Agroforestry Systems (2006) 67:107–114
DOI 10.1007/s10457-004-2370-4

Diversity of glomale mycorrhizal fungi in maize/sesbania intercrops and maize monocrop systems in southern Malawi☆

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Received 27 August 2002; accepted in revised form 22 August 2004

Key words: Farming systems, Management practices, Soil organisms

Abstract

The study investigated diversity and frequency of occurrence of glomale (Arbuscular- or Vesicular Arbuscular-) mycorrhizal fungi on three farming systems in a drought prone and nitrogen deficiency site in southern Malawi. The farming systems comprised of two agroforestry systems of *Sesbania sesban* (L) Merr intercropped with maize and *Sesbania macrantha* E Phillips & Hutch. intercropped with maize and a maize monocrop systems without fertilizer, with nitrogen, phosphorus and a combination of nitrogen and phosphorus. Species diversity and species frequency of occurrence were examined in soil samples obtained in the dry and wet seasons. Twelve glomale mycorrhizal species were recorded, four species being in the genus *Acaulospora*, four in *Glomus*, two in *Gigaspora* and two in *Scutellospora*. Species diversity in the two agroforestry systems were not significantly ($p \leq 0.05$) different but had lower species diversity than maize monocrop with only *Sesbania macrantha* intercropped with maize significantly ($p \leq 0.05$) lower. Species diversity was significantly increased by the inorganic nitrogen fertilizer. Inorganic phosphorus fertilizer had no effect. The study shows that the occurrence and persistence of glomale species are influenced by agroforestry combinations, and that the spores of most species are tolerant to dry conditions. Only four species responded to fertilizer application with the occurrence of spores of some species high and some low. Management practices have great implication in the persistence of spore propagules of glomale species.

Introduction

Short duration fallows using *Sesbania sesban* and *Sesbania macrantha* have been found to improve crop yield and soil fertility (Kwesiga and Coe 1994). The type of fallow influences soil fertility levels (Ikerra et al. 2001) and may also influence the diversity of soil organisms and the microbial processes in soil. Thompson (1987) observed bare fallow to lead to disorders that were manifested as phosphorus (P) deficiency in sunflower and linked this to decline in mycorrhizal numbers.

Many studies on soil fertility have often focused on soil chemical and physical properties, disregarding soil biological properties. Differences exist in the relationship of *Sesbania* species with soil organisms. For example, *S. sesban* is susceptible to root-knot nematode disease but *S. macrantha* is not (Karachi 1995). *S. sesban* has also been proven

☆The order Glomale was revised in 2001 and upgraded to a phylum Glomeromycota.

to improve soil fertility through nitrogen fixation in Zambia (Kwesiga and Coe 1994) but no studies were undertaken on *S. macrantha*.

Glomale fungi (Arbuscular Mycorrizal Fungi-AMF), keystone organisms that form an interface between the soil and plant roots, are sensitive to changes in soil and plant conditions (Power and Mills 1995). Glomale fungi, which are widespread in tropical soils, form association with a wide range of plant species, including most commercial crops (Sieverding 1991) and agroforestry trees (Atayese et al. 1993). The association enhances processes of nutrient uptake, soil aggregate stability, control root diseases and alleviate water stress problems (Read et al. 1992). Soil conditions, plant communities and seasonal changes affect the plant mycorrhizal association (Read et al. 1992).

The effect of tree fallows on glomale mycorrhizal fungi is not well documented. The objectives of this study were: (1) to determine the effects of two short-term, dry season *Sesbania* relay fallows on glomale mycorrhizae species diversity and species frequency of occurrence, (2) determine whether the variables are modified by application of inorganic nitrogen and phosphorus fertilizers and (3) evaluate seasonal changes in diversity and frequency of occurrence. The study was undertaken to complement research by Ikerra et al. (2001), done at the same time and same system that showed dry season fallow with *S. sesban* and *S. macrantha* to result in increase in nitrogen.

Materials and methods

Site description

The site is located at Makoka Agricultural Research station, near Zomba in southern Malawi (15°30′S, and 35°15′E) at 1030 m above sea-level. The total rainfall ranges from 560–1600 mm, with a 30-year mean of 1024 mm. Rainfall is unimodal, most coming between November and March, followed by a prolonged dry season. In this study, wet season refers to the November to April cropping season and dry season refers to the May to October season.

The soils are ferric lixisols (FAO) or oxic Haplustalf (USDA). The top soil (0–20 cm) has 52% sand and 37% clay; pH (1:2.5 soil:water suspension) = 6.0; organic C = 1.33%; total N = 0.09%; bicarbonate-EDTA extractable P = 5.1 mg kg^{-1}; KCl extractable Ca = 6.4 $cmol_c$ kg^{-1}, KCl extractable Mg = 1.7 $cmol_c$ kg^{-1} and bicarbonate-EDTA extractable K = 0.19 $cmol_c$ kg^{-1}. Nitrogen was the most limiting nutrient at the site and there was no response to added P at the site (Ikerra et al. 2001).

Experimental design and management

The experiment was established in December 1992 and maintained in subsequent years. The present study began in March 1995. The sampled treatments were arranged in a $3 \times 2 \times 2$ factorial design with three farming systems (no tree, *S. sesban* and *S. macrantha* at 7400 trees ha^{-1}), two inorganic nitrogen fertilizer rates (0 or 24 kg N ha^{-1}) applied as calcium ammonium nitrate (CAN) and two inorganic phosphorus fertilizer rates (0 or 40 kg P ha^{-1}) applied as triple super phosphate (TSP). Treatments were replicated three times in a randomized complete block design. Plot size was 5.7 m × 11.25 m.

Maize hybrid NSCM 41 was planted on 0.3–0.4 m high ridges in December 1995 and 1996 at a spacing of 0.30 m × 0.75 m (44,400 plants ha^{-1}). After maize germination, *Sesbania* seedlings were planted on the same ridges at a spacing of 0.9 m × 1.5 m (7400 trees ha^{-1}). Inorganic nitrogen and phosphorus fertilizer were applied singly and in combination at two and six weeks after planting. Plots were weeded manually, twice. As is the practice in the region, maize was harvested in late April each year. After harvest, the trees were allowed to grow through the dry season and cut in October. The non-woody biomass and litter, plus the maize stover, were placed in the open ridges and covered with soil during land preparation in October. The wood was removed as fuelwood. After the first rain in late November or early December, maize and trees were planted on the ridges.

Soil sampling and processing

Soils were sampled in the dry season of July 1995, after maize harvest and the wet season of March 1996 during the cropping season. Soil samples were taken from all 36 plots. For each plot, five

sub-samples were collected to a depth of 25 cm from the soil surface on a diagonal of the plot. The other diagonal was sampled in the second season. One 50 g sub-sample was collected from each point and pooled to make a composite sample of 250 g, homogenized, air-dried and stored at 4 °C until processing.

The study used spore characteristics to determine glomale species. Extracted spores were compared against pre-determined morphotypes. Pre-determined morphotypes of intact spores were subjected to destructive examination, morphotype characterization done by using a compound microscope with the aid of Normarski differential interference optics up to a magnification of 1000 × under oil immersion. Spores were mounted on Poly Vinyl Lactophenol Glycerol (PVLG) and Meltzer's reagent (5:1 v/v).

Glomale spores were extracted from five 50 g sub-samples retrieved from the composite sample. Spores were isolated from the soil by sucrose centrifugation (Jenkins 1964), modified by using 710 and 45 μm mesh sieves (Walker et al. 1982) and sucrose concentration of 50% w/v. Spores were examined with a 40 × stereomicroscope, aided by both reflected light and white background (specifically used for color determination) and a transmitted light (to aid morphological character recognition). Only fresh spores were counted in small Petri dishes. Fresh spores were recognized by the appearance of the oily contents as either a diffuse milky white substance or as multiple oil globules, or one of a few large oil droplets within the spore, and the absence of parasitism.

Spore morphotypes, now fully characterized, were confirmed within the morphological characteristic ranges for the known glomale mycorrhizal taxa successfully cultured from soils collected earlier in March 1995. The spore cultures are all preserved as live and slide specimens at the National Museums of Kenya. Species were identified using conventional methods (Morton 1988), INVAM species description and species description by Schenck and Perez (1990). Reference collections at the University of Pretoria, Republic of South Africa and the National Museums of Kenya were used to confirm some of the species. The source of reference materials for Kenya is the University of Kent and Forestry Commission (Edinburgh) in the United Kingdom.

The presence or absence of spores of each species was recorded for each sub-sample and fresh spores of each species were counted in each sub-sample. The spore count data was used to calculate diversity index and the presence/absence data was used to calculate species frequency of occurrence using Genstat 6.1.

Computations and statistics

The diversity was derived from the Shannon–Weiner diversity index, which is a measure of community diversity and takes into account both species richness and evenness (Shannon 1948). The Shannon–Weiner index was computed according to the formula: $\Delta_{\mathrm{Sh}} = -\sum(X_{\mathrm{i}}/X_0)\ \log(X_{\mathrm{i}}/X_0)$ where X_{i} = the spore abundance for an individual species and X_0 = the total spore abundance of the population (all glomale species). The resulting ANOVA was used to determine differences in diversity between different treatments.

The frequency of occurrence binary data of dependent non-continuous variables was analysed using logistic regression. A logit transformation was done on the binary data. For each species in a plot, occurrence was recorded in a 0–5 sub-sample. The resulting analysis of deviance table was used to determine significant treatment effects. The logistic model gave predicted (probabilities or proportions) values. Predicted values from the fitted logistic regression models were used to examine the nature of various treatment effects. All calculations were done using Genstat 6.1.

Results

Species composition

Twelve glomale species were recorded from the study site. Spores of four species appeared to closely resemble *Acaulospora rehmii* Sieverding & Toro, *Glomus etunicatum* Becker & Gerdemann, *Gigaspora margarita* Becker & Hall and *Scutellospora cerradensis* Spain & Miranda. Five species had morphological characters affiliated to *Acaulospora* aff. *delicata* Walker, Pfeiffer & Bloss, *Acaulospora* aff. *scrobiculata* Trappe, *Glomus* aff. *aggregatum* Schenck & Smith, *Glomus* aff. *globiferum* Koske & Walker, and *Scutellospora* aff.

dipupurascens Morton & Koske. Spores of *Acaulospora* sp., *Gigaspora* sp. and *Glomus* sp. lacked sufficient material to accurately determine the species. *Gigaspora* sp., successfully established in pot culture, had spore morphological characters that strongly overlapped with *G. margarita* species. Except *Acaulospora* sp., *Glomus* sp. and *G. margarita*, all other species were successfully pot cultured on *Senna siamea* (Lam.). Irwin and Barneby (syn. *Cassia siamea* Lam.), *Senna spectabilis* (DC) Irwin and Barneby (syn. *Cassia spectabilis* DC), *Sorghum bicolor* (L.) Moenche, *Zea mays* L., *Sesbania sesban* (L) Merr, *S. macrantha* E Phillips and *Gliricidia sepium* (Jacq.) Walp.

Species diversity

The Shannon–Weinner diversity index assumes that all species are represented in the sample and provides a measure of species richness. Therefore based on the assumptions made for the diversity index and the need to emphasize on species richness, the Shannon-diversity index was used.

Analysis of variance of diversity index data showed farming systems and the application of inorganic fertilizer to have significant effects on AMF species diversity. Species diversity in the three farming systems differed, with diversity being lower in these agroforestry systems than in the maize monocrop system (Table 1). The decline was more prominent in the agroforestry system with *S. macrantha*/maize intercrop than in the *S. sesban*/maize intercrop system (Table 1). Species diversity of the *S. macrantha*/maize intercrop was, however, not significantly different from *S. sesban*/maize intercrop system. The fertilizer effect was evident in plots with inorganic nitrogen fertilizer, glomale species diversity being significantly ($p \leq 0.05$) higher with inorganic nitrogen fertilizer than without (Table 1). Inorganic phosphorus fertilizer had no effect on glomale species diversity (Table 2).

Table 1. Shannon diversity index of glomale fungi under different agroforestry combinations and fertilizer levels in southern Malawi.

Factors	Shannon diversity index
Farming systems	
S. sesban	1.43
S. macrantha	1.30
Monocrop	1.53
Fertilizer regimes	
−Nitrogen	1.33
+Nitrogen	1.51
−Phosphorus	1.43
+Phosphorus	1.42

Shannon index: SED comparing three farming systems = 0.08, two nitrogen levels = 0.07 and two phosphorus levels – 0.07. Values with differences greater than 2SED are significantly different.

Table 2. Shannon diversity index of glomale fungi under different phosphorus levels in the dry and wet season in southern Malawi.

Factors	Shannon diversity index
Dry season	
−Phosphorus	1.55
+Phosphorus	1.40
Wet season	
−Phosphorus	1.30
+Phosphorus	1.43

Shannon index: SED for comparing two phosphorus levels = 0.09. Values with differences greater than 2SED are significantly different.

Frequency of occurrence of species

Season had the greatest effect on the frequency of occurrence of glomale spores. Season significantly ($p \leq 0.05$) affected all glomale species, spores of nine species being predominant in the dry season and three in the wet season (Table 3).

Only four species were affected by farming systems (Table 3). Farming systems significantly ($p \leq 0.05$) affected the frequency of occurrence of *Gigaspora* sp. and *S. dipurpurascens* and slightly ($p \leq 0.1$) affected *A. scrobiculata* and *G. globiferum*. The species differed in their association with farming systems with *A. scrobiculata* higher and *S. dipurpurascens* least in *S. sesban*/maize intercrop system and *G. globiferum* higher and *Gigaspora* sp. least in *S. macrantha*/maize intercrop system. The remaining species were not affected.

Effect of inorganic fertilizer was observed on a few glomale species; four species were significantly ($p \leq 0.05$) affected and two species slightly ($p \leq 0.1$) affected (Table 4). The spores of *A. rehmii* were higher and spores of *S. dipurpurascens* lower in plots with inorganic nitrogen. A slight decline was, however, observed in spores of

Table 3. Probability of frequency of occurrence of glomale species in two seasons and three farming systems in southern Malawi.

Glomale species	Season[a]			Farming systems[b]			
	Dry	Wet	*p*-value[c]	Monocrop	SS	SM	*p*-value[c]
Acaulospora aff. *delicata*	0.14	0.27	0.002	0.21	0.22	0.19	0.89
Acaulospora rehmii	0.38	0.24	0.003	0.37	0.28	0.28	0.18
Acaulospora aff. *scrobiculata*	0.34	0.15	0.001	0.21	0.32	0.21	0.06
Acaulospora sp.	0.12	0.03	0.001	0.12	0.05	0.06	0.12
Glomus aff. *aggregatum*	0.06	0.15	0.003	0.13	0.08	0.11	0.42
Glomus etunicatum	0.76	0.52	0.001	0.66	0.58	0.67	0.29
Glomus globiferum	0.13	0.24	0.006	0.14	0.18	0.25	0.09
Glomus sp.	0.19	0.01	0.001	0.13	0.12	0.06	0.11
Gigaspora margarita	0.11	0.02	0.001	0.05	0.10	0.05	0.22
Gigaspora sp.	0.28	0.09	0.001	0.21	0.23	0.12	0.04
Scutellospora cerradensis	0.59	0.27	0.001	0.44	0.37	0.48	0.18
Scutellospora aff. *dipurpurascens*	0.14	0.01	0.001	0.09	0.02	0.12	0.003

Fungal species with *p*-value ≤ 0.05 have significantly different probability of occurrence. SS = *Sesbania sesban*/maize intercrop and SM = *Sesbania macrantha*/maize intercrop.
[a]Each number represents means of 15 observations (sub-samples), average of four fertility regimes and three farming systems.
[b]Each number represents means of 15 observations (sub-samples), average of four fertility regimes and two seasons.
[c]*p*-value is the test of the hypothesis of no difference between treatments.

Table 4. Probability of frequency of occurrence of glomale species at four fertility regimes in southern Malawi.

Fertility regimes:	0	N	P	N × P	N	P	N × P
Glomale species	Mean species occurrence				*p*-values		
Acaulospora aff. *delicata*	0.23	0.17	0.23	0.19	0.19	0.79	0.77
Acaulospora rehmii	0.23	0.33	0.27	0.41	0.01	0.25	0.74
Acaulospora aff. *scrobiculata*	0.26	0.27	0.21	0.26	0.54	0.54	0.69
Acaulospora sp.	0.06	0.03	0.08	0.13	0.54	0.03	0.20
Glomus aff. *aggregatum*	0.09	0.09	0.11	0.12	0.86	0.38	0.88
Glomus etunicatum	0.70	0.53	0.66	0.67	0.12	0.38	0.08
Glomus globiferum	0.19	0.18	0.20	0.19	0.79	0.79	1.0
Glomus sp.	0.16	0.10	0.07	0.09	0.60	0.11	0.25
Gigaspora margarita	0.06	0.08	0.06	0.08	0.4	1.0	1.0
Gigaspora sp.	0.19	0.17	0.17	0.22	0.68	0.68	0.35
Scutellospora cerradensis	0.48	0.44	0.30	0.50	0.11	0.24	0.02
Scutellospora aff. *dipurpurascens*	0.10	0.01	0.11	0.08	0.02	0.15	0.07

Fungal species with *p*-value ≤ 0.05 have significantly different probability of frequency of occurrence. Each mean value represents means of 15 observations (sub-samples), an average of two farming systems and two seasons. *p*-value for nitrogen (N) is the significant level for testing whether there is a main effect of nitrogen (N) on species frequency of occurrence. *p*-value for phosphorus (P) is the significant level for testing whether there is a main effect of phosphorus (P) on species frequency of occurrence. *p*-value for nitrogen × phosphorus (N × P) is the significant level for testing for nitrogen (N) by phosphorus (P) interaction effect on species frequency of occurrence.

S. dipurpurascens in plots with a combination of inorganic nitrogen and phosphorus fertilizer. Spores of *Acaulospora* sp. were higher in plots with inorganic phosphorus fertilizer whereas *S. cerradensis* was variably affected with spores least in plots with inorganic phosphorus and highest in plots with a combination of inorganic nitrogen and phosphorus. The spores of *G. etunicatum* were slightly lower in plots with inorganic fertilizer.

Discussion

The study was undertaken to determine whether agroforestry systems differ in their effects on glomale species, as measured by spores, and whether this effect would be modified by fertilizer and season. Malawi is a region prone to drought and spores are propagules likely to withstand drought conditions, hence they were used to assess diversity

and species frequency of occurrence. The spores are the most preserved source of inoculum in prolonged drought conditions (Babara and Hetrick 1984).

Except for three glomale species whose specific taxa could not be established, the species recovered from this site are found in other biogeographic regions, suggesting adaptations over a wide range of habitats. The species *A. rehmii*, *G. aggregatum*, *G. globiferum*, *S. cerradensis* and *S. dipurpurascens* are reported for the first time in Africa. Species that have been reported in Africa are *G. etunicatum* (Gaur et al. 1999), *G. margarita* (Gaur et al. 1999; Dalpe et al. 2000); *A. scrobiculata* (Shepherd et al. 1996) and *A. delicata* (Ba et al. 1996).

The agroforetry systems *S. sesban*/maize intercrop and *S. macrantha*/maize intercrop had lowering effects on the diversity of glomale fungi. *S. sesban* and *S. macrantha* are closely related species, implying the possibility of plant species associations with mycorrhizal fungi to be a hereditary trait.

The lower species diversity in the two *Sesbania* agroforestry systems, compared to maize monocrop system may be linked with a combination of factors: root turnover, changes in nitrogen and root biomass. In temperate climates where root growth by perennial plants is more or less continuous, Baylis (1969) found that few spores were produced despite high levels of colonisation and suggested lack of evolutionary stimulus for spore production if root growth was not intermittent. Baylis (1969) also observed a New Zealand bush soil to have fewer spores compared to soils carrying native grasses or those of cultivation and suggested that the native grass soils were subjected to intermittent root growth and drying that stimulates sporulation. At the *Sesbania* spp. agroforestry site, trees were left longer in agroforestry plots as dry season fallow and hence tree roots lasted longer than maize roots. Maize plants were in active growth for a period of only four months, thereafter maize was harvested in the dry season, leaving maize roots to decay. This may explains the high species diversity in maize monocrop systems.

The study also investigated whether application of fertilizer and season would modify glomale fungi. Only inorganic nitrogen had an effect on glomale species diversity. The high species diversity in plots with inorganic nitrogen is similar to observations made by Sreenivasa et al. (1990), who noted increase in spores with increase in nitrogen in the form of nitrate and ammonium nitrate. Chambers et al. (1980) observed high concentrations of inorganic nitrogen compounds to reduce mycorrhizal colonisation, and the reduction was generally greater with ammonium than nitrate. The differences between the two sources of nitrogen were linked to mycorrhizal preference for ammonium than nitrate. Under the same system where the studies on glomales were undertaken, Ikerra et al. (2001) observed most soil inorganic nitrogen increases at the *Sesbania* site to be due to nitrate rather than ammonium. This may explain the high species diversity in plots with inorganic nitrogen fertilizer. The site is deficient in nitrogen (Ikerra et al. 2001) and glomale diversity seemed to be affected more by changes in nitrogen than phosphorus. This may imply that glomale fungi response to fertilizer amendment could be highly dependent on the most deficient nutrient in the soil, in this case nitrogen, with changes in the most deficient nutrient affecting glomale species in that soil.

The frequency of occurrence of individual spores of glomale species showed marked variations with season and slight variation with farming systems and fertility regimes. There was no trend in frequency of occurrence of spores of species in the same family or genus. Spores of most species seemed to occur in the dry season. Guadarrama and Sanchez (1999) suggested root senescence as a factor that contributed to high spore numbers in the dry season. Considering that southern Malawi is prone to drought, most species adapted to a dry season are likely to prolong survival of the fungi and also maintain the inoculum potential of soils longer under drought conditions. The high occurrence of spores is a favourable strategy of species survival particularly under dry conditions as less sporulating species that are in the form of mycelia and root fragments become non-viable in prolonged dry conditions (Barbara and Hetrick 1984).

Studies on frequency of occurrence of spores of glomale species showed *A.* aff.*scrobiculata*, *S. dipurpurascens*, *G.* aff.*globiferum* and *Gigaspora* sp. to respond to changes in farming systems. There are numerous studies that have reported specific associations between glomale species and plant species/farming systems. Khalil et al. (1992)

also noted four *Glomus* species to be most abundant around the rhizosphere of soya beans (*Glycine max* (L) Merr.), *Gigaspora* species second most abundant and *Acaulospora* species the least. *A*. aff. *delicata*, *A*. *rehmii*, *Acaulospora* sp. *G*. aff. *aggregatum*, *G*. *etunicatum*, *Glomus* sp., *G*. *margarita* and *S*. *cerradensis* were not affected by farming systems. As in this study, there were no generic or family trends observed in the association of spores of glomale species with the plant species. The occurrence of spores in the rhizosphere of the host plants is considered as an indicator of mycorrhizal incidence. There are reports of positive correlation between spore number and root colonization (Onguene 2000). The weakness of use of spores to determine host/plant associations excludes non-sporulating species that may be dominant colonizers in the root system.

The differential response in spore production of glomale species to different types of fertilizer dismisses the generalization that inorganic fertilizers always have a lowering effect on all glomale species. This study showed sporulation of a few species not to be affected by inorganic fertilizer.

Studies by Sieverding (1991) showed *G*. *etunicatum* to be more prevalent in soils with high inorganic input. At the *Sesbania* spp/maize intercrop and maize monocrop site the spores of *G*. *etunicatum* were less frequent in plots with inorganic fertilizer. There is still limited record on the effects of fertilizer on all spores of glomale species and the mechanisms governing preference.

There is need to investigate further the composition and distribution patterns of glomale species in different farming systems. Such a study will facilitate the utilization and management of glomale fungi to improve root functions and subsequent productivity in farming systems. Improved fallows with agroforestry trees affect the diversity and frequency of occurrence of glomale species. The choice of agroforestry tree species and soil management would therefore have great implication in the manipulation and conservation of glomale species.

Acknowledgements

We would like to thank ICRAF for providing financial support through Ford Foundation and Rockefeller Foundation. We are particularly grateful to R. Coe of ICRAF's Research and Support unit for providing statistical support, L. Verchont for reading through the manuscript, J. Awimbo of Training and Capacity facilitating logistics and all ICRAF Malawi staff for data collection.

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