**CBM:s Skriftserie 3:53–80. Uppsala 2001.**

# Distribution and diversity of arbuscular mycorrhizal fungi in traditional agriculture on the Niger inland delta, Mali, West Africa.

**Sara Friberg**

*Friberg, S. 2001. Distribution and diversity of arbuscular mycorrhizal fungi in traditional agriculture on the Niger inland delta, Mali, West Africa. – CBM:s Skriftserie 3: 53–80.*

A diverse community of arbuscular mycorrhizal fungi (AMF) produces a beneficial and stable symbiosis with most plant communities. In this study, we determined diversity, richness and relative abundance of AMF species in the semi-arid Niger inland delta of Mali, West Africa.

The 10 sites ranged from annually inundated fields to arid fields of rice, sorghum, millet and natural vegetation, and were sampled using four transects per site. To determine possible correlations with soil characters we analysed pH, extractable phosphorus (P), total P, organic matter and particle fractions. The plant parameters assessed were density, species diversity and richness. A 4.5 months pot culture with *Sorghum bicolor* was used to enhance sporulation of indigenous AMF species. By comparing this with INVAM references (International Culture Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi), we could identify seven AMF species: *Glomus aggregatum, Glomus clarum, Glomus claroideum, Glomus occultum,* an undescribed *Glomus* species, *Acaulospora morrowiae* and an undescribed *Entrophospora* species.

The undescribed G*lomus* species had the greatest range for every measured parameter, was totally dominant in three samples and produced most spores in both the arid and inundated sites. AMF species richness ranged from 1 to 5 per 2500 $m^2$ site, showing no correlation to plant species richness. Intense AMF root colonisation and sporulation were found in the interval pH 5.6 to 7.1 and 0 to 13mg P $kg^{-1}$ soil. To investigate the most important variables influencing AMF, we used a multivariate principal component analysis. The highest and most consistent AMF data was found in the annually inundated sites. The study showed that traditional, monospecific, low input, untilled agriculture of inundated rice, sorghum and millet is promoting an extremely high and relatively diverse inoculum potential of AM fungi.

*Sara Friberg, Swedish Biodiversity Centre, Swedish University of Agricultural Sciences, P. O. Box 7007, SE-750 07 SWEDEN. E-mail: axebo@hotmail.com*

## Introduction

### Arbuscular mycorrhiza in general

Mycorrhiza (modern Latin of Greek words *mykes* = fungi, *rhiza* = root) were discovered 100 years ago, but were not seriously included in the multidisciplinary science of biology until the 1980's. The very special mycorrhizal group considered here, arbuscular mycorrhiza (AM) is often still neglected when issues of botany, soil biology or microbial ecology are discussed. One reason may be that the methods available today for studying AM are very specific and time consuming. From a conservation perspective, a reason for neglect may be the assumed global abundance of AM fungi (AMF), although the functional diversity and the effects of local species extinction of AMF have not been studied. Nevertheless, research and interest have expanded exponentially during the last two decades, especially in agricultural sciences.

There are seven groups of mycorrhizal fungi, all of which build a living bridge between plant roots and bulk soil in most ecosystems. In 1973, Rambelli suggested the term "mycorrhizosphere" to substitute "rhizosphere" because of the significant and dynamic microbial interactions found in the soil of mycorrhizal roots. The morphologically and functionally different groups of mycorrhizal fungi are distinguished by having the plant exchange compartment either outside (ectomycorrhiza) or inside (endomycorrhiza) the root epidermis cells (Smith and Read 1997). AM is an endomycorrhiza and has got its name from the distinct fungal tree-shaped, short-lived structure that develops in plant root cells (arbus = tree). Earlier, the name vesicular-arbuscular fungi (VAM) was used, but since not all fungi in the group produce vesicles, the term AMF is preferred. AM is the most widespread group, found from the Arctic's to the tropics, and is the dominating mycorrhiza in deserts, grasslands, agroecosystems and broad-leaved forests in temperate to tropical biomes (Smith and Read 1997). On the other hand, AMF is the least diverse group of mycorrhizal fungi on a species level, containing only 154 species in the order Glomales of the division Zygomycetes (Morton and Benny 1990). The species concept used is phylogenetic, based on the inherited morphology and biochemistry of AMF spores (Morton *et al.*1995). Distinct from the other groups of mycorrhizal fungi, AMF lack sexual reproduction. Furthermore, AMF lack plant host specificity and are obligate symbionts, germinating but not growing in the absence of responding plant roots (Smith and Read 1997). The wide range of hosts has only been marginally screened, but a compilation by Trappe (1987), based on 6500 plant species (e.g. 3% of the unknown but estimated number of angiosperms), suggested that the range covers 50% of the dicots and 50% of the monocots. Many bryophytes (Smith and Read 1997) and pteridophytes (Gemma *et al.* 1992) also develop AM symbiosis. There are reports of AM-plants with such different adaptations as being aquatic (Cooke and Lefor 1998), epiphytic (Gemma and Koske 1995), halophytic or desert cacti, rainforest trees (Smith and Read 1997), $C_3$ and $C_4$-grasses (Hetrick *et al.* 1991), and agricultural crops (Smith and Read 1997). One of the first terrestrial plants, *Aglaophyton,* in a 400 million year old fossil, shows arbuscules identical to the type found in roots today (Pirozynski and Dalpé 1989, Taylor *et al.* 1995). The long co-evolutionary history of plants and AMF, as proved by this finding, probably explains the lack of host specificity and the global distribution of AMF.

When it became known that AM-plants show increased fecundity compared to non-AM plants, the interest for AM symbiosis arose, especially in agricultural research. An AMF mycelium increases the absorptive root surface area of a plant 100-fold (Smith and Read 1997). AM-plants thus have increased macro- and micronutrient content (Clark and Zeto 1996, Solaiman and Hirata 1996). Due to unknown reasons, this is also seen at low soil phosphorus levels (Smith and Read 1997) or low to high pH-levels (Clark and Zeto 1996). In general, AMF-plants also exhibit an increased rate of photosynthesis (Dixon *et al.* 1994), and tolerance to drought (Osonubi *et al.* 1992) and salinity (Rosendahl and Rosendahl 1991). Resistance to

root pathogens also increases (Smith and Read 1997), primarily due to AMF occupying the root niche and to increased plant vigor. Another feature important in the establishment of seedlings is the transport of photoderivatives from an unshaded to a shaded plant via the AMF mycelium (Eissenstat and Newman 1990).

As AM is a mutualistic symbiont, AM fungi drain up to 20% of photosynthetic carbon (Jakobsen and Rosendahl 1991) and in return, provide plants with large amounts of nutrients (P, N, K, Zn etc) and water from the soil. AMF also produce glycoprotein extracellularly on the mycelia in the bulk soil, which together with the physical network of hyphae, helps to aggregate soil (Wright and Upadhyaya 1998), thus improving aeration and water percolation. The carbon inflow to soil attracts soil microbes; altogether producing a functionally diverse and dynamic soil biota (Schreiner *et al.* 1997), which is fundamental for plant nutrition in natural systems and sustainable agriculture.

The benefit of an AM symbiosis depends on when in a plants life stage its roots are colonised by AM fungi (Solaiman and Hirata 1996). The outcome is also affected by the growth rate of both the fungi and plant. Moreover, the AM symbiosis is also influenced by the composition of plant and fungal species (Schreiner *et al.* 1997), by the hierarchical structure of AMF species in the root niche, and by their inherited genetic and functional diversity (Smith and Gianinazzi-Pearson 1988). Additionally, the outcome of an AM symbiosis is affected by soil properties, soil and plant treatments, and the presence, and amount, of soil microbes being mutualists, commensalists, inhibitors or parasites. The above ground macro- and microclimate are also factors influencing the symbiosis.

An AM fungus cannot be regarded as an individual. What we may call an intact AM fungus is in fact a community of thousands of individually distinct, motile DNA-nuclei, building and inhabiting a network of non-septate (non-cross walled) hyphae inside and between root epidermis cells. Intact hyphae have been proved to extend at least 12 cm from a colonised root (Jakobsen *et al.* 1992).

A new AMF infection of roots can start from anywhere, when all compartments are considered as independent propagules. But the life cycle of an AM fungus starts from an asexually produced, thick-walled spore, produced on a hyphal tip either inside the root or in the bulk soil, depending on the fungal species. When mature, the spore separates from the hypha and is totally dependent on passive dispersal. If the spore is produced in the soil surface layer, it may be spread by wind, water or by any soil digging animal such as humans, voles, earthworms and root collecting birds (Terwilliger and Pastor 1999; Koske and Gemma 1990). AM spores can be produced more than 1.20m down in the soil profile (Thompson 1991) and are then heavily dependent on the frequency of passing roots to grow. Without plants, AM fungi can survive for a few years in the form of spores if not heavily parasitized (Smith and Read 1997).

Depending on the AMF family, one to several germ tubes grow a few millimetres from the AM spore, carrying the stored lipid content and hundreds to thousands of nuclei. But an AMF spore is unable to metabolise its own reserves without the presence of a root (Bécard and Piché 1989). It is not known what type of signal system the AM symbionts are using, but McArthur and Knowles (1992) showed that ethylene production in potato roots, promoted by high levels of soil phosphorus, prevented AMF colonisation. If an AM responding plant root is present, germination and hyphal growth is promoted, directing the germ hyphae towards the fine root tips. An appressorium is developed, which is used as an attachment onto the root surface. From the appressorium, an intraradical mycelium develops between and inside the plant cells in the epidermal layer of the root. In the plant cells, the hyphae produce arbuscules by dichotomous branching and a simultaneous plant response invaginating the cell plasmalemma. The AM symbiosis is thus established. Via the vast absorptive surface area of the arbuscule/plasmalemma, carbon is delivered from the plant, promoting growth of the mycelial

network in the bulk soil. Water and protein bound phosphorus is transported from the bulk soil back to the arbuscular compartment and delivered to the plant. The AMF stores some photosynthetic derivatives as lipids in elliptical vesicles produced by many fungi on both intraradical and extraradical hyphae. When a threshold level of colonisation is achieved (e.g. a certain amount of carbon is allocated), most AMF species start to sporulate (Gazey *et al.* 1992; Pearson and Schweiger 1993).

**Arbuscular mycorrhiza, diversity and disturbance**

To understand the contributions of AMF to ecosystems (including agriculture) and how to manage them, Abbott *et al.* (1995) stressed the importance of assessing its diversity, as it has been shown that the exchange activity and beneficial outcomes vary with fungal and plant species composition. Rarely one AM fungal species, but mostly three and occasionally nine species of different families and suborders, occupy the root system at the same time (Morton *et al.* 1995). The AMF diversity does not follow, but may regulate, patterns of plant diversity: if one AMF species or indigenous species becomes extinct in a habitat, there may be significant shifts in how plants acquire resources in that habitat (Allen *et al.* 1995). The interspecific genetic diversity of AMF probably overrides the intraspecific diversity, which is why conservation and research should also deal with the adaptations of isolated species. As the molecular methods to describe specific and interspecific diversity are so far only developed for a few AMF species, taxonomy still must rely on the time consuming methods of morphology and histochemistry.

High AMF diversity ranges from 10-18 species per 25g subsample in $1m^2$ plots of dry tropical forest, forest edge and grassland in Costa Rica (Johnson and Wedin 1997), to 43 species found in apple rootstock plantings across 18 states of the US (Miller *et al.* 1985). Along a 355km latitudinal gradient along the eastern US, 4.6 species on average, and 23 species in total, were found associated with two plant species along 1km transects across Atlantic barrier dunes (Koske 1987). A relatively low species richness of AMF has been found in true semi-arid to arid areas. However, Stutz and Morton (1996) showed that AMF species richness in arid ecosystems could be comparable to the richness found in most other plant communities if an adequate root soil sampling technique and several successive trap cultures were used to propagate the slow-growing and/or non-sporulating fungi. AMF diversity has been reported to decrease with the moisture gradient of a tall grass prairie (Anderson *et al.* 1984) and with temperature gradients in coastal sand dunes (Koske 1987). Some species, like *Glomus intraradices*, are reported to have a vast soil parameter range, while others, like *Acaulospora* species, are restricted to acidic soils in the tropics. Wang *et al.* (1997) showed that spores of *Glomus* species have different temperature and pH preferences for germination.

As AMF are below ground organisms, they spread slowly over short distances, using plants as "stepping stones". The distribution that we see today therefore can be said to rely on historical processes (Ricklefs and Schuluter 1993; Morton *et al.* 1995). Plants have better means of dispersal in time and space than AMF, as seeds and pollen are produced above ground and have co-evolved with the behaviour of above ground animals. However, proof of AM symbiosis in more than 90% of the endemic flora of the isolated Hawaii islands (Koske and Gemma 1990), suggests a historical long-distance co-dispersal of plants and AM fungi by oceanic waters, winds and birds (Koske *et al.* 1992; Gemma and Koske 1995).

When a plant establishes itself, the plant and the soil dwelling AMF community must co-adapt to develop a symbiosis (Allen *et al.* 1995). Allen *et al.* (1995) state that plants of arid and semi-arid regions are facultatively mycorrhizal in comparison to most tropical trees that are believed to be obligatory AM, and thus it seems less likely that the fungi control the plant's distribution in such areas. This statement is a bit contradictory,

as semi arid to arid environments have an extremely patchy distribution of vegetation, which may even differ from year to year, so the survival of AM fungi and the establishment of AM symbiosis may be locally obstructed. As vegetation in such areas is patchily distributed due to the spatial heterogeneity of nutrients being too easily volatilised, leached or too firmly bound, they theoretically would depend more on AMF for establishment than plants in rich or nutrient homogenous environments. Moreover, plants in disturbed areas of low fertility would benefit from a diverse AMF community, as there is then a larger chance of adaptation to environmental changes (Abbott and Gazey 1994). As an example, AMF that are scarce in undisturbed areas may increase after disturbance and mitigate disturbance effects (Jasper *et al.* 1989). In the subtropics, one such periodical disturbance is the shift from the rainy to dry season. Dodd *et al.* (1990) report that the number of AMF spores in tropical savannahs decreases during the dry season due to wilt of the vegetation, which prevents carbon allocation to AM fungi and hence hinders growth and sporulation. Additionally, soil surface temperatures above 60°C kill AMF spores (Thompson 1989) which decreases the infectivity potential in the surface layer.

Periodical inundation is another disturbance affecting the distribution of plant diversity. Until recently, inundation was thought to prevent AMF development, but Cooke and Lefor (1998) now report that young plants on developing shorelines were colonised by AM fungi, suggesting that this phenomenon is common in the development of vegetation associated with fluctuating water, nutrient and oxygen conditions.

Subtropical and tropical soils often have low amounts of available phosphorus, due to long-term exposure to optimal weathering conditions. The availability of phosphorus is also constrained by acidity (pH <6.5) and alkalinity (pH >7.5), which are both common features of tropical and subtropical soils. Less than 1% of the total soil phosphorus is available in the soil solution (Mullen 1998), serving as the central conversion point between the geochemical and biological pools in the overall phosphorus cycle. Phosphorus is an essential macronutrient to all living organisms, making up the backbone structure of DNA. Phosphorus assimilated by an organism will be recycled by other organisms during decomposition, either directly or indirectly. AM fungi are as effective in finding and delivering phosphorus from uniformly distributed fertilisers as from enriched patches in the soil (Cui and Caldwell 1996) if and when the AM symbiosis is established.

Agricultural management is another disturbance affecting the development and function of AM. Abiotically, tillage disrupts the hyphal network, which delays the AMF infectivity rate on plant roots in the coming season (Jasper *et al.* 1989). Biotically, inter-cropping of a legume with a cereal promotes AMF proliferation more than monocropping either of them (Harinikumar *et al.* 1990). The importance of soil parameters to AMF species diversity is not well known, but overall AMF production in the form of spore propagules may increase with soil pH, organic carbon (Johnson *et al.* 1991) and clay (Day 1987), and decrease with increasing amounts of soil phosphorus (Johnson *et al.* 1991). Superphosphate is reported to have a negative effect while rock phosphate enhances the AMF indigenous inoculum (Barea *et al.* 1980). Harinikumar and Bagyaraj (1989) showed that root colonisation and spore numbers increased during the season following treatment with farmyard manure and straw. Likewise, Douds *et al.* (1995) found a higher species richness in soils treated with farmyard manure compared to when inorganic fertilisers were used, but what process is causing the differences is not clear. Joner and Jakobsen (1995) report that the branching and growth of AMF hyphae was stimulated by the encounter of microsites rich in organic matter. An increased percentage of oxygen in the soil gas, due to aggregation stability and enhanced aeration, may be one factor (Smith and Read 1997). Alternatively, the transformation and decomposition rate of soil organic material, increasing the respiration of carbon dioxide, has

been proven to stimulate AMF (Bécard and Piché 1989).

**Objective of the study**

The objective of this study was to assess the diversity and relative abundance of AMF in representative traditional agriculture sites on the Niger inland delta of Mali. We also wanted to investigate if the AMF species present, and their relative abundance, were correlated with the status of soil phosphorus, pH, organic matter, plant diversity, plant density and any agricultural treatments, such as fallow or water regime. Additionally, the aim of the study was to discuss possible agricultural benefits of the AMF inoculum found at the different sites, and cautionary aspects when converting traditional agriculture to modern methods.

## Study area and methods

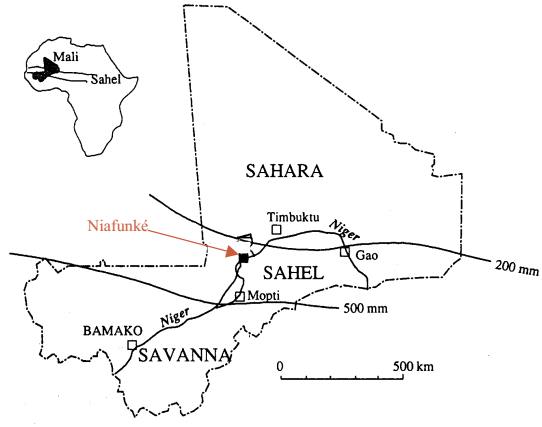
**Study area**

The study area was located in the Sahel belt of Mali in West Africa, where the Niger River forms an inland delta (Fig 1a, 1b). In total, 10 sites were sampled, all situated within a 25km radius from the village Niafunké (4 00'W, 15 59'N). The bushland of the Sahel, rich in woody herbs, grasses and scattered leguminous trees, is extensively used as grazing land for large herds of primarily cow. The annual inundation of the river creates temporary lakes and wetlands. African and asian rice (*Oryza glaberrima* Steud., *O. sativa* L.) are sown in depressions either before or after inundation. In the latter case, the rice nursery is established on the shore and rice is then transplanted up to three times, following the receding waterline. Close to the villages, millet (*Pennisetum glaucum* (L.) R.Br., syn. *P. typhoides*) and sorghum (*Sorghum bicolor* (L.) Moench.) are sown on the sand dunes after the heavy rains in July-August (200mm year$^{-1}$ in the area of Niafunké). After harvest, all fields are freely grazed and additional manure is rarely added. Crops are not rotated in time nor space, but intercrops are cultivated when seeds are available on the market. On the dunes, the wild water-melon (*Citrullus lanatus* (Thunb.) Matsumara & Nakai) is sown as an intercrop. In the inundated depressions, Bambara groundnut (*Vigna subterranea* (L.) Verdc.), potatoes (*Solanum tuberosum* L.) and gombou (*Abelmoschus esculentus*

Table 1: Plant and management data (For site codes, see Fig.1). Total species richness includes crops and native plants. Total average distance is an estimate of plant density/plant cover, also given as an estimated number of individuals per site. The crop and water regimes in brackets indicate what treatment was used before the fallow started in 1973 for iLN and 1993 for iG1-3r

| Site | Tot species richness Nov. -98 | Tot average distance (m) Nov. -98 | Total no. individuals (50x50m) | Major crop (per year) | Crop distance (m) | Water regime (per year) |
|---|---|---|---|---|---|---|
| *I*LR | 1 | 0.2 | 62500 | rice | 0.2 | inundation |
| *I*LS | 4 | 0.9 | 3075 | sorghum | 1.0 | inundation |
| *I*LM | 8 | 0.7 | 5100 | millet | 1.0 | inundation |
| *i*LN | 13 | 0.5 | 10000 | natural veg. | – | (inundation -73) |
| *i*G1r | 5 | 5 | 100 | fallow (rice) | (0.2) | (inundation - 93) |
| *i*G2r | 0 | 50 | 1 | fallow (rice) | (0.2) | (inundation - 93) |
| *i*G3r | 9 | 10 | 25 | fallow (rice) | (0.2) | (inundation - 93) |
| *A*MN | 3 | 40 | 1.5 | natural veg. | – | arid |
| *A*MM | 22 | 0.7 | 5100 | millet | 1.0 | arid |
| *A*NM | 21 | 0.7 | 5125 | millet | 1.0 | arid |

**a)**




**b)**

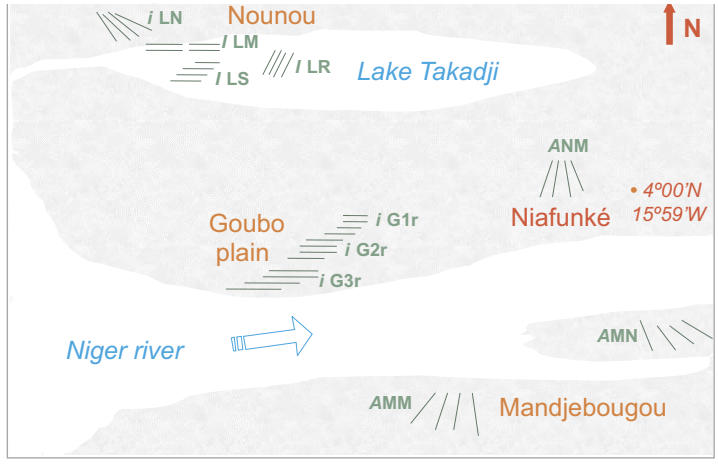



Figure 1: **a)** Mali in West Africa. **b)** Study area in the semi-arid Niger inland delta (4°00'W, 15°59'N). Bars represent transects (n = 4/site). Site codes: 1st letter signifies the water conditions being either I = inundated yearly since historical time, i= historically inundated but now arid (iLN since -73, iG1-3r since -93), and A = historically arid; 2nd letter signifies area or village being either L = Lake Takadji, G = Goubo (field no. 1, 2 and 3), N = Niafunké and M = Mandjebougou; and 3rd letter signifies the vegetation type being either R = rice, r = fallow from rice, S = sorghum, M = millet or N = natural vegetation.

(L.) Moench.) are often sown as intercrops. Perennial intercrops such as cassava (*Manihot esculenta* Crantz), laurel (*Laurus nobilis* L.), henne (*Indigofera tinctoria* L.) and mango (*Mangifera indica* L.) are sometimes planted along the upper rim of the inundated depressions. The native annuals and perennials on the dunes are cut back at time of crop establishent, but are never totally removed. Some are collected as fodder, medicine or wood for charcoal production, or left detached on the ground as wind erosion traps. Sometimes, especially on the dunes, pit traps for wind deposition are dug. So far, tillage has never been used in the traditionally cultivated study area. In one site, a fungicide (*Sijolan* in French) was mixed with millet seeds before sowing to prevent mildew and black soot.

In co-operation with the staff of the

Table 2. Soil properties at 10 traditional agricultural sites (n=4) in the semi arid Niger inland delta, Mali, West Africa. The value given is the average ± 1 standard deviation, counted on 2:1 top:subsoil. (For site codes, see Fig.1). Extractable P was assessed using NaCO3. * Preliminary assessment based on 1 transect sample/site.

| Site | Depth (cm) | pH (2:1 aq.dest) | SOM (%) | Extract. P (mg/kg soil) | Total P* (mg/kg soil) | Ex. P: Tot. P (%) | Soil type* (% fraction) |
|---|---|---|---|---|---|---|---|
| *I*LR | 0–40 | 5.8 ± 0.1 | 7.6 ± 1.2 | 6.0 ± 1.1 | 27.0 | 22.2 | Sand |
| *I*LS | 0–40 | 6.0 ± 0.3 | 10.6 ± 0.5 | 11.8 ± 2.7 | 27.7 | 42.7 | Clay |
| *I*LM | 0–45 | 7.0 ± 0.1 | 2.6 ± 0.3 | 3.4 ± 1.4 | 9.50 | 35.5 | Sandy loam |
| *I*LN | 0–45 | 6.2 ± 0.1 | 8.6 ± 0.5 | 6.4 ± 1.0 | 25.4 | 25.11 | Clay |
| *i*G1r | 0–25 | 5.4 ± 0.2 | 6.8 ± 0.4 | 5.4 ± 2.2 | 43.5 | 12.5 | Clay |
| *i*G2r | 0–25 | 5.9 ± 0.1 | 6.7 ± 0.3 | 1.4 ± 0.7 | 34.8 | 4.0 | Clay |
| *i*G3r | 0–25 | 5.8 ± 0.4 | 6.8 ± 0.2 | 3.3 ± 2.6 | 43.8 | 7.5 | Clay |
| *A*MN | 0–25 | 5.5 ± 0.4 | 7.3 ± 0.2 | 5.8 ± 3.8 | 23.8 | 24.3 | Clay |
| *A*MM | 0–30 | 8.0 ± 0.2 | 1.1 ± 0.3 | 28.7 ± 9.3 | 62.3 | 46.1 | Sandy clay |
| *A*NM | 0–45 | 7.0 ± 0.1 | 0.7 ± 0.1 | 2.5 ± 1.2 | 5.3 | 46.7 | Sand |

multidisciplinary development project of the lake district of Niafunké (PDZL-II) and a parallel swedish minor field study-project (MFS) of soil properties (Friberg *et al* 2000), four agriculturally representative villages were chosen (Fig. 1b). The field sampling was carried out in November and December 1998, in the dry season (18 to 30°C), just before the inundation of the Niger River. Site locations and site codes are given in Fig. 1b.

Site information on crop and management regimes is presented in Table 1. Soil properties assessed in the MFS-project, using the same sampling regime and time, as here, are presented in Table 2. For transect data see Appendix 1.

**Soil sampling**

To cover the spatial heterogeneity of each 2500 $m^2$ site, soil was sampled along four transects (a, b, c, d), each with a length of 40 meters and situated 10 meters apart (Fig. 1b), giving four pooled soil samples per site. Each pooled sample was produced by collecting soil with a traditional hoe from dug pits along a transect in one bucket, and then mixing the soil was cautiously before subsampling ca 200g of soil for physical and chemical analyses. This procedure was done twice per transect, giving one top soil sample collected from 20 dug pits and one sub soil sample collected from 10 deepened pits. The depth of pits at each site differed, due to variation in root depth between sites, and varied between 25 and 45cm. The soil content of the top soil and sub soil buckets were mixed after subsampling, giving a mixed AMF transect sample of 2:1 (top soil: sub soil) of 400g of soil to use as a pot culture inoculum. Additionally, roots (assumed to contain more AMF propagules than bulk soil) were gathered from each transect to counteract a possible low AMF inoculum potential when setting up the pot culture. All samples were air dried in the shade for one week before transport.

**Soil analyses**

The physical and chemical soil properties were assessed in a separate MFS project. For further details, see Friberg *et al* 2000. A brief description of the methods is given here: Soil pH was analysed in air dried, 2mm sieved soil after 24 hrs in 2:1 water and two repeated 30 minute shakes. The amount of extractable phosphorus (P) in the soil was measured using the P-Olsen Method (Olsen *et al.* 1954). Following Olsen and Sommers (1987), the total amount of soil P was

assessed on one topsoil subsample and one subsoil subsample from each site, as a preliminary screening. The percentage of soil organic material (SOM) in the 2mm sieved soil was indirectly measured by comparing the dry weight after 6 hrs at 105°C with the dry weight after 4 hrs at 550°C (the standard Loss on Ignition Method). Some water adsorbed to clay may be included in the results for SOM. A rough estimate of the soil types was based on a top soil subsample from each site, where dispargation, sedimentation and hydrometry were used to achieve soil particle fractionating (Gee and Bauder 1986) and the international soil textural triangle.

**Plant taxonomy and plant density**

Data on vernacular names, crop history, agricultural treatments, vegetation periods, crop distances etc were collected during field walks and interviews with farmers. Voucher specimens of native plants occurring within the 2500m$^2$-site (50´50 m) were collected. After identification, the herbaria sheets were deposited at the Uppsala Herbaria (UPS) in Sweden for storage. The plant species diversity was investigated according to taxonomic literature of Western and Northern Africa (Maire 1957; Hutchinson 1958; Hubbar and Milne-Redhead 1959; Berhaut 1967; Bondet *et al.* 1986; El Amin 1990; Maydell 1992; Hedberg and Edwards 1995), as there is no flora of Mali at present. As the chosen time of sampling was in the dry season, after harvest and grazing, no specimens of cultivars could be collected at any of the sites. Despite the grazing, most native plants were still identifiable. Plant sampling was carried out two weeks after soil sampling, which is why no native specimens could be collected from the sites at Lake Takadji (*I*LR, *I*LS and *I*LM ), as they had been competely inundated in the meantime.

Overall plant density per site was roughly estimated as the average distance (m) between plants, based on observations of the amount of native plants and the distance between crops made during fieldwork.

**AMF pot culture**

A pot culture, with each pot representing a single transect, was set up at the Swedish University of Agricultural Sciences (SLU), Department of Microbiology, Uppsala. There are several reasons for setting up a pot culture. Firstly, we wanted to dilute the parasitic pressure on the AMF propagules in the soil. Secondly, our aim was to induce AMF sporulation in all samples at the same time, in order to get spores of similar developmental stages. Thirdly, by maximizing the availability of roots for AMF colonization, and by optimizing the conditions for nutrient, water, light and temperature, we intended to promote AMF sporulation. The "trap culture" was set up according to the recommendations of Morton *et al.* (1993), based on the experiences at INVAM (International collection for Arbuscular and Vesicular-arbuscular Mycorrhizal fungi), West Virginia, USA. The recommended host genera is sorghum, due to the fact that 1000 AMF isolates, of 98 species in all six genera, have been able to grow and sporulate in pots with *Sorghum sudanense* (Piper) Stapf at INVAM (Morton 1993).

A subsample of 200g from each transect soil inoculum (see Soil sampling) was diluted with 800g autoclaved medium sized sand and mixed before being poured into a one liter pot. Sand was chosen as a diluting substrate, as it is inert and does not affect inoculum pH, which was confirmed by a trial. After 24 hrs of incubation with water, a local sorghum variety from Northern Mali (group durra membranaceum, CIRAD, Bamako, Mali) was sown as a host plant, at a density of 25 plants pot$^{-1}$. Each pot was then covered with coarse, autoclaved sand to prevent unintentional dispersal of AMF. The 10x4 pots were randomly placed in a climate chamber, where subtropical conditions were imitated as follows: 75% humidity, 12 hrs of 24°C and 480 mmol m$^{-2}$s$^{-2}$ light intensity and 12 hrs of 18°C in darkness. After seedling emergence, the pots were watered daily with deionized water to keep 60% of the Water Holding Capacity (WHC). Every second week, the pots were given diluted UWA nutrient solution poor in phosphate according to Hill *et al.* (1979). The total

amount of minerals given in successive doses were: 74.0 N, 58.5 K, 6.2 Ca, 4.8 Mg, 14.5 P, 32.9 S, 10.9 Cl, 3.7 Mn, 1.3 Zn, 0.53 Cu, 0.08 Mo, 0.13 Na (in kg $ha^{-1}$).

The pot culture was run for 4.5 months. During the last week, the moisture regime was successively lowered to 30% of WHC to stop the growth of plants and to enhance sporulation of the existing AMF species.

**AMF root colonisation**

To assess the success of the AMF inoculum in the pot cultures, we determined root colonisation one month after sowing. From each pot, three core borer samples (Æ1.5cm, 7cm deep) were collected. The roots were rinsed, cut, mixed, cleared and stained for fungal structure (Kormanik and McGraw 1982) and placed in a petri dish. The hairline intersect counting method (Newman 1966) was used on 15 random spots per petri dish, covering 0.15m of 1m roots per sample. As we considered that the root colonisation percentage was too low, we added a small amount (0.1g) of dried, cut root pieces from the vegetation of the associated transects in Mali. Suspended in water, the roots were added to each pot two months after sowing.

After harvest and taxonomic sampling, we determined the AMF root colonisation again in each pot by sampling a section on each side of where the AMF taxonomy section had been sampled 5.5 months from sowing. The WHC had been kept at 10% and the pots stored at room temperature over the month after harvest. We used the same clearing and staining method as above, but did the counting according to Giovanetti and Mosse (1980) and Kormanik and McGraw (1982), using a gridline intersect method where 0.85m of 1m root sample was covered.

**AMF taxonomy**

At 4.5 months from sowing, a section (1/4) of the trap culture was cut out, chopped and mixed. A subsample of 50ml was taken for AMF spore extraction by centrifugation in sucrose gradients (Daniels and Skipper 1982). Diluted with water, we counted intact spores on 30 random fields of view per petri dish by microscopy to obtain the relative abundance per species and the total spore numbers $g^{-1}$ freshweight soil. The spore morphotypes were separated and transferred to object glasses and identified by investigating the range of, and mean, spore and saccule sizes, colours and distances between spore and saccule. To further examine the organisation and histochemistry of spore subcellular structure, we mounted slides with 2´30 spores to PVLG media and Melziers' reagent, according to Schenck and Pérez (1990). INVAM isolates and voucher specimens were used as taxonomic references.

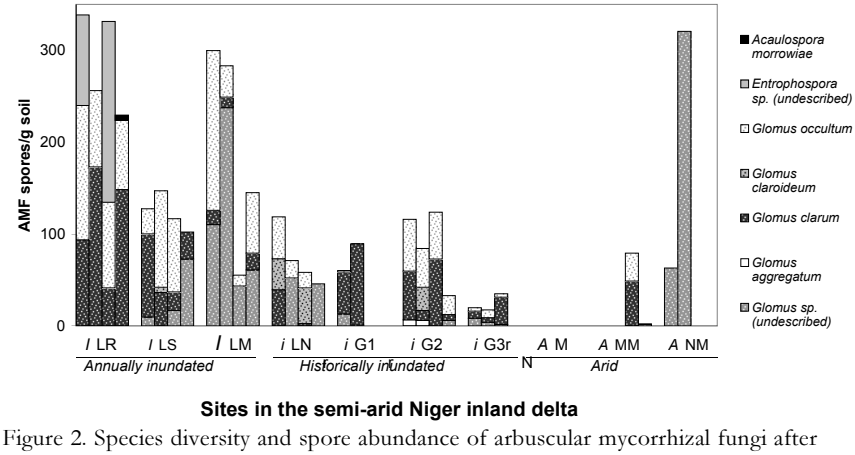



Figure 2. Species diversity and spore abundance of arbuscular mycorrhizal fungi after 4.5 months of trap culture. Each pot represents a transect. The sites are arranged according to water regime. (For site codes see Fig.1b)

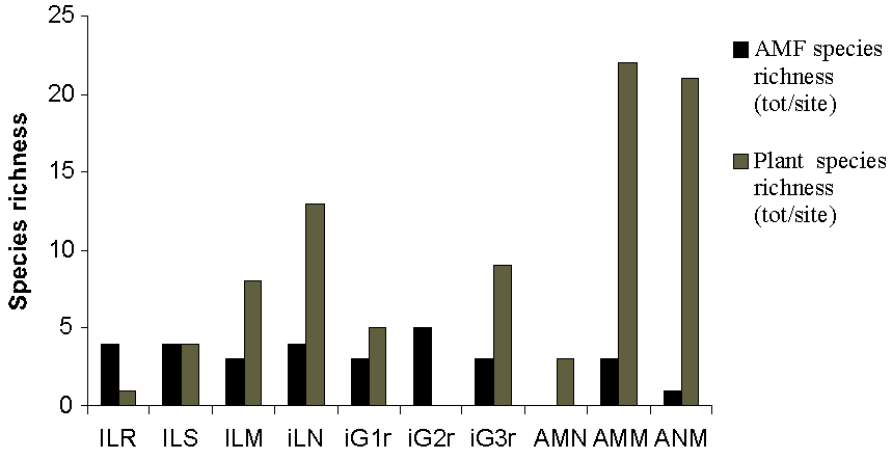



Figure 3. Species richness comparison. Site codes see Fig. 1b.

**Statistical analyses**

Means and standard deviations (StDev) were produced in Microsoft Excel (Windows 97). Correlation within and between the soil parameters and the AMF data were initially determined by performing linear regressions in Microsoft Excel (Windows 97). A single ANOVA analysis was simultaneously carried out to prove the validity of the regression.

A multivariate principal component analysis (PCA) was performed according to Wold *et al.* (1987) in the Unscrambler – program (Camo AS 1996) for all quantitative data (See Appendix 1). The first component, *X-axis,* explains the greatest part of the total variation in the data set and consequently directs the grouping of samples from left to right in the graph. The second component, *Y-axis,* explains the grouping of samples from bottom up in the graph. It is calculated differently from component one, using residual variation instead of the least square fit, to describe the second most influential direction of maximum variation in the data set. The variables furthest away from the origin are the most influential, meaning that they are either parallel (cos 0 = 1) or oppositely angled (cos

Table 4: Data on arbuscular mycorrhizal fungi (AMF) after 4.5 months of trap culture with Sorgum bicolordurra membranaceum in soil from the Niger inland delta in the Sahel belt of Mali, West Africa. (For site code, see Fig. 1).

| Site | % Root colonisation (1 month) | % Root colonisation (4.5 months) | No. Spores per g fw soil (4.5 months) | Species richness (4.5 months) |
|---|---|---|---|---|
| *I*LR | 5.9 ± 7.2 | 73.0 ± 4.4 | 169.9 ± 31.9 | 2.8 ± 0.5 |
| *I*LS | 5.3 ± 4.6 | 46.2 ± 11.1 | 72.4 ± 11.2 | 2.8 ± 0.5 |
| *I*LM | 3.8 ± 3.5 | 55.0 ± 5.9 | 115.0 ± 68.4 | 2.8 ± 0.5 |
| *i*LN | 7.4 ± 7.9 | 32.8 ± 12.1 | 43.1 ± 18.9 | 2.3 ± 1.0 |
| *i*G1r | 1.9 ± 1.0 | 1.1 ± 0.4 | 0 | 0 |
| *i*G2r | 1.2 ± 1.0 | 1.1 ± 1.9 | 12.0 ± 23.1 | 1.0 ± 1.2 |
| *i*G3r | 0.4 ± 0.6 | 3.2 ± 1.3 | 22.0 ± 26.4 | 1.3 ± 1.5 |
| *A*MN | 1.0 ± 0.7 | 24.7 ± 26.4 | 51.1 ± 22.8 | 3.0 ± 0.8 |
| *A*MM | 0.6 ± 0.8 | 11.4 ± 22.8 | 10.5 ± 8.4 | 2.3 ± 1.5 |
| *A*NM | 2.5 ± 1.4 | 14.0 ± 8.4 | 56.4 ± 89.8 | 0.5 ± 0.6 |

Table 3. Plant diversity. (For site codes, see Fig.1). Authors are given after family and species name. Abbreviations: * voucher specimens deposited at the Uppsala Herbaria (UPS) in Sweden; AM = reported in literature to develop arbuscular mycorrhiza; (F) vernacular name in French; (S) Souraï; MC = major crop; IC = inter crop; X = Native plant; F= >5 individuals/site; mc, ic, x, xf = as above, but not present in 1998, although frequent in the years before.

| PLANT FAMILY | Plant species and authority | *I*LR | *I*LS | *I*LM | *i*LN | *i*G1r | *i*G2r | *i*G3r | *A*MN | *A*MM | *A*NM |
|---|---|---|---|---|---|---|---|---|---|---|---|
| AIZOACEAE | *Glinus lotoides* L. * | | X | | X | | | X | | | |
| | *Zaleya pentandra* (L.) Jeffrey * | | | | | | | | | X | |
| AMARANTACEAE | *Aerva Sp.* * | | | | | | | | | | X |
| | *A. javanica* (Burm. f.) Juss ex Schultez * | | | | X | | | | | | |
| | *Alternantera sessilis* (L.) R. Br. ex Roth * | | | | XF | | | X | | | |
| | *Amaranthus graecizans* L. * | | | | | | | | | X | |
| ANACARDIACEAE | *Mangifera indica* L. | | | IC | | | | | | | |
| ASCLEPIADACEAE | *Leptadenia hastata* (Pers.) Decne. * | | | | X | | | | | X | X |
| | *L. pyrotechnica* (Forsk.) Decne. * | | | | X | | | | | X | X |
| | *Pergularia daemia* (Forssk.) Chiov. * | | | | X | | | | | | |
| BALANITACEAE | *Balanites aegyptiaca* (L.) Del. * | | | | | | | | | X | X |
| BORAGINACEAE | *Heliotropium baclei* Johnston * | | X | | | | | | | X | |
| | *H. subulatum* (Hochst. ex A. DC.) Vatke * | | | | | | | | | | X |
| CAPPARIDACEAE | *Boscia angustifolia* A. Rich. * | | | | | | | | | | X |
| | *B. salicifolia* Oliv. * | | | | | | | | | | X |
| | *Maerua crassifolia* Forssk. * | | | | | | | | | X | X |
| CELASTERACEAE | *Maytenus senegalensis* (Lam.) Exell * | | | | | | | | | X | |
| COMPOSITAE | *Pulicaria undulata* L.* | | | | X | | | | | | |
| | *Sp.** | | | | | | | | | | X |
| CONVOLVULACEAE | *Sp.** | | | | | | | X | | | |
| CUCURBIATACEAE | *Citrullus lanatus* (Thunb.) Matsumara & Nakai * | | | | | | | | | | XF |
| | *Cucumis Sp.* L. * AM | | | | XF | | | | | | |
| | *Sp.** | | | | | | | X | | | |
| CYPERACEAE | *Cyperus rotundus* L. ("*eu-rotundus*" Maire & Weiller) * AM | | | | X | | | XF | | | |
| | *Sp.** | | | | X | | | | | X | X |
| ELATINACEAE | *Bergia suffruticosa* (Del.) Fenzl. * | | X | | XF | | | XF | X | XF | |
| EUPHORBIACEAE | *Euphorbia thymifolia* L. * | | | | | | | | | X | X |
| | *Manihot esculenta* Crantz AM | | | IC | | | | | | | |

Table 3. continued

| PLANT FAMILY | Plant species and authority | *I*LR | *I*LS | *I*LM | *i*LN | *i*G1r | *i*G2r | *i*G3r | *A*MN | *A*MM | *A*NM |
|---|---|---|---|---|---|---|---|---|---|---|---|
| GRAMINEAE | *Cenchrus biflorus* Roxb. * [AM] | | | | X | | | | X | XF | XF |
| | *Chloris lampropriata* Stapf * | | | | X | | | | | | |
| | *Echinocloa stagnina ?* "Le Bourgou" (F) | | | | | xf | xf | xf | | | |
| | *Eragrostis tremula* Hochst. ex Steud. * | | | | | | | | | X | X |
| | *Hyparrhenia rufa* (Nees) Stapf * | | | | | | | | | | X |
| | *Oryza glaberrima* Steud. * | xf | | | | xf | xf | xf | X | XF | |
| | *O. sativa* L. [AM] cult. Chinois, Maître D'Oro (F) | MC | | | | mc | mc | mc | | | |
| | *Pennisetum glaucum* (L.) R.Br. [AM] cult. Haini (S) | | | MC | | | | | | MC | MC |
| | *Sorghum bicolor* (L.) Moench. [AM] cult. Saba, Sotta, Hambo (S) | | MC | | | | | | | | |
| | *Tragus berteronianus* Schult. * | | | | | | | | | XF | |
| LEGUMINOSAE | *Acacia albida* Del. * [AM] (Syn. *Faidherbia albida*) | | | | | | | | | X | |
| | *A. ehrenbergiana* Hayne * | | | | | | | | | | X |
| | *A. raddiana* Savi (syn. *A. tortilis* Hayne) * | | | | | | | | | | X |
| | *Aeschynomenae sp.* * | | | | | XF | | | | | |
| | *A. tambacoundensis* Berh. * | | | | | | | XF | | | |
| | *Alycicarpus zeyheri* Harv. * | | | | | | | | | X | X |
| | *Indigofera tinctoria* L. | | | IC | | | | | | | |
| | *I. senegalensis* Lam. * | | | | | X | | | | | |
| | *Prosopis juliflora* (Sw.) DC. * [AM] | | | | | | | | | | X |
| | *Vigna subterranae* (L.) Verdc. | | | IC | | | | | | | |
| LAURACEAE | *Laurus nobilis* L. | | | IC | | | | | | | |
| MALVACEAE | *Abutilon pannosum* (Forstf.) Schlechtend. * | | | | | | | | | X | |
| MALVACEAE ? | "L'Oseil rouge" (F) | | | IC | | | | | | | |
| PALMAE | *Hyphaene thebaica* Mart. * | | | | | | | | | X | |
| POLYGALACEAE | *Polygala crisptera* DC. * | | | | | | | | | | X |
| SOLANACEAE | *Solanum tuberosum* L. * [AM] | | | IC | | | | | | | |
| RHAMNACEAE | *Zizyphus mauritiana* Lam. * | | | | | | | | | X | |
| TILIACEAE | *Corchorus fascicularis* Lam. * | | | | | XF | | | | | |
| ULMACEAE | *Celtis integrifolia* Lam. * | | | | | | | | | X | |
| ? | "L'Aimé du lapin" (F) | | | X | | | | | | | |
| Total number of plant species per site: | | 2 | 4 | 8 | 13 | 6 | 2 | 10 | 3 | 22 | 21 |
| Total number of plant families per site: | | 1 | 4 | 8 | 8 | 4 | 2 | 9 | 2 | 15 | 11 |

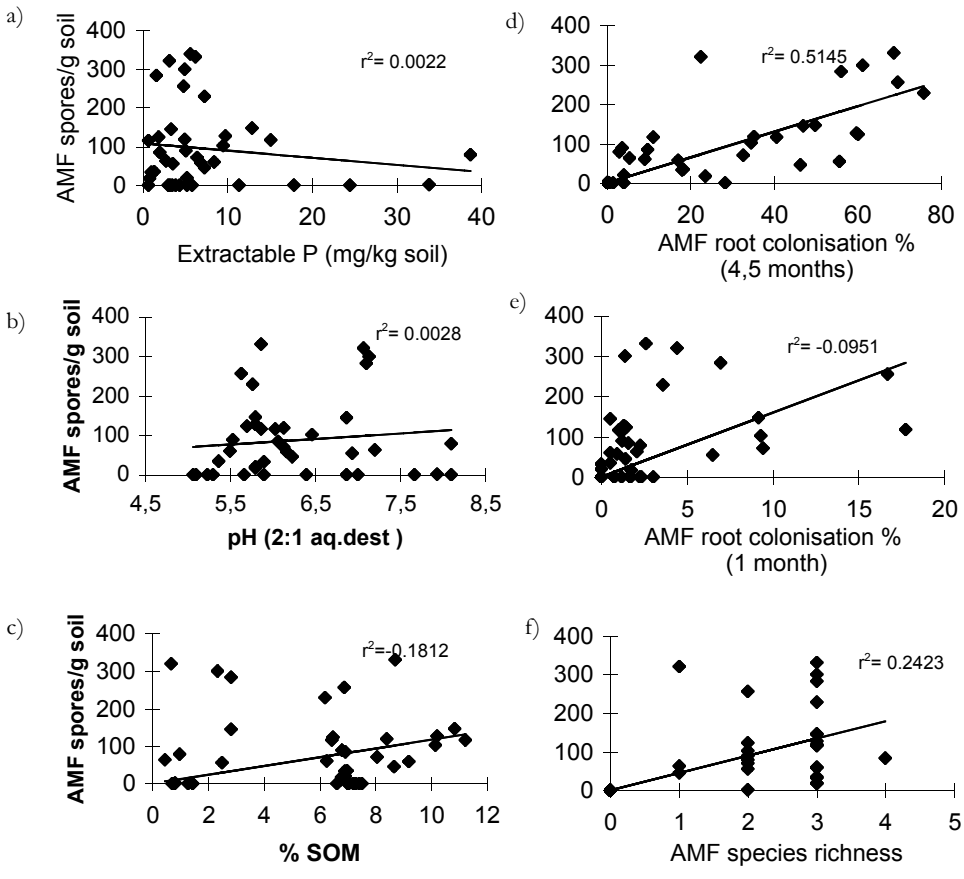



Figure4: Regression analyses: a, b, c) Correlations of AMF and soil parameters. The clustering of data may be more important than the correlation. d, e, f) Correlations of AMF parameters. The r-square value obtained is given in each figure

180 = -1) to the components. When site samples are grouped around a variable, it means they score high values of it.

A mathematical transformation of variables was performed when necessary to achieve a normal distribution as a base for linear statistics, in order to give them all the same possibility to influence the multivariate model (Ö(*AMF spore numbers g-1 soil*), Ö(*% AMF root colonisation 4.5 months*); $\log_{10}$ (*plant distance, m*)). We did not include the variables *Extractable P* and *% AMF root colonisation at 1 month* in the model, as they both had a very low influence (appearing close to the origin) and only disturbed the relationship between the other parameters. As the data used were of different units, types and ranges, a standardisation (each transect-data subtracted by the site mean and divided by the site standard deviation) was performed on transformed data to give all variables the same chance to influence the estimation of the components (Camo AS 1996).

## Results

### AMF data

After 4.5 months of trap culture, AMF root colonisation and sporulation was found in nine of 10 sites, with species richness ranging in total

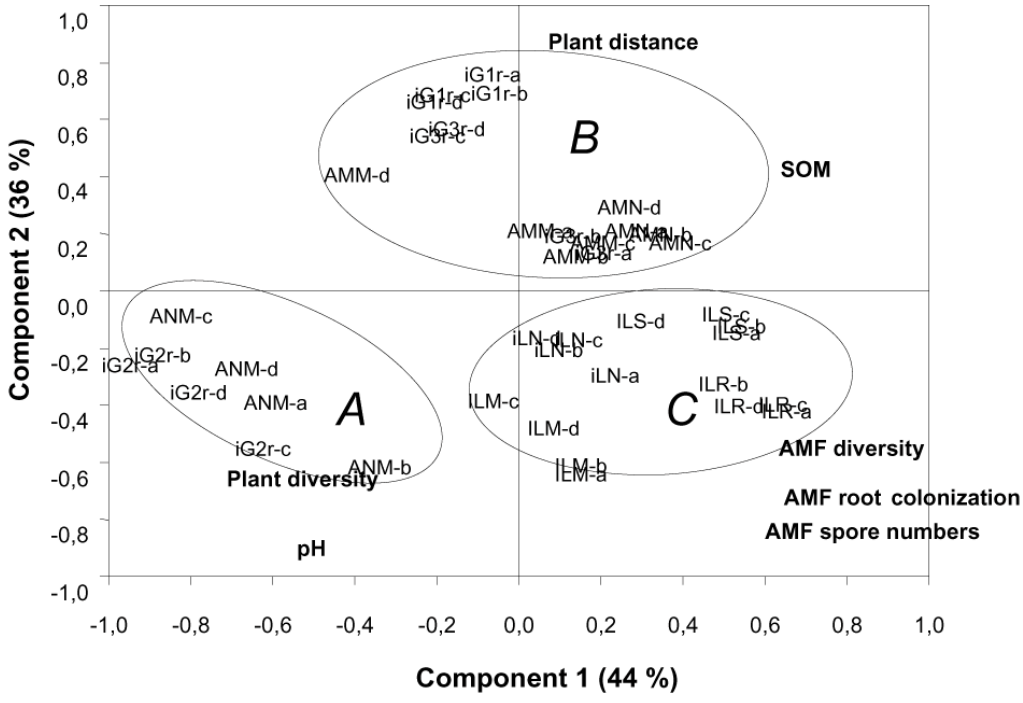



Figure 5. Principal component analysis(PCA) of AMF-, soil-, and plant-data from 10 (n=4) sites in traditional agriculture in the semi-arid Niger inland delta of Mali, West-Africa. (Site codes see Fig. 1; Raw data see Appendix 1). The grouping of data by PCA is interpreted by the authors in the following way with circles representing: A) historically arid sites; B) uncovered historically arid or flooded sites; and C) covered historically flooded sites now arid (iLN) or still yearly flooded.

from 1 to 5 in those sites. The species richness varied within the site. When comparing the transects, the site species richness ranged from 0.5±0.6 to 2.3±1.5 and 2.8±0.5. (Table 3 ). AMF root colonisation per site obtained after one month ranged from 0.4 to 7.4% whereas 1.1 to 73.0% of roots where colonised at the final harvest (4.5 months) (Table 3). The total numbers of AMF spores produced by the site inoculum varied between 17.9±14.3 and 288.9±54.4 $g^{-1}$ soil (Table 3). For parameter results per transect, see Appendix 1.

In total, the trap culture revealed seven species of AM fungi (see Fig. 2). Five of them belonged to the Glomus genera in Glomaceae and the other two belonged to different genera in the Acaulosporaceae family. The species were *Glomus aggregatum* (Schenk and Smith), *Glomus claroideum* (Schenck and Smith), *Glomus clarum* (Nicolson and Schenck) (synonymous with *Glomus manihotis* according to Morton and Bentivenga, unpublished), *Glomus occultum* (Walker), an undescribed *Glomus* species, *Acaulospora morrowiae* (Spain and Schenck) and an undescribed *Entrophospora* species. The distribution of species communities within sites and the relative abundance of spore numbers are shown in Fig. 2. The most frequent species were *Glomus occultum*, *Glomus clarum* and the undescribed *Glomus* species, occurring in 80% of the sites. Less frequent were *Glomus claroideum* (30%), followed by *Glomus aggregatum*, *Acaulospora morrowiae* and the *Entrophospora* species, found in 10% of the sites. The glomacean family dominated, found in 90% of the assessed area.

At INVAM, monospecific cultures of the following species and sites were set up for live voucher collection and multiplication: *Glomus*

*clarum* from site *I*LR and *A*MM; *Glomus occultum* from *I*LR; *Glomus claroideum* from *i*LN; the undescribed *Glomus* species from *A*MM and the undescribed *Entrophospora* species from *I*LR. A minimum of 125 spores is needed, so not all species could be accessed on this occasion.

**AMF response to plant and soil parameters**

The relationship between plant species richness (found in Nov-98) and AMF species richness is shown in Fig. 3 and shows no correlation. The scientific names of the plants found per site are presented in Table 4). Plant species richness was up to seven times higher in the arid sites compared to the inundated sites (Fig 3 and Table 4). One exception to this was the completely open *A*MN, situated in the middle of an island in the Niger river. This sampled site had only five plant individuals per 2500m$^2$ (Table 1). The site most diverse in terms of AMF species was one of the uncovered, formerly inundated sites in fallow after rice cultivation (iG2r), closely followed by annually inundated sites of low plant species richness (*I*LR, *I*LS, *I*LM ), and the formerly inundated site now rich in natural vegetation species (*i*LN) as well as one of the arid sites of high plant species richness (*A*MM) (Fig 2 and 3). It should be remebered that plant species richness and plant density does not correlate (Table 1).

By using regression analysis, it was found that there was no correlation's between the investigated soil parameters and AMF (Fig. 4 a,b,c). The only linear correlation found was between AMF spore numbers and AMF root colonisation percentage after harvest ($r^2 = 0.6$) when comparing the whole data set (N=40) (Fig 4 d,e,f). But when considering the clustering of data, another picture appears: AMF spore numbers >100g$^{-1}$ were only found at 1.4 to 7.3 mg P kg$^{-1}$ soil (Fig 4 a), and at soil pH of 5.6 to 7.1 (Fig. 4 b), but within a wide range of SOM (0.6 to 8.7%) (Fig. 4 c). Final AMF root colonisation of >50% was only found at low to moderate P-levels (1.6 to 12.9 P mg kg$^{-1}$), at soil pH of 5.6 to 7.1, and at a wide range of SOM (2.5 to 10.2%) (See Appendix 1).

The multivariate analysis of soil, plant and AMF variables for the different sites is shown in Fig. 5 Together, the components explain 80% of the grouping of data. The principal component analysis enabled separation of inundated, arid and bare fallow sites. The variable "plant species richness", "pH", soil organic matter and all the AMF parameters all exerted a high influence on component one. "Plant distance", measured in meters (m) was the only variable with influence on component two. There were two outlier transects in the data set, meaning that they have a high influence. One was *A*NM-b, which was from an arid site, but had extreme sporulation numbers by one single, dominating species (the undescribed *Glomus* species). The other outlier transect, *i*G2r-b, was from a site with no plant cover, but delivered the highest AMF species richness found in any sample (four species).

## Discussion

**AMF response to sampling and trap culture**

Data of soil biota often differ as much within a site as between sites (Stenberg 1999), which is why the aims of the study must direct the sampling procedures. If the aim is to assess the field level diversity, a transect-sampling technique, like the one used in this study, would be accurate, preferably complemented by a split of the pooled transect samples into sub replicates. All 10 sites were sampled metrically, despite differences in plant cover, which may have diluted the AMF inoculum in sparsely vegetated sites, but gives an estimate of the average field level diversity. The addition of roots after two months of culturing may have been an important counteraction to overcome the differences in inoculum propagule density. The aim of the trap culture was not to mimic the actual conditions of the sites, but to optimise the conditions for AMF propagules in general. The relatively high numbers of colonisation, sporulation and species richness, achieved after 4.5 months, proved that the pot culture method was successful in culturing many, if not all, dwelling AMF fungi. No control pots were used, but contamination seems to have been avoided, as there was no sporulation found in

11 of the randomly placed 40 pots. The variation and inconsistency in the arid to semi-arid sites confirms the need for successive pot culture cycles (e.g. several periods of water treatments to respond and channel the allocated carbon into hyphal growth, colonisation and sporulation) as suggested by Stutz and Morton (1996).

**AMF response to inundation**

The annually inundated sites on the Niger inland delta of Sahel (*I*LR, *I*LS, and *I*LM*)* had the highest and most consistent scores of AMF root colonisation, AMF spore numbers, and AMF species richness (Table 3, Fig. 2). Additionally, the number of spores produced per g soil in the study area were up to 10 times higher than in reports from semi-arid to arid areas (see Stutz and Morton 1996, Jakobsen 1997). However, in contradiction, Hayman (1982) reported that the infectivity of AMF propagules decreases in wet and anoxic soils. Another common feature of inundated soils is high organic material content, attracting a wide array of soil organisms and enhancing the parasitic pressure on AMF spores (Smith and Read 1997). The longer the soil is submerged under water, the more AMF viability is decreased (Ilag *et al.* 1987). Consequently, rice has been considered an unsuitable pre-crop when managing AMF in rotation systems (Brandon and Mikkelsen 1979, Thompson 1991). All these reports contradict our results.

Recently though, it has been confirmed that AMF are present, and even are beneficial to plants, in waterlogged ecosystems. For example, Solaiman and Hirata (1996) report that AMF innoculated paddy rice plants have higher grain yield, P level and micronutrient content (Zn, Cu, Fe, and Mn) than non-mycorrhizal plants throughout all growth stages. According to Solaiman and Hirata (1996), soil fertility dictates at which life stage AMF colonisation of rice roots is most successful. The less fertile the soil, the earlier a successful root colonisation was established by inoculated AM fungi in transplanted rice. In a more fertile soil, AMF root colonisation rate had an extended lag phase. The same authors reported in 1995 that to benefit most from an AM symbiosis, rice should be innoculated as early as possible in the nursery, because their observations were similar to those of Ilag *et al.* (1987), that AMF root colonisation rate decreases with increased time of paddy conditions. It is not clear though if a decrease in root colonisation rate is only due to rapid growth of plant roots, or if AM fungi simply stop growing at a certain point in paddy conditions and allocate carbon to sporulation? Rice has roots similar to several cyperaceae species, producing an air filled tube cover where AM fungi have been found to thrive. Such roots were dense in *I*LR, where the highest scores of all AMF parameters were obtained, despite the long inundation time (four months) compared to the other less inundated sites. What is important to consider is the cropping system used in Lake Takadji, called *riz de decrue*, meaning that rice plants are transplanted successionally (up to three times) before being established at the site after inundated water has receded (through infiltration and evaporation). Probably, each rice plant has been colonised both in the nursery site and in the transplanted site by AM fungi. That may be one reason why the soil of *I*LR had such a diverse and fast growing AMF population, responding very well to the trap culture technique used Why would periodic waterlogging increase the AMF diversity and inoculum potential? If deteriorated every season, the transplanting of rice, and possible dispersal by water and wind, may add a considerable amount of AMF propagules to the inundated soils from the surroundings. Water has been suggested as an important medium for the dispersal of AMF propagules (and other soil micro-organisms) to soils (Koske *et al.* 1992). Dispersal by water may cover distant areas, but is probably also important within and between sites. In Lake Takadji, the water rises from, and recedes back to, a Niger River inlet, crossing the bottom of a depression where rice is cultivated and where the highest consistent AMF data was obtained. Smaller and larger depressions, like the ones in Sahel, are filled with surface run-off during the rainy season. This surface run-off contains nutrients, clay and possibly AMF propagules

from surrounding dunes. Likewise, suspended material eroded by wind may be deposited on the slopes of the depressions when dry, and on the water surface during inundation. Wind-eroded material may contain AMF propagules from the surrounding landscape. Efficient dispersal of AM fungi is also achieved by freely moving large herds of animals and by humans working on the fields. But why was the AMF inoculum from the inundated sites of our study higher in comparison to the inoculum from drained or arid sites in the area? Could there be unknown direct or indirect effects of waterlogging that are beneficial to the development of AM fungi? The water shelters the surface soils from high temperature fluctuations and slows down decomposition rates, allowing broader, more time consuming, successive resource scavenging by more functionally diverse microbial populations. Inundation can also be considered as a disturbance, inducing a temporary shift in the soil environment from aeroby to anaeroby, directing the soil biota to alternative, slower respiratory pathways or to dormancy or death. When the water recedes, a new disturbance regime takes place, allowing for niche and resource competition. Nutrients from the "bank" of organic material are quickly released through the fast aerobic respiration process, having a fertilising effect on the plants, and attracting more microbes and mesofauna. Additionally, the carbon dioxide respiration rate in the soil increases with a more numerous, diverse and active microbial community, which has been proven to have a stimulating effect on AMF hyphal growth (Bécard and Piche 1989), and indirectly promote the rate of root colonisation.

**AMF response to aridity**

In arid sites, the high surface soil temperature has an almost sterilising effect on the alluvial (A) horizon, only possibly sustaining crustaceans, some saprophytic or parasitic fungi and free-living diazotrophic bacteria. In contrast to wet soils, the decomposition rate of organic material in/on arid soils will be more similar to a burning process, where substances are quickly lost to the atmosphere. A study of the AMF communities in dunes in the Namib Desert revealed that moisture is important for opportunistic growth in arid sites as well, but on a microsite level (Jakobson 1997). Jacobson showed that more resilient spores were produced in the dunes when moisture was low, which assures AMF survival when plants are lost due to drought. In our study, we assessed three formerly inundated sites that had been arid for five years (*i*G1r, *i*G2r and *i*G3r) and three truly arid sites (*A*MN, *A*MM and *A*NM). All sites had a remarkably low amount of AMF root colonisation, AMF spore productivity and AMF diversity in comparison with the annually inundated sites, although individual transect inoculum samples varied from having zero to very high scores. The multivariate analysis separated the truly arid soils of Mandjebougou and Niafunké into unvegetated or plant diverse soils, while the now drained soils of Goubo were held intact, but grouped together with the unvegetated and organically rich *A*MN soils. The reasons are probably complex

**AMF response to soil organic matter, pH and phosphorus**

This study cannot show why there is a higher and more consistent AMF development and spore production in soils rich in organic matter. *A*MN, the only site where sporulation was not discovered, was rich in soil organic matter (7.8%), but was instead lacking plant cover for a very long time, which is why we conclude that next to inundation, plant cover is the second most important factor affecting the presence of AMF. Then thirdly comes the influence of soil organic matter.

Soil organic matter shelters the soil from insolation and binds water. Soil organic matter also has a buffering capacity, retaining and releasing nutrients as well as humic acids and carbon dioxide, which can act as solvents of inorganic nutrients bound to the clay. Soil organic matter contains organic forms of nitrogen. Ortas *et al* (1996) showed that the phosphorus uptake by AM colonised sorghum plants was enhanced by increased nitrogen availability. That would in turn

increase the plant growth and likewise the allocation of carbon to the AMF, which may explain the more opportunistic growth of AMF fungi in soils rich in organic matter, in the presence of roots.

Soil pH and extractable phosphorus may be more influential than this study could reveal, and were difficult to compare due to their extreme differences in varying water regimes, soil types and plant cover. Apparently, soil pH and phosphorus do influence certain fungal species and their ability to colonise roots (Fig. 4). Sylvia *et al.* (1993) observed a decrease in all AMF parameters; by different AM fungi from a wide array of habitats, when extractable P exceeded 10-mg $kg^{-1}$ soil. Only two sites in our study had $P^{Olsen}$ >10 mg $kg^{-1}$ soil (*I*LS 11.8±2.7 and *A*MM 28.7±9.3, see Table 2), which may explain why extractable P did not have much influence in our study. The rough estimates of total soil phosphorus in our study, ranging from 5 to 62 mg $kg^{-1}$ (extractable P contributing with 4 to 47%, see Table 2), were extremely low compared to values from many other areas in the world, ranging from 350 to 4700 mg $kg^{-1}$ (McCullum 1996). It is very important to investigate this further, to know if the plants, with the help of AMF, are actually mining the soil for its phosphorus content, as suggested by van der Pol and Traoré (1993). If so, rock phosphate must be added to the soils to maintain both plants and AMF in the area.

**AMF response to plant density and plant species richness**

To maintain productive AMF communities, plant cover seems to be more important than plant diversity or plant species richness, but less important than inundation and the presence of soil organic material. As AMF propagules cannot survive by themselves for more than one to a few years in the soil, revegetation is essential for AMF survival. Koske and Gemma (1997) found a total lack of AMF propagules in unvegetated sites, but after planting with inoculated grass species, an AMF population was established in less than a year. Al Agely and Reeves (1995) showed that the AMF root colonisation of *Oryzopsis hymenoides* (Gramineae), a common plant on inland dunes in the western US, was positively correlated to plant cover in comparison to diversity. In site *A*MN of this study, which was a dune isle naturally unvegetated since the sorghum fields were abandoned 100 years ago and probably only ever had very scattered annuals after the rains each year, showed a complete lack of AMF spores. A very low percentage of root colonisation indicated that AMF were still present, but unable to reproduce even when the soil was densely seeded with sorghum plants in the trap culture experiment. The reason for this is probably a combination of low AMF potential and that the AMF species present in the arid sites are (or have turned into) K-strategists

A denser plant community helps the colonising obligate AMF to spread extensively, with less propagule being lost to passive stochastic dispersal. A denser plant cover also produces a higher litterfall and greater amount of root biomass to the soil organisms, hence directly increasing the percentage of organic material in the soil and indirectly assuring soil system sustainability. However, plant diversity may be important in maintaining a diverse AMF community - and vice versa. Van der Heijden *et al.* (1998) showed that AMF diversity determined plant diversity, ecosystem variability and productivity in European calcareous grassland and in some North-American old-fields. In European calcareous grassland, eight of 11 plant species were dependent on certain AMF taxa to produce enough biomass to stay competitive in the plant community. This result was roughly equal in microcosms with the most effective single combinations of plant-AMF species as when mixing all the actual plant and AMF taxa. Although AMF diversity has been proven to dictate plant diversity, as discussed above, plants ultimately regulate AMF communities. To study how individual plant species influence the community structures of AMF, a sampling technique comparing mycorrhizosphere soils of several plant species in different sites would be needed. In our study, we were not studying

specific diversity relationships, but were looking for congruent patterns of plant and AMF species richness, but, as mentioned, no such correlation's were detected.

In the Niger inland delta in the Sahel belt of Mali, overall plant species richness and plant cover increases after rainfall or inundation, which is why the results obtained in the dry season before inundation may be underestimations of these parameters, but are still comparable as site differences probably remain proportionally the same throughout the year.

**AMF communities**

AMF species richness was as high in one of the arid sites (*A*MM) as in any of the inundated sites, indicating that AMF diversity may be as high, but less evenly distributed, in arid sites (Stutz and Morton 1996). When present in an arid site, AMF can also produce spore numbers as high as in inundated sites (>300 $g^{-1}$ soil). If correctly assessed (see paragraph 4.8), the actual *Glomus* species in *A*NM produced those spore numbers despite a rather low root colonisation (<25%).

Rice roots were dense in all transects of the rice field (*I*LR), which was the only site where *Entrophopora* species and *Acaulopora morrowiae* were detected, the latter genera frequently found in acid soils (Allen *et al.* 1995). *Acaulospora* species have been reported from upland rice (Ammani and Rao 1996). *Glomus clarum* is reported to have increased the plant biomass of *Acacia albida* (syn. *Faidherbia albida*) and *A. nilotica* during drought stress in sterile soil (Osonubi *et al.* 1992), both tree species being very important to the Sahel ecosystem. *Glomus aggregatum*, and *Glomus clarum* have been found in irrigated and dryland rice in Brazil (Pozzebon, *et al.* 1992).

**Two undescribed species of AMF**

The undescribed *Glomus* species (Glomaceae) were present in 80% of the sites. Mostly, it shared a niche with *Glomus clarum* and/or *Glomus occultum*, but in three cases it dominated completely, ability not found in other AM fungi in the study. The spores of the undescribed *Glomus* species are externally very similar to *Glomus intraradices*, but have one extra cell wall layer when studied subcellularly. The environmental range where this species was found on the Niger inland delta of Mali, was very broad. It occurred in inundated, drained and arid clays, loams and sands of 0.5 to 11% SOM, 5.4 to 7.9 soil pH and 0.8 to 33.8 mg P $kg^{-1}$soil. It was also found in uncovered sites as well as in sites with the highest plant species richness. It was not found in the rice field, but in the five years of fallow after rice. Earlier, these undescribed *Glomus* species had only been found in arid sites; once in the Namib desert in Africa; twice in the semi arid region of the western U.S.; and once in the dunes of the Assategue island outside Virginia, eastern U.S. (INVAM database). In this study, the undescribed *Glomus* species was the most productive sporulater in both arid and inundated sites (*A*NM-b: 320.5 $g^{-1}$, *I*LM-b: 237.5 $g^{-1}$). What is not known is to what extent it is beneficial to the plants.

Another undescribed species, *Entrophospora* species (Acaulosporaceae) only occurred in two replicates in the inundated rice field (*I*LR), the only site where the undescribed *Glomus* species could not be detected. This *Entrophosphora* species was the second best sporulater in the study (197.2 $g^{-1}$), and shared a root niche with *Glomus clarum* and *Glomus occultum*.

**Agricultural and conservation importance of the AMF found**

In human society, the combination of natural conditions and soil degradation, together with the colonially created fatalism and poverty, have led to an agricultural situation where nutritional losses are greater than the inputs. Crop yields are reported to mine the soil, even when fertilised (Van der Pol and Traoré 1993). Phosphorus deficiency in soils in tropical areas is one of the limiting factors in the establishment of tree plantations and agricultural crops (Sanchez 1995). In such systems where nutrients are low, AM fungi are a resource to rely on and should be cautiously maintained. Locally adapted species should not be suppressed or allowed to become

extinct by unconsciously introducing new crops, AMF inoculum from elsewhere or new agricultural methods and treatments. In restoration of grasslands, AMF are important (Miller and Jastrow 1992). Likewise, in restoration of watersheds AM fungi should not be underestimated (Cooke and Lefor 1998). The unknown status of soil phosphorus on the Niger inland delta in Mali, led us to assess not only the soil phosphorus but the species richness and abundance of the indigenous arbuscular mycorrhizal fungi. These data need to be complemented by local studies of growth yield responses to AMF in different fertiliser regimes and intercropping systems, but can still serve as a practical indication for agriculture. To maintain and increase the local diversity and inoculum potential, phosphorus levels should be kept low (<20 mg/kg soil), land kept vegetated (not less than one plant $m^{-2}$ if annuals) or periodically inundated. The pH range of 5.6 to 7.1 where AMF respond the most, is not easy to regulate in naturally acidic or alkaline soils. But, denser vegetation on the dunes, where pH is often high, would decrease the pH locally by root exudes. Additionally, increased plant cover would add organic material to the soil, which facilitates aggregation and infiltration. The AMF species found might have adaptations that are suggested for further study. For instance, the co-evolution of AM fungi and African rice, *Oryza glaberrima*, originating from the area, and the functional diversity of the two undescribed species, especially the undescribed *Glomus* species abundant in arid and inundated sites, are suggested. Additionally, the intercropping of AM trees and annual or perennial rhizobium-symbiosed legumes, all preferably native species from Northern or Western Africa, would together maintain and stimulate the AM fungi and, indirectly, the agricultural crops and the ecosystem as such.

*Acknowledgements* – First of all, I wish to thank my supervisor Monica Kling, Department of Microbiology, Swedish University of Agricultural Sciences (SLU), who initiated me into the field of arbuscular mycorrhiza and who has given me mental and practical support and space in critical moments during the project. She also encouraged me to get in touch with Joseph B. Morton at the International Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi (INVAM), West Virginia University (WVU), USA, who welcomed my visit to INVAM. Without his tremendous taxonomic knowledge and generous supervision, this project could never have been carried out. All the following people and institutions have given additional important support: the Swedish Biodiversity Centre (CBM) by creating and teaching the international masters programme in biodiversity, SLU; the Department of Microbiology, SLU, for accepting and supporting me as a student in a very friendly atmosphere; the Swedish International Development Cooperation Agency (Sida) and the Swedish Royal Academy of Forestry and Agriculture (KSLA) for financing the two projects; M.S. Traoré, his staff and the farmers of PDZL-II in Mali for extraordinary housing, informing, field assistance and interpretation from Souraï and Bambara to French; G. Jacks Swedish Royal Faculty of Technology, (KTH) for logistics and field assistance in Mali and help with soil chemical analyses; C. Sydstrand (SLU) and A. Lindberg (SLU) for being co-workers in the field in Mali and for soil chemical analyses and report writing of the MFS-project; B. Jacks for sharing her knowledge and friendship with people in Mali; M. Erikson (Dept. of Microbiology, SLU) for technical assistance; M. Almlöf (Dept. of Microbiology, SLU) for help with watering the pot culture; M. Thulin (Dept. of Syst. Botany, Uppsala,) for initial identification of plant vouchers; INVAM and staff (WVU, USA) for help with AMF identification and assistance; M. Johansson and B. Stenberg (Dept. Microbiology, SLU) for PCA-analysis; and finally L. Torstensson (Dept. Microbiology, SLU) for revision of the article.

## References

Abbott, L. K., Robson, A. D., and Scheltema, M. A. 1995. Managing soils to enhance Mycorrhizal benefits in Mediterranean agriculture. – Critical Reviews in Biotechnology 15: 213–228.

Abbott, L. K. and Gazey, C. 1994. An ecological view of the formation of VA mycorrhizas. – Plant and soil 159: 69–78.

Al Agely, A. K. and Reeves, F. B. 1995. Inland sand dune mycorrhizae: effects of soil depth, Moisture and pH on colonization of Oryzopsis hymenoides. – Mycologia 87: 54–60.

Allen, E. B., Allen, M. F., Elm, D. J., Trappe, J. M., Molina, R., and Rincon, E. 1995. Patterns of regulation of mycorrhizal plant and fungal diversity. Plant and Soil 170: 47–62.

Ammani, K. A. and Rao, A. S. 1996. Effect of two arbuscular mycorrhizal fungi, *Acaulospora spinosa* and *A. scrobiculata* on upland rice varieties. Microbiological Research 151: 235–237.

Barea, J.M., Escudero, J. L., and Azcon de Aguilar, C. G. 1980. Effects of introduced and Indigenous VA fungi on nodulation, growth and nutrition of *Medicago sativa* in Phosphate fixing soils as affected by P–fertilizers. Plant and soil 54: 283–296.

Bécard, G. and Piché, Y. 1989. New aspects on the acquisition of biotrophic status by a Vesicular-arbuscular mycorrhizal fungus, *Gigaspora margarita*. – New Phytol. 112: 77–83.

Berhaut, Jean. 1967. Flore du Sénégal. 2nd ed. – Éditions Clairafrique, Dakar.

Bethlenfalvay, G. J., Dakessian, S. and Pacovsky, R. S. 1984. Mycorrhizae in southern California desert: ecological implications. – Can.J. Bot. 62: 519–524.

Bondet, G; Lebrun, J. P. and Demarge, R. 1986. Catalogue des Plantes Vasculaires du Mali. – Institut d'Élévage et de Médécine Vétérinaire des Pays Tropicaux, France.

Brandon, D. M. and Mikkelsen, D. S. 1979. Phosphorus transformations in alternately Inundated California soils: 1. Cause of plant phosphorus deficiency in rice crops and – Correctional methods. Soil Sci. Soc. Am. J. 43: 989–994.

Camo A. S., 1996. Method reference. In: The Unscrambler 6.0 User's Guide. – Trondheim, Norway. pp. 21–89.

Clark, R. B. and Zeto, S. K. 1996. Mineral acquisition by mycorrhizal maize grown on acid and alkaline soil. – Soil Biology and Biochemistry 28: 1495–1503.

Cooke, J. C. and Lefor, M. W. 1998. The mycorrhizal status of selected plant species from Connecticut wetlands and transition zones. Restoration and Ecology 6: 214–222.

Cui, M. and Caldwell, M. M. 1996. Facilitation of plant phosphate acquisition by arbuscular Mycorrhizas from enriched soil patches. – New Phytol. 133: 461–467.

Daniels, B. A. and Skipper, H. D. 1982. Methods for the recovery and quantitative estimation of propagules from soil. In: Schenck, N.C. (ed.) Methods and Principles of Mycorrhizal Research. – American Phytopathological society Press, St Paul, AMN, U.S.A., pp. 29–35.

Day, L. D., Sylvia, D. M., and Collins, M. E. 1987. Interactions among vesicular–arbuscular mycorrhizae, soil, and landscape position. – Soil Sci. Soc. Am. J. 51: 635–639.

Dodd, J. C., Arias, I., Koomen, I., and Hayman, D. S. 1990. The management of populations of vesicular–arbuscular mycorrhizal fungi in acid–infertile soils of a savannah ecosystem. II: The effects of pre–crops on the spore populations of native and introduced VAM fungi. – Plant and Soil 122: 241–247.

Douds, D. D., Galvez, L., Janke, R. R. and Wagoner, P. 1995. Effect of tillage and farming System upon populations and distribution of vesicular–arbuscular mycorrhizal fungi. – Agriculture, Ecosystems and environment 52: 111–118.

Dixon, R. K., Rao, M. V., and Garg, V. K. 1994. Water relations and gas exchange of Mycorrhizal Leucaena leucocephala seedlings. – J. Tropical Forestry Science 6: 542–552.

Eissenstat, D. M. and Newman, E. I. 1990. Seedling establishment near large plants. Effects of vesicular–arbuscular mycorrhizas on the intensity of plant competition. – Functional Ecology 4: 95–99.

El Amin, Mohamed Hamza. 1990. Trees and Shrubs of the Sudan. – Ithaca Press, Exeter.

Friberg, S., Lindberg, A. and Sydstrand, C. 2000. Analyse de phosphore, pH, matière organique dans la delta intérieur de Mali. Minor Field Study, Sida/SLU, Sweden.

Gazey, C., Abbott, L. K., and Robson, A. D. 1992. The rate of development of mycorrhizas affects the onset of sporulation and production of external hypha by two species of *Acaulospora*. – Mycol. Res. 96: 643–650.

Gee, G. W. and Bauder, J. W. 1986. Particle size analysis. – In: Klute, A. (ed.). Physical and Mineralogical Methods. Soil Science Society of America, Madison, pp. 383–411.

Gemma, J. N. and Koske, R. E. 1995. Mycorrhizae in Hawaiian epiphytes. – Pacific Science 49: 175–180.

Giovannetti, M. & Mosse, B. 1980. An evaluation of techniques for measuring vesicular-

arbuscular mycorrhizal infection in roots. – New Phytol. 84: 489–500.

Hayman, D. S. 1982. Influence of soils and fertility on activity and survival of vesicular-arbuscular mycorrhizal fungi. – Phytopathology 72: 1119–1125.

Harinikumar, K. M. and Bagyaraj, D. J. 1989. Effect of cropping sequence, fertilizers and farmyard manure on vesicular-arbuscular mycorrhizal fungi in different crops over three consecutive seasons. – Biol. Fertil. Soils 7: 173–175.

Harinikumar, K. M., Bagyaraj, D. J., and Mallesha, B.C. 1990. Effect of intercropping and organic soil amendments on native VA mycorrhizal fungi in an oxisol. – Arid Soil Research and Rehabilitation 4: 193–197.

Hedberg, I. and Edwards, S. 1995. Flora of Ethiopia and Eritrea.

Hetrick, B. A. D., Wilson, G. W. T. and Leslie, J. F. 1990. Root architecture of warm-and cool-season grasses: relationship to mycorrhizal dependence. – Can. J. Bot. 69: 112–118.

Hill, J., Robson, A. D. and Loneragan, J. F. 1979 The effect of copper supply and shading on copper translocation from old wheat leaves. – Annals of Botany 43:449–457.

Hubbar, C. E. and Milne-Redhead, E. 1959. Flora of Tropical East Africa. – Crown agents For Oversea Governments and Administration, London.

Hutchinson, J. and Dalziel, J.L. 1958. Flora of West Tropical Africa. 2nd ed. – Whitefriars Press Ltd, London.

Ilag, L. I., Rosales, A. M., Elazegui, F. A., and Mew, T. W. 1987. Changes in the population of infective endomycorrhizal fungi in a rice-based cropping system. Plant and Soil 103: 67–73.

Jacobson, K. M. 1997. Moisture and substrate stability determine VA–mycorrhizal fungal community distribution and structure in an arid grassland. J. Arid Environments 35. 59–75.

Jakobsen, I., Abbott, L. K., and Robson, A. D. 1992. External hyphae of vesicular–arbuscular mycorrhizal fungi associated with Trifolium subterraneum L. 1: Spread of hyphae and phosphorus inflow into roots. – Phytol. 120: 371–380.

Jakobsen, I. and Rosendahl, L. 1991. Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber plants. – New Phytol. 115: 77–83.

Jasper, D. A., Abbott, L. K. and Johnson, N. C. and Wedin, D. A. 1997. Soil carbon, nutrients and mycorrhizae during conversion of dry tropical forest to grassland. – Ecological Applications 7: 171–182.

Johnson, N. C., Zak, D. R., Tilman, D. and Pfleger, F. L. 1991. Dynamics of vesicular-arbuscular mycorrhizal fungi during old field succession. – Oecologia 86: 349–358.

Joner, E. J. and Jakobsen, I. 1995. Growth and extracellular phophatase activity of arbuscular mycorrhizal hyphae as influenced by soil organic matter. – Soil Biology and Biochemistry 27: 1153–1159.

Kormanik, P. P and McGraw, A. C. 1982. Quantification of vesicular–arbuscular mycorrhizae in plant roots. In: Schenck, N.C. (ed.) Methods and Principles of Mycorrhizal Research. – American Phytopathological Society Press, St Paul, AMN, U.S.A., pp. 37–45.

Koske, R. E. 1987. Distribution of VA mycorrhizal fungi along a latitudinal temperature gradient. – Mycologia 79: 55–68.

Koske, R. E. and Gemma, J. N. 1990. VA mycorrhizae in strand vegetation of Hawaii: evidence for long–distance codispersal of plants and fungi. – Amer. J. Bot. 77: 466–474.

Koske, R. E., Gemma, J. N., and Flynn, T. 1992. Mycorrhizae in Hawaiian Pteridophytes: occurrence and evolutionary significance. – American Journal of Botany 79: 843–852.

Koske, R. E. and Gemma, J. N. 1997. Mycorrhizae and succession in plantings of beachgrass in sand dunes. – Am. J. Bot. 84(1): 118–130.

Kush, G. S. 1997. Origin, dispersal, cultivation and variation of rice. – Plant Molecular Biology 35: 25–34.

McArthur, D. A. J. and Knowles, N. R. 1992. Resistance response of potato to vesicular arbuscular mycorrhizal fungi under varying abiotic phosphorus levels. – Plant Physiology 100: 341–351.

Maire, R. 1957. Flore de l'Afrique du Nord. – Paul Lechevalier, Paris.

Maydell, H-J. von. 1992. Arbres et Arbustes du Sahel: leurs caractéristiques et leurs utilisations. Version francaise. 3rd ed. – Verlag Josef Margraf, Weikersheim.

McCullum, R. E. 1996. Soil phosphorus and potassium. – In: Brady, N. C., and Weil, R. R. (eds.), The Nature and properties of Soils, 11th ed. – Prentice Hall Int., Inc.New Jersey, Chap. 14.

Miller D. D., Domoto, P. A., and Walker, C. 1985. Mycorrhizal fungi at eighteen apple rootstock plantings in the United States. – New Phytol. 100: 379–391.

Miller, R. M. and Jastrow, J. D. 1992. The role of mycorrhizal fungi in soil conservation. – ASA–special publication 54: 29–44. Proceedings of a symposium on Mycorrhizae in sustainable agriculture, Denver, Colorado, 31 Oct. 1991.

Morton, J. B. and Benny, G. L. 1990. Revised classification of arbuscular mycorrhizal fungi (Zygomycetes): a new order, Glomales, two new suborders, Glomineae and Gigasporineae, and two new families, Acaulosporaceae and Gigasporaceae, with an emendation of Glomaceae. – Mycotaxon 37 471–491.

Morton, J. B., Bentivenga, S. P., and Wheeler, W. W. 1993. Germ plasm in the International Collection of Arbuscular and Vesicular–Arbuscular Fungi (INVAM) and procedures for Culture development, documentation, and storage. – Mycotaxon 48: 491–528.

Morton, J. B. 1993. Problems and solutions for the integration of Glomalean taxonomy, systematic biology, and the study of mycorrhizal phenomena. – Mycorrhiza 2: 97–109.

Morton, J. B., Bentivenga, S. P., Bever, J. D. 1995. Discovery, measurement, and interpretation of diversity in arbuscular mycorrhizal fungi (Glomales, Zygomycetes). – Can. J. Bot., 73 (Suppl.1): S25–S32.

Newman, E. I. 1966. A method of estimating the total length of root in a sample. – J. Appl. Ecol. 3: 139.

Olsen, S. R., Cole, C. V., Watanabe, F. S. and Dean, L. A. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. – U.S. Dept of Agriculture, Circular 939, Washington DC.

Olsen, S. R. and Sommers, L. E. 1987. Phosphorus. – In: Page, A. L., Miller, R. H. and Keeney, D. R. (eds.). Methods of Soil Analysis (2nd ed): Chemical and Microbiological Properties. – Series Agronomy Part 9, No 2. Am. Soc. of Agronomy, Inc. Madison, Wisconsin, U.S.A.

Ortas, I., Harris, P. J. and Rowell, D. L. 1996. Enhanced uptake of phosphorus by mycorrhizal sorgum plants as influenced by forms of nitrogen. Plant and Soil 184: 255–264.

Osonubi, O., Bakare, O. N., and Mulongoy, K. 1992. Interactions between drought stress and vesicular arbuscular mycorrhiza on the growth of *Faidherbia albida* (syn. *Acacia albida*) and *A. nilotica* in sterile and non-sterile soils. – Biology and Fertility of Soils 14: 159–165.

Pearson, J. N. and Schweiger, P. 1993. *Scutellospora calospora* (Nicol. & Gerd.) Walker & Sanders associated with subterranean clover: dynamics of colonisation, sporulation, and soluble carbohydrates. – New Phytologist 124: 215–219.

Pirozynski, K.A. and Dalpé, Y. 1989. Geological history of the Glomaceae, with particular reference to mycorrhizal symbiosis. – Symbiosis 7: 1–36.

Pozzebon, E., Antoniolli, Z. I., and Thomas, P. S. 1992. Associations of vesicular-arbuscular mycorrhizal fungi with inundation-irrigated and dryland rice. – Lavoura-Arrouzeira 45: 5–9.

Ramaswamy, S. and Sanders, J. H. 1992. Population pressure, land degradation and sustainable agricultural technologies in the Sahel. – Agricultural Systems 40: 361–378.

Rambelli, A. 1973. The rhizosphere of mycorrhizae. – In: Marks, G. L., and Koslowski, T. T. (eds.) Ectomycorrhizae. – Academic Press, New York. pp. 299–343.

Ricklefs, R.E., and D. Schuluter. 1993. Species Diversity: an introduction to the problem. – In: Ricklefs, R. E. and Schuluter, D. (eds.) Species Diversity in Ecological Communities. Historical and Geographical Perspectives. – University of Chicago Press, pp. 1–10.

Rosendahl, C. N. and Rosendahl, S. 1991. Influence of vesicular–arbuscular mycorrhizal fungi (*Glomus* spp.) on the response of cucumber (*Cucumis sativus* L.) to salt stress. – Environmental and Experimental Botany 31 : 313–318.

Sanchez, P. A. 1995. Science in Agroforestry. – Agrofor. Syst. 30: 6–55.

Schenck, N. C. and Pérez, Y. 1990. Manual for the identification of VA mycorrhizal fungi. 3rd ed. – Synergistic, Gainesville, Florida, U.S.A.

Schreiner, R. P, Mighara, K. L., McDaniel, H., and Bethlenfalvay, G. J. 1997. Mycorrhizal fungi influence plant and soil functions and interactions. – Plant and Soil, 188: 199–209.

Smith, S. E. and Gianinazzi–Pearson, V. 1988. Physiological interactions between symbionts in vesicular-arbuscular mycorrhizal plants. – Ann. Rev. Plant Physiol. Plant Mol. Biol. 39: 221– 224.

Smith, S. E. and Read, D. J. 1997. Mycorrhizal symbiosis, 2nd ed. – Academic Press, Inc.,

U.S.A.

Solaiman, M. Z. and Hirata, H. 1995. Effects of indigenous arbuscular mycorrhizal fungi in paddy fields on rice growth and N, P, K nutrition under different water regimes. – Soil Science and Plant Nutrition (Japan) 41: 505–514.

Solaiman, M. Z. and Hirata, H. 1996. Effectiveness of arbuscular mycorrhizal colonization at nursery stage on growth and nutrition in wetland rice (*Oryza sativa L.*) after transplanting under different soil fertility and water regimes. – Soil Science and Plant Nutrition (Japan) 42: 561–571.

Stenberg, B. 1999. Monitoring soil quality of arable land: microbiological indicators. – Acta Agric. Scand., sect. B, Soil and Plant Sci. 49: 1–24.

Stutz, J. C. and Morton, J. B. 1996. Successive pot cultures reveal high species richness of arbuscular endomycorrhizal fungi in arid ecosystems. – Can. J. Bot. 74: 1883–1889.

Sylvia, D. M., Wilson, D. O., Graham, J. H., Maddox, J. J., Millner, P., Morton, J. B., Skipper, H. D., Wright, S. F., and Jarstfer, A. G. 1993. Evaluation of vesicular arbuscular mycorrhizal fungi in diverse plants and soils. Soil biology and Biochemistry, 25: 705–713.

Terwilliger, J. and Pastor, J. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. – OIKOS 85: 83–94.

Tews, L. L. and Koske, R. E. 1986. Toward a sampling strategy for vesicular–arbuscular mycorrhizas. – Transactions of the British Mycological Society 87: 353–358.

Thompson, J. P. 1991. Improving the mycorrhizal condition of the soil through cultural practices and effects on growth and phosphorus uptake by plants. – In: Johansen, C., Lee, K. K. and Sahrawat, K. L. (eds). Phosphorus nutrition of grain legumes in the semi-arid tropics. ICRISAT, India, pp. 117–137.

Thompson, J.P. 1989. Soil sterilisation methods to show VA mycorrhizae aid P and Zn nutrition of wheat in vertisols. – Soil Biology and Biochemistry 22: 229–240.

Trappe, James M. 1987. Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. – In: Safir, Gene R. (ed). Ecophysiology of VA mycorrhizal plants. CRC Press, Inc. Florida, Chapt. 2.

Wang, C-L., Tschen, J. S. M. and Wang, C. L.1997. Factors on the spores germination of arbuscular mycorrhizal fungi, *Glomus* spp. Archives of international Medicine, 157: 109–116.

Van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf–Engel, R., Boller, T., Wiemken, A., and Sanders, I. R. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. – Nature 396: 69–72.

Van der Pol, F. and Traoré, B. 1993. Soil nutrient depletion by agricultural production in Southern Mali. – Fertilizer research 36: 79–90.

Wold, S., Esbensen, K. and Gelati, P. 1987. Principal Component Analysis. – Chemometrics Intel. Lab. Sys. 2: 37–52.

Wright, S. F. and Upadhyaya, A., 1996. Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. – Soil Science 161: 575–586.

Appendix 1. Raw soil, plant and AMF data from 10 sites in the semi-arid Niger inland delta, Mali, West Africa. (Site codes see Fig.1b).

| Site transect | Depth cm | Pot No. | % Root col. 1m | 4.5m | Spores /g soil | Extr P mg/kg | % | Tot P mg/kg | SOM % | pH aq 2:1 | Soil type | Main Crop 98 | Water regime |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *I*LR-a | 0-40 | 1 | 0.91 | 77.55 | 338.5 | 5.64 | 20.89 | 27.00 | 8.48 | 5.87 | Sand | rice | flood |
| *I*LR-b | 0-40 | 2 | 16.67 | 69.66 | 256 | 4.79 | | | 6.87 | 5.63 | | rice | flood |
| *I*LR-c | 0-40 | 3 | 2.60 | 68.73 | 331.3 | 6.24 | | | 8.70 | 5.87 | | rice | flood |
| *I*LR-d | 0-40 | 4 | 3.59 | 75.89 | 229.3 | 7.32 | | | 6.18 | 5.77 | | rice | flood |
| *I*LS-a | 0-40 | 5 | 1.30 | 59.82 | 127.3 | 9.77 | 35.27 | 27.71 | 10.21 | 5.80 | Clay | sorghum | flood |
| *I*LS-b | 0-40 | 6 | 9.15 | 49.91 | 146.8 | 12.91 | | | 10.85 | 5.80 | | sorghum | flood |
| *I*LS-c | 0-40 | 7 | 1.30 | 40.55 | 116.6 | 15.11 | | | 11.22 | 5.87 | | sorghum | flood |
| *I*LS-d | 0-40 | 8 | 9.28 | 34.55 | 101.9 | 9.52 | | | 10.14 | 6.47 | | sorghum | flood |
| *I*LM-a | 0-45 | 9 | 1.38 | 61.21 | 299.8 | 4.95 | 52.07 | 9.50 | 2.34 | 7.13 | Sandy | millet | flood |
| *I*LM-b | 0-45 | 10 | 6.97 | 56.10 | 283.1 | 1.62 | | | 2.83 | 7.10 | loam | millet | flood |
| *I*LM-c | 0-45 | 11 | 6.49 | 55.68 | 55.1 | 3.57 | | | 2.50 | 6.93 | | millet | flood |
| *I*LM-d | 0-45 | 12 | 0.51 | 47.03 | 145.1 | 3.33 | | | 2.83 | 6.87 | | millet | flood |
| *I*LN-a | 0-45 | 13 | 17.73 | 35.24 | 118.5 | 4.95 | 19.46 | 25.42 | 8.40 | 6.13 | Clay | nat.veg. | (flood -73) |
| *I*LN-b | 0-45 | 14 | 9.41 | 32.57 | 70.9 | 6.44 | | | 8.05 | 6.13 | | nat.veg. | (flood -73) |
| *I*LN-c | 0-45 | 15 | 0.92 | 16.95 | 58.2 | 6.85 | | | 9.20 | 6.17 | | nat.veg. | (flood -73) |
| *I*LN-d | 0-45 | 16 | 1.42 | 46.38 | 45.6 | 7.29 | | | 8.67 | 6.23 | | nat.veg. | (flood -73) |
| *I*G1r-a | 0-25 | 25 | 0.53 | 8.99 | 60.2 | 8.44 | 19.42 | 43.46 | 6.25 | 5.50 | Clay | fallow (rice) | (flood -93) |
| *I*G1r-b | 0-25 | 26 | 1.23 | 3.49 | 89.3 | 5.11 | | | 6.81 | 5.53 | | fallow (rice) | (flood -93) |
| *I*G1r-c | 0-25 | 27 | 0 | 0.00 | 0 | 5.20 | | | 7.01 | 5.30 | | fallow (rice) | (flood -93) |
| *I*G1r-d | 0-25 | 28 | 0 | 0.14 | 0 | 3.03 | | | 7.29 | 5.07 | | fallow (rice) | (flood -93) |
| *I*G2r-a | 0-25 | 29 | 1.02 | 10.95 | 115.9 | 0.68 | 1.95 | 34.83 | 6.43 | 6.03 | Clay | fallow (rice) | (flood -93) |
| *I*G2r-b | 0-25 | 30 | 1.58 | 9.63 | 84.2 | 2.01 | | | 6.93 | 6.07 | | fallow (rice) | (flood -93) |
| *I*G2r-c | 0-25 | 31 | 1.44 | 60.19 | 123.5 | 1.88 | | | 6.49 | 5.70 | | fallow (rice) | (flood -93) |
| *I*G2r-d | 0-25 | 32 | 0 | 17.98 | 32.9 | 1.01 | | | 6.90 | 5.90 | | fallow (rice) | (flood -93) |
| *I*G3r-a | 0-25 | 33 | 0 | 3.90 | 19.6 | 5.23 | 11.93 | 43.79 | 6.93 | 5.80 | Clay | fallow (rice) | (flood -93) |
| *I*G3r-b | 0-25 | 34 | 1.76 | 23.49 | 17.1 | 0.83 | | | 6.78 | 5.80 | | fallow (rice) | (flood -93) |
| *I*G3r-c | 0-25 | 35 | 0.54 | 18.22 | 34.9 | 1.31 | | | 6.98 | 5.37 | | fallow (rice) | (flood -93) |
| *I*G3r-d | 0-25 | 36 | 0 | 0.00 | 0 | 5.83 | | | 6.62 | 6.40 | | fallow (rice) | (flood -93) |
| *A*MN-a | 0-25 | 17 | 0.76 | 0.44 | 0 | 3.89 | 16.33 | 23.84 | 7.40 | 5.10 | Clay | nat.veg. | arid |
| *A*MN-b | 0-25 | 18 | 1.72 | 3.95 | 0 | 3.45 | | | 7.51 | 5.23 | | nat.veg. | arid |
| *A*MN-c | 0-25 | 19 | 3.03 | 0.00 | 0 | 4.36 | | | 7.21 | 5.67 | | nat.veg. | arid |
| *A*MN-d | 0-25 | 20 | 2.24 | 0.00 | 0 | 11.40 | | | 7.04 | 5.90 | | nat.veg. | arid |
| *A*MM-a | 0-30 | 21 | 0 | 0.13 | 0 | 24.51 | 39.34 | 62.29 | 1.29 | 8.10 | Sandy | millet | arid |
| *A*MM-b | 0-30 | 22 | 0.75 | 1.34 | 0 | 17.84 | | | 1.45 | 7.67 | clay | millet | arid |
| *A*MM-c | 0-30 | 23 | 2.26 | 2.81 | 79.2 | 38.71 | | | 0.97 | 8.10 | | millet | arid |
| *A*MM-d | 0-30 | 24 | 1.66 | 0.00 | 1.9 | 33.81 | | | 0.80 | 7.93 | | millet | arid |
| *A*NM-a | 0-45 | 37 | 2.06 | 5.26 | 62.7 | 2.76 | 52.57 | 5.25 | 0.46 | 7.20 | Sand | millet | arid |
| *A*NM-b | 0-45 | 38 | 4.41 | 22.35 | 320.5 | 3.17 | | | 0.66 | 7.07 | | millet | arid |
| *A*NM-c | 0-45 | 39 | 2.33 | 0.00 | 0 | 3.24 | | | 0.78 | 6.87 | | millet | arid |
| *A*NM-d | 0-45 | 40 | 1.18 | 28.27 | 0 | 0.64 | | | 0.71 | 7.00 | | millet | arid |

Appendix 1. Continued

| Site transect | Plant ssp | AMF ssp | AMF species diversity GLOMACEAE | | | | ACAULOSPORACEAE |
|---|---|---|---|---|---|---|---|
| *I*LR-a | 1 | 3 | *G. clarum* | | *G. occultum* | | *Entrophospora sp.* |
| *I*LR-b | | 2 | *G. clarum* | | *G. occultum* | | |
| *I*LR-c | | 3 | *G. clarum* | | *G. occultum* | | *Entrophospora sp.* |
| *I*LR-d | | 3 | *G. clarum* | | *G. occultum* | | *Acaulospora morrowiae* |
| *I*LS-a | 4 | 3 | *G. clarum* | | *G. occultum* | *G. sp.* | |
| *I*LS-b | | 3 | *G. clarum* | *G. claroideum* | *G. occultum* | | |
| *I*LS-c | | 3 | *G. clarum* | | *G. occultum* | *G. sp.* | |
| *I*LS-d | | 2 | *G. clarum* | | | *G. sp.* | |
| *I*LM-a | 8 | 3 | *G. clarum* | | *G. occultum* | *G. sp.* | |
| *I*LM-b | | 3 | *G. clarum* | | *G. occultum* | *G. sp.* | |
| *I*LM-c | | 2 | | | *G. occultum* | *G. sp.* | |
| *I*LM-d | | 3 | *G. clarum* | | *G. occultum* | *G. sp.* | |
| *i*LN-a | 13 | 3 | *G. clarum* | *G. claroideum* | *G. occultum* | | |
| *i*LN-b | | 2 | | | *G. occultum* | *G. sp.* | |
| *i*LN-c | | 3 | *G. clarum* | *G. claroideum* | *G. occultum* | | |
| *i*LN-d | | 1 | | | | *G. sp.* | |
| *i*G1r-a | 5 | 3 | *G. clarum* | | *G. occultum* | *G. sp.* | |
| *i*G1r-b | | 2 | *G. clarum* | | | *G. sp.* | |
| *i*G1r-c | | 0 | | | | | |
| *i*G1r-d | | 0 | | | | | |
| *i*G2r-a | 0 | 3 | *G. aggregatum* | *G. clarum* | | *G. occultum* | |
| *i*G2r-b | | 4 | *G. aggregatum* | *G. clarum* | *G. claroideum* | *G. occultum* | |
| *i*G2r-c | | 2 | | *G. clarum* | | *G. occultum* | |
| *i*G2r-d | | 3 | | *G. clarum* | | *G. occultum* | *G. sp.* |
| *i*G3r-a | 9 | 3 | | *G. clarum* | | *G. occultum* | *G. sp.* |
| *i*G3r-b | | 3 | | *G. clarum* | | *G. occultum* | *G. sp.* |
| *i*G3r-c | | 3 | | *G. clarum* | | *G. occultum* | *G. sp.* |
| *i*G3r-d | | 0 | | | | | |
| *A*MN-a | 3 | 0 | | | | | |
| *A*MN-b | | 0 | | | | | |
| *A*MN-c | | 0 | | | | | |
| *A*MN-d | | 0 | | | | | |
| *A*MM-a | 22 | 0 | | | | | |
| *A*MM-b | | 0 | | | | | |
| *A*MM-c | | 2 | | *G. clarum* | | *G. occultum* | |
| *A*MM-d | | 2 | | | | *G. occultum* | *G. sp.* |
| *A*NM-a | 21 | 1 | | | | *G. sp.* | |
| *A*NM-b | | 1 | | | | *G. sp.* | |
| *A*NM-c | | 0 | | | | | |
| *A*NM-d | | 0 | | | | | |