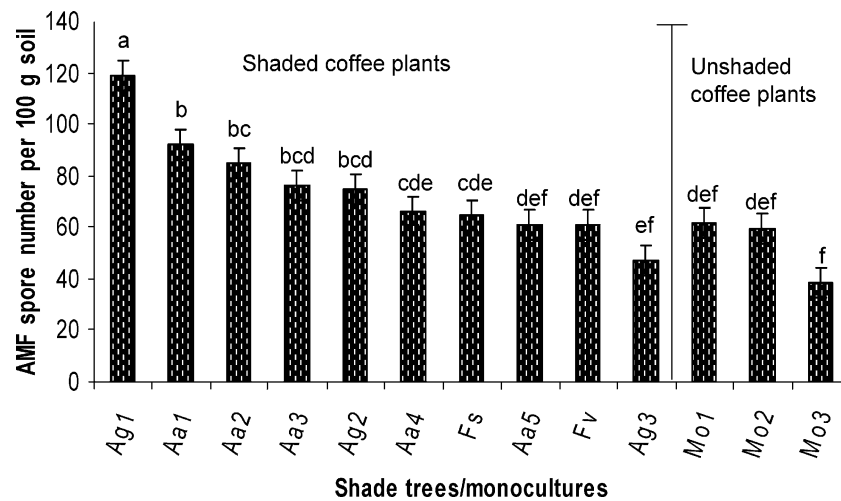
## Results and discussion

### Shade trees and coffee management practices

Of the ten coffee shade trees investigated, eight were legumes belonging to two genera (*Acacia* and *Albizia*; Table 1). The age of the coffee plants was estimated to be approximately 6–26 years and that of the shade tree species 15 to more than 100 years (Table 1). Coffee crops were hand planted at all sites investigated except the Yabbu2, Yayu1 and Yayu4 sub-sites, which had naturally growing plants. The shaded sites were either grazed virgin land (seven sites) or tilled farmlands, whereas the unshaded coffee plants were all on tilled lands.

### Enumeration of AMF spores

AMF spores were recovered at varying densities from all sites investigated, regardless of soil management and production system. The overall AMF spore density at the individual sites ranged from 38 to 119 per 100 g of dry soil. Spore numbers showed variations with respect to site (type and age of shade tree species), age of coffee plants, sampling points and depth profiles. There were significant differences ( $n = 13$ ,  $F = 18.61$ ,  $p < 0.001$ ) in number of AMF spores between sites. The highest AMF spore counts were recorded at the Agaro site (under the canopy of *A. gummifera*), followed by Yayu1, Yabbu2 and Yayu4 (all under the canopy of *A. abyssinica*) and Yayu3 (under the canopy of *A. gummifera*; Fig. 1). The lowest density of AMF spores was recorded in soil samples collected from Yayu5 (unshaded coffee; Fig. 1). Analysing the combined spore densities of coffee plant root zones under shade trees and comparing them with those of unshaded coffee plants revealed a strongly significantly ( $F = 25.84$ ,  $p < 0.001$ )



**Fig. 1** The overall AMF mean spore density of the 13 sampling sites, regardless of soil profile and sampling point. Abbreviations: *Ag1* *Albizia gummifera* 1 (Agaro), *Aa1* *Acacia abyssinica* 1 (Yayu1), *Aa2* *Acacia abyssinica* 2 (Yabbu2), *Aa3* *Acacia abyssinica* 3 (Yayu4), *Ag2* *Albizia gummifera* 2 (Yayu3), *Aa4* *Acacia abyssinica* 4 (Melko1), *Fs*

*Ficus sur* (Shabel), *Aa5* *Acacia abyssinica* 5 (Yabbu1), *Fv* *Ficus vasta* (Yayu2), *Ag3* *Albizia gummifera* 3 (Yabbu3), *Mo1* monoculture 1 (Melko2), *Mo2* monoculture 2 (Shabe2) and *Mo3* monoculture 3 (Yayu5). Significant differences between sites are indicated by different letters above the bars. Bars represent means+SE

higher mean value associated with shade trees. Likewise, grouping the three sites with *A. gummifera*, five with *A. abyssinica*, two with *Ficus* species and three with unshaded coffee plants revealed significant differences ( $n=4$ ,  $F=17.96$ ,  $p=0.001$ ) between these groups. There was also a significant difference ( $p<0.05$ ) between the tree legumes and *Ficus* shade tree species, but there was no significant difference ( $p>0.05$ ) between the latter group and unshaded coffee plants.

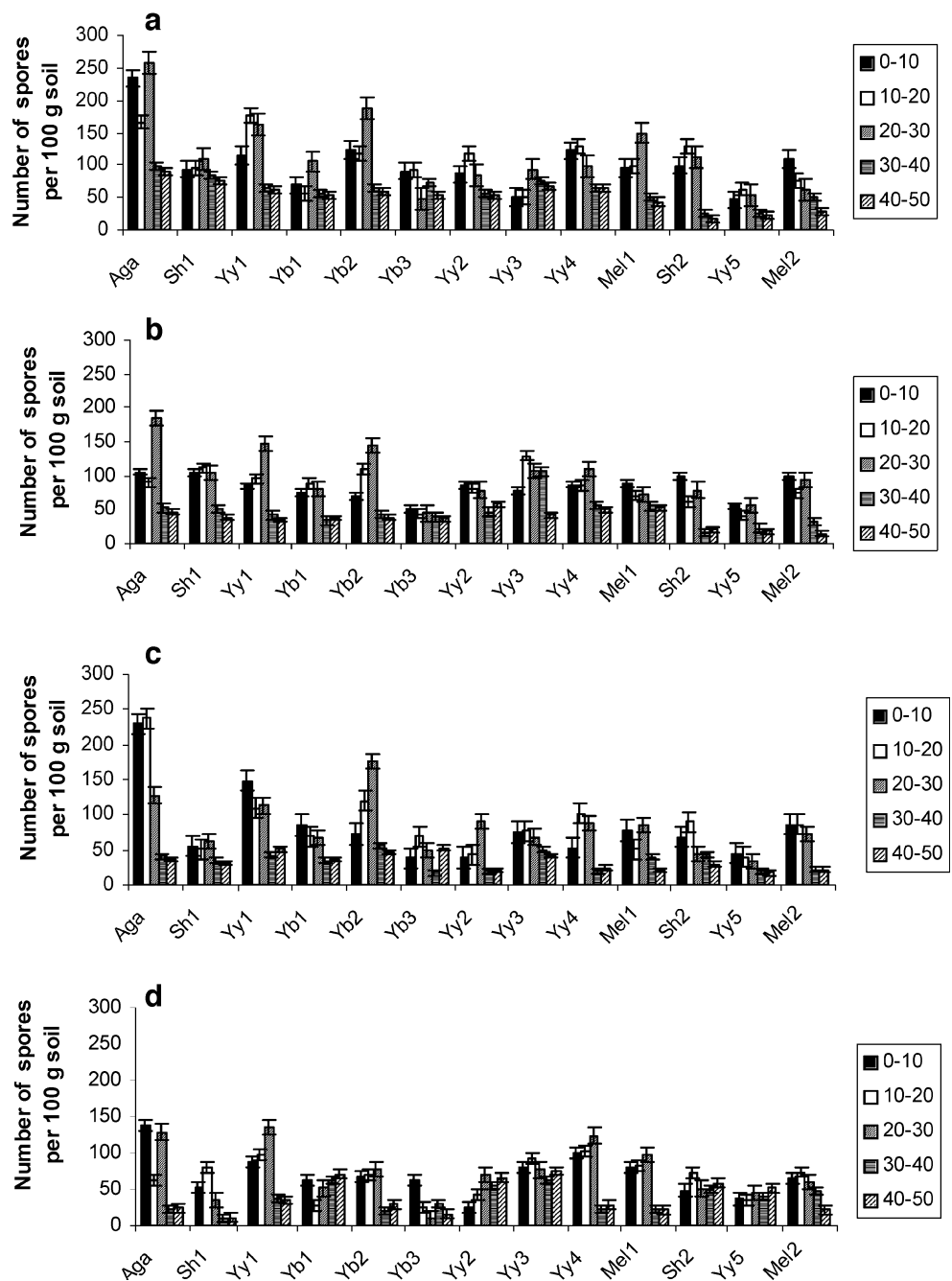
The lands beyond the canopy of coffee plants shaded by leguminous plants were grazed virgin land with the exception of Yayu3, which was a tilled plot of land from which maize had been harvested in the previous year. Maize is also a suitable host for AMF. Legumes, however, are generally more mycotrophic than other plants (Plenchette et al. 2005). In coffee plantations, legume intercropping has been found to increase the concentration of AMF spores in the soil (Colozzi and Cardoso 2000). It appears that this kind of interaction is mutualistic because nitrogen fixation demands high P (Hokka et al. 2004), which is supplied by AMF, and fixed nitrogen can be transferred to non-nitrogen fixing plants (coffee and other plants) via AM fungal hyphae without entering the soil solution (Mårtensson et al. 1998). The higher spore densities recorded under the legume shade trees (this study) strongly support their use as agroforestry trees for coffee growers. Remarkably, these tree species are among the most preferred plants by the farmers for coffee production (Muleta et al. unpublished).

The mean spore density of AMF was not related to diameter at breast height, average canopy diameter or altitude. Although not fully significant, the age of shade tree species ( $n=10$ ,  $r=-0.59$ ,  $p=0.07$ ) or coffee plants ( $n=13$ ,

$r=-0.43$ ,  $p=0.14$ ) and mean spore density of AMF were slightly negatively correlated. It appeared that the age (directly or indirectly) of both shade tree species and coffee plants gave rise to low AMF spore counts in cases where both shade trees and their understorey coffee plants had ages exceeding 30 and 20 years, respectively (Table 1; Fig. 1). In shaded cacao plantations, AMF mean spore density has been shown to decrease in the plant age order nursery 6 months>young (20 years)>mature (20–30 years)>old (40–70 years old; Cuenca and Meneses 1996). Aged roots probably have lower starch concentrations and exudates, which may put stress on both myco- and autotrophs.

Mean spore density was found to be significantly higher ( $n=4$ ,  $F=20.21$ ,  $p=0.001$ ) at the CB of the stems compared with the CR, CE and OC at all sites investigated, regardless of the land use system or shade tree species (Fig. 2a–d). The mean spore values obtained at CR were not significantly different ( $p>0.05$ ) from those at CE but significantly higher ( $p<0.05$ ) than at OC (the CE spore numbers were intermediate between CR and OC). Observation of the highest AMF mean spore density at CB (this study) is in agreement with another study under the canopy of *Acacia* species (He et al. 2004), although the two study areas differ in climatic conditions. Furthermore, reports from southern Ethiopia indicate that beneath common coffee shade tree species such as *C. africana* and *M. ferruginea* (trees scattered on maize fields), the proportion of colonised roots decreases with increasing distance laterally from the tree trunk (Asfaw 2003). AMF survive better when they are close to the host crop on which they develop (Kabir 2005). This is probably because of their obligate biotrophic nature of existence, as close to tree trunks, there are more roots

**Fig. 2** Mean AMF spore density per 100 g soil in samples collected from fields of small-holder agroforestry and monocultural/unshaded coffee systems at different sampling points **a** canopy base (CB), **b** canopy radius (CR), **c** canopy edge (CE) and **d** outside canopy (OC). Abbreviations: *Aga* Agaro (*A. gummifera*), *Sh1* Shabe1 (*F. sur*), *Yy1* Yayu1 (*A. abyssinica*), *Yb1* Yabbu1 (*A. abyssinica*), *Yb2* Yabbu2 (*A. abyssinica*), *Yb3* Yabbu3 (*A. gummifera*), *Yy2* Yayu2 (*F. vasta*), *Yy3* Yayu3 (*A. gummifera*), *Yy4* Yayu4 (*A. abyssinica*), *Mel1* Melko1 (*A. abyssinica*), *Sh2* Shabe2 (monoculture), *Yy5* Yayu5 (monoculture) and *Mel2* Melko2 (monoculture). Bars represent means+SE



that can be colonised by potential propagules and more spores are expected.

AMF spore density was highest in the topsoil (0–30 cm soil depth), with most peaks at 20–30 regardless of site, sampling point relative to stems, tree species or land use system, and decreased gradually with increasing soil depth (Fig. 2a–d) as also observed by other investigators (Oehl et al. 2004; Kabir 2005; Muleta et al. unpublished). This distribution of AMF spores is most likely related to the higher organic matter (Osorio et al. 2002) and/or root biomass in the topsoil. On the other hand, Guadarrama and Álvarez-Sánchez (1999) reported that high temperature and

light intensity (stresses), which are silent features of surface soils, can also augment AMF sporulation.

In the present study, the observed decrease in spore density in the deepest soil layers (30–50 cm soil depth) at CB and CR (Fig. 2a,b) was more noticeable in soil samples collected from the root zones of monoculture coffee plants (17.3–29.0 spores per 100 g at CB) than those of agroforestry coffee systems (50.3–98.7 spores per 100 g soil at CB; Fig 2a). The main reason for the higher spore numbers in the deeper soil layers in the agroforestry is probably the presence of more roots in the deeper soil layers in these shaded coffee systems (Cardoso et al. 2003).

## AMF genera

At all sites investigated, members of the Glomeromycota had more or less similar frequencies of occurrence in both production systems except for *Entrophospora*, which were rare in the monoculture (unshaded) coffee fields. *Glomus* (31.2%) followed by *Acaulospora* (26.7%) dominated at all sites surveyed, in keeping with results from the Bonga natural coffee forest (Muleta et al. 2007). The relative abundance of *Glomus* in many ecosystems regardless of degree of disturbance or land use system has been frequently reported (Daniell et al. 2001; Wubet et al. 2004). The dominance of *Glomus* observed in this study could therefore be very important for the highly mycotrophic coffee plants (Habte and Bittenbender 1999), as the monocultural production systems in particular invariably involve a certain degree of soil disturbance.

Other genera identified in terms of their abundance were *Scutellospora* (15.8%), *Gigaspora* (14.0%) and *Entrophospora* (5.5%). A considerable proportion of unidentifiable spores (6.8%) were also encountered in both cultural production systems. At certain sub-sites such as Yayu1 (under the canopy of *A. abyssinica*), Yayu2 (under the canopy of *F. vasta*), Yayu5 (unshaded coffee) and Shabel (under the canopy of *F. sur*), one or two of the genera *Gigaspora*, *Scutellospora* and *Entrophospora* were either rarely encountered or not detected (data not shown). We suggest that soil disturbance particularly selects AM fungi with a certain degree of adaptability and eliminates others. For instance, the Shabel site where *Scutellospora* was not identified was close to a wetland where it suffers from recurrent flooding during the rainy season (June to October), which may have had an adverse effect on AMF diversity (Pattinson and McGee 1997). At least six other sub-sites with shade tree species (Fig. 1) showed better total counts of AMF spores than this particular sub-site.

Although *Entrophospora* (cf. above) had a limited distribution in most sites studied, it was not detected at all at the Yayu5 site (unshaded coffee plants), and all other sites showed better total AMF spore counts than this sampling site (Fig. 1). Besides the lengthy age of monoculture coffee plants (Table 1), the land OC at this site was tilled farm land close to homestead garden. The absence or lower abundance of *Entrophospora* at most sites might be attributed to the yearly/periodical disruption of the extra-radical hyphae of this fungus induced by human activities during coffee plant management, as Menéndez et al. (2001) have demonstrated that tillage and cereal monoculture negatively affect the more labile *Entrophospora* but favour the resistant *Glomus* species.

Considering the distribution down the soil profile, *Glomus*, *Acaulospora* and *Gigaspora* maintained a more or less similar distribution in shaded coffee plots (data not

shown). However, in unshaded coffee plants, only the distribution of *Glomus* was similar with increasing soil depth, unlike *Acaulospora* and *Gigaspora*, the vertical distribution of which decreased with depth (from 34.6 to 8.3% and 14.3 to 3.8%, respectively). *Entrophospora* was different from that of the other genera in that its occurrence steadily decreased with soil depth (from 8.0 to 1.4%) in the agroforestry coffee systems, but it was not encountered at all at depths of 30–50 cm in monocultural coffee systems. The situation for *Scutellospora* was different because its occurrence (both relatively and absolutely) gradually increased down the soil profile in both cultural coffee production methods (from 9.6 to 34.8% in agroforestry systems and from 11.5 to 41.7% with a peak of 60.0% at 30–40 cm for monocultural systems). We have no obvious explanation for this observation. However, *Scutellospora* is particularly sensitive to soil disturbance (Jansa et al. 2003). Perhaps this genus has developed a strategy to take refuge at deeper soil layers beyond possible disturbance level, as *Scutellospora* has also been detected at soil depths of 50–70 cm in intensively managed maize fields (Oehl et al. 2005). On the other hand, Ho (1987) indicated that AMF adapt differently to a range of temperature conditions. Taking this into account, *Scutellospora* may also prefer the relatively stable temperature of the sub-soil compared with the topsoil, where either hoeing/farming or clearing could expose it to high ambient temperatures.

In conclusion, the results of the current work show that a number of the shade trees studied, particularly the tree legumes, are ideal for agroforestry systems because most of them presented high AMF spore counts even in deep soil layers. Low spore densities or absence of some AMF genera at some study sites imply, however, that these sites had been subjected to mechanical disturbance. Because AMF spores provide only a static picture of the AMF community (Clapp et al. 1995; Redecker et al. 2003; Oehl et al. 2004, 2005), molecular methods that directly involve plant roots and/or spores in combination with the morphological tools may assist in providing a fuller picture of the AMF community composition in the investigated areas.

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## References

- Aga E, Bryngelsson T, Bekele E, Salomon B (2003) Genetic diversity of forest arabica coffee (*Coffea arabica* L.) in Ethiopia as

- revealed by random amplified polymorphic DNA (RAPD) Analysis. *Hereditas* 138:36–46
- Asfaw Z (2003) Tree species diversity, topsoil conditions and arbuscular mycorrhizal association in the Sidama traditional agroforestry land use, southern Ethiopia. Doctoral dissertation. SLU, Acta Universitatis agriculturae Sueciae. Silvestria vol. 263
- Brundrett M, Bougher N, Dell B, Grove T, Malajezuk N (1996) Working with Mycorrhizas in forestry and agriculture. Australian Centre International Agricultural Research, Canberra
- Cardoso IM, Boddington C, Janssen BH, Oenema O, Kuyper TW (2003) Distribution of mycorrhizal fungal spores in soils under agroforestry and monocultural coffee systems in Brazil. *Agrofor Syst* 58:33–43
- Clapp JP, Young JPW, Merryweather JW, Fitter AH (1995) Diversity of fungal symbionts in arbuscular mycorrhizae from a natural community. *New Phytol* 87:259–265
- Colozzi A, Cardoso EJBN (2000) Detection of arbuscular mycorrhizal fungi in roots of coffee plants and *Crotalaria* cultivated between rows. *Pesqui Agropecu Bras* 35:2033–2042
- Cuenca G, Meneses E (1996) Diversity patterns of arbuscular mycorrhizal fungi associated with cacao in Venezuela. *Plant Soil* 183:315–322
- Daniell TJ, Husband R, Fitter AH, Young JPW (2001) Molecular diversity of arbuscular mycorrhizal fungi colonising arable crops. *FEMS Microbiol Ecol* 36:203–209
- Dubale P, Mikru Z (1994) Ecology and soils of major coffee growing regions of Ethiopia. In: Dubale P (ed) Mineral fertilization of coffee in Ethiopia. IAR, Addis Ababa
- Gole TW, Denich M, Teketay D, Vlek PLG (2002) Human impacts on *Coffea arabica* genetic pools in Ethiopia and the need for its in situ conservation. In: Rao R, Brown A, Jackson M (eds) Managing plant genetic diversity. CAB International, Wellingford, UK, pp 237–247
- Graham JH (2001) What do root pathogens see in mycorrhizas? *New Phytol* 148:357–359
- Guadarrama P, Álvarez-Sánchez FJ (1999) Abundance of arbuscular mycorrhizal fungi spores in different environments in a tropical rain forest, Vera Cruz, Mexico. *Mycorrhiza* 8:267–270
- Habte M, Bittenbender HC (1999) Reactions of coffee to soil solution P concentrations and arbuscular mycorrhizal colonization. *J South Pacific Agric* 16:29–34
- He X, Pen-Mouratov S, Steinberger Y (2004) Research Note: Spatial variation of AM fungal spore numbers under canopies of *Acacia raddiana*. *Arid Land Res Manage* 18:295–299
- Ho I (1987) Vesicular arbuscular mycorrhizae of halophytic grasses in the Alvard desert of Oregon. *Northwest Sci* 61:148–151
- Höfner W (1987) Nährstoffstatus der Böden in den Kaffeeanbaugeländen Äthiopien. In: Matter HE, Westpal A (eds) 20 Jahre Agrarforschung des Tropeninstituts in Äthiopien. Äthiopien. Tropeninstitut, Giessen, pp 55–56
- Hokka V, Mikola J, Vestberg M, Setälä H (2004) Interactive effects of defoliation and an AM fungus on plants and soil organisms in experimental legume-grass communities. *Oikos* 106:73–84
- Jansa J, Mozafar A, Kuhn G, Anken T, Ruh R, Sanders IR, Frossard E (2003) Soil tillage affects the community structure of mycorrhizal fungi in maize roots. *Ecol Appl* 13:1164–1176
- Kabir Z (2005) Tillage or no-tillage: Impact on mycorrhizae. *Can J Plant Sci* 85:23–29
- Mårtensson AM, Rydberg I, Vestberg M (1998) Potential to improve transfer of nitrogen in intercropped systems by optimizing host–endophyte combinations. *Plant Soil* 205:57–66
- Menéndez AB, Scervino JM, Godeas AM (2001) Arbuscular mycorrhizal populations associated with natural and cultivated vegetation on a site of Buenos Aires province, Argentina. *Biol Fertil Soils* 33:373–381
- Muleta D, Assefä F, Nemomissa S, Granhall U (2007) Composition of coffee shade tree species and density of indigenous arbuscular mycorrhizal fungi (AMF) spores in Bonga natural coffee forest, southwestern Ethiopia. *Fore Ecol Manage* 241:145–154
- Oehl F, Sieverding E, Ineichen K, Ris E, Boller T, Wiemken A (2005) Community structure of arbuscular mycorrhizal fungi at different soil depths in extensively and intensively managed agroecosystems. *New Phytol* 165:273–283
- Oehl F, Sieverding E, Mäder P, Dubois D, Ineichen K, Boller T, Wiemken A (2004) Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. *Oecologia* 138:574–583
- Osorio NW, Alzate JM, Ramírez GA (2002) Coffee seedling growth as affected by mycorrhizal inoculation and organic amendment. *Commun Soil Sci Plant Anal* 33:1425–1434
- Pattinson GS, McGee PA (1997) High densities of arbuscular mycorrhizal fungi maintained during long fallows in soils used to grow cotton except when soil is wetted periodically. *New Phytol* 136:571–580
- Plenchette C, Clermont-Dauphin C, Meynard JM, Fortin JA (2005) Managing arbuscular mycorrhizal fungi in cropping systems. *Can J Plant Sci* 85:31–40
- Redecker D, Hijri I, Wiemken A (2003) Molecular identification of arbuscular mycorrhizal fungi in roots: Perspectives and problems. *Folia Geobot* 38:113–124
- Sieverding E (1991) Vesicular–arbuscular Mycorrhiza management in tropical agrosystems. GTZ, Eschborn and Hartmut Bremer, Friedland
- Tafesse A (1996) Agroecological zones of Southwest Ethiopia. Universität Trier, Trier
- Taye E (2001) Report on woody plant inventory of Yayu national forestry priority area. IBCR/GTZ, Addis Ababa
- Thompson JP (1987) Decline of vesicular-arbuscular mycorrhizas in long fallow disorder of field crops and its expression in phosphorus deficiency in sunflower. *Aust J Agric Res* 38:847–867
- Wubet T, Kottke I, Teketay D, Oberwinkler F (2003) Mycorrhizal status of indigenous trees in dry afro-montane forests of Ethiopia. *Fore Ecol Manage* 179:387–399
- Wubet T, Weiß M, Kottke I, Teketay D, Oberwinkler F (2004) Molecular diversity of arbuscular mycorrhizal fungi in *Prunus africana*, an endangered medicinal tree species in dry afro-montane forests of Ethiopia. *New Phytol* 161:517–528