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ORIGINAL PAPER

Effect of agricultural management practices on arbuscular mycorrhizal fungal abundance in low-input cropping systems of southern Africa: a case study from Zimbabwe

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Abstract Previous research, mostly in temperate agricultural systems, has shown that management practices such as fallow period, tillage, crop rotation, and phosphorus (P) fertilizer applications can influence the abundance of arbuscular mycorrhizal fungi (AMF), but relatively little is known about their effect in smallholder farmers' fields in sub-Saharan Africa. In this study, we evaluated the effect of four subsistence crops that form associations with AMF, moderate P fertilization, tillage, and fallow period on the subsequent AMF abundance on three contrasting low fertility soils in south-western Zimbabwe. Arbuscular mycorrhizal fungal abundance was estimated based on early mycorrhizal colonization of maize (*Zea mays* L.) or lablab (*Lablab purpureus* L.) following the various treatments. The previously grown crop significantly affected AMF abundance ($p<0.001$). It was highest after lablab followed by pigeonpea (*Cajanus cajan* L.), maize, and groundnut (*Arachis hypogaea* L.), and there were significant positive correlations between AMF abundance and aboveground biomass of pigeonpea, lablab, and maize. Contrary to much previous research, P fertilization, fallowing, and tillage did not significantly decrease AMF abundance. In smallholder farmers' fields in the semi-arid tropics of sub-Saharan Africa, therefore, growing vigorous mycorrhizal plants prior to the dry season could be more important than minimizing P fertilizer applications, fallow periods, and tillage to maintain or increase AMF abundance.

Keywords Arbuscular mycorrhizal fungi · Management practices · Subsistence farming · Semi-arid tropics

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Introduction

Arbuscular mycorrhizal fungi (AMF) are present in most agroecosystems and colonize roots of a majority of agricultural crops (Smith and Read 1997). These fungi have the potential to increase the uptake of phosphorus (P) to the plant (Sanders and Tinker 1971) and may be more important than the roots themselves as organs of P uptake (Smith et al. 2003). A recent meta-analysis showed that significant increases in mycorrhizal colonization resulted in yield promotions averaging 23% (Lekberg and Koide 2005), which could be of particular importance for smallholder farmers in sub-Saharan Africa who often farm on low fertility soils and have little or no access to mineral fertilizers (Twomlow et al. 1999).

Studies undertaken over the past 30 years have shown that common management practices such as cultivation of non-mycorrhizal crops (Harinikumar and Bagyaraj 1988; Gavito and Miller 1998), P fertilizer applications (Black and Tinker 1979; Lu et al. 1994), fallow periods (Harinikumar and Bagyaraj 1988; Kabir and Koide 2002), and intensive tillage (Kabir et al. 1997 Kabir 2005) may have negative effects of varying degrees on AMF abundance (Lekberg and Koide 2005). Whereas a majority of these studies have been undertaken in high-input, temperate agroecosystems, less is known about effects of management practices commonly employed by smallholder farmers in low-input tropical agroecosystems.

We report on results from two experiments conducted in collaboration with farmers in south-western Zimbabwe. These farmers grow a number of mycorrhizal crops such as maize (*Zea mays* L.), sorghum (*Sorghum bicolor* L.), groundnut (*Arachis hypogaea* L.), and cowpea (*Vigna unguiculata* L. Walp.; Howeler et al. 1987; Dodd et al. 1990). Fields are typically tilled to a depth of 10 to 15 cm using animal-drawn moldboard plows to control weeds and prepare a seed bed prior to planting. Farmers are also encouraged to till their fields at end of the cropping season (so-called winter tillage) to reduce weed densities and conserve water prior to the 6-month dry season (Twomlow et al. 1999). While this practice may be important to combat weeds and reduce water loss, it could reduce AMF abundance due to a combined effect of disturbance and reduction of potential hosts between cropping cycles. Based on these common practices, the objective with Experiment 1 was to determine the effect of different mycorrhizal crops and moderate P fertilizations on AMF abundance. Experiment 2 was conducted to determine the impact of dry-season fallow period and winter tillage on subsequent AMF abundance and weed density.

Materials and methods

Experimental sites

Experiments were conducted in three contrasting soils of low fertility, typical of the low-input smallholder farming systems of southern Zimbabwe: A fine sandy soil formed over deposits of Kalahari Sands, corresponding to either a Oxyaquic Haplustalf (USDA) or a Stagni-Vertic Luvisol (FAO), a black clay with shrink and swell properties that corresponds to either a Vertic Haplustoll (USDA) or a Vertic Phaeozem (FAO), and a coarse-grained granitic sand corresponding to either a Typic Ustochrept (USDA) or a Eutric Arenosol (FAO), hereafter referred to as the fine sand, black clay, and granitic sand, respectively (Moyo 2001). The fine sand and black clay were located on smallholder farmers fields in the Tsholotsho communal area (27° 49.73′ E; 19° 51.07′ S, 1,120 masl), and the granitic sand was located on the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) research fields in Lucydale (28° 24.46′ E; 20° 25.64′ S, 1,378 masl). Selected soil characteristics are summarized in Table 1. The mean annual rainfall for both Tsholotsho and Lucydale is 540 mm (ICRISAT, unpublished data) and is concentrated during the growing season between the months of November and April. The average yearly maximum and minimum temperatures are 26°C and 11°C.

Table 1 Characteristics of soils used in Experiments 1 and 2

Soil property	Soil		
	Black clay	Fine sand	Granitic sand
pH (in water 1:1, *w*/*v*)	7.9	6.2	4.2
Organic C (%)	1.1	0.4	0.4
Available N (mg NO_3^- kg^{-1})	5.9	1.1	5.3
Total N (%)	0.09	0.03	0.01
Available P (Olsen, mg kg^{-1})	1.8	2.1	1.8
Total P (%)	0.04	0.03	0.04
Sand (%)	48	90	92
Silt (%)	11	7	4
Clay (%)	41	3	4

Soil for all analyses was collected from the upper 15 cm prior to planting of Experiment 1

Experiment 1—effect of crop rotation and P fertilization

Year 1 The fine sand and black clay were tilled using the host farmers' animal-drawn moldboard plows to a depth of 15 cm on 17 December 2000, and the granitic sand at the on-station site was tilled using a tractor-drawn disc plow to a depth of 20 cm on 20 December 2000, the normal practice at this site. Groundnut (var. Natal Common), lablab bean (*Lablab purpureus* var. Rongai), pigeonpea (*Cajanus cajan* var. ICPL 87091), and maize (hybrid SC 513) were all planted at a depth of between 2 and 5 cm according to local practices for each variety in the fine sand, black clay, and granitic sand on 19, 21, and 28 December, respectively. Although lablab and pigeonpea are not commonly grown by smallholder farmers in Zimbabwe today, they were included in the study due to their potential as high-quality animal feed (lablab) and drought resistance (pigeonpea). The in-row distance between seeds was 10 cm for groundnut, 15 cm for lablab bean, and 20 cm for pigeonpea, with a distance between rows of 45 cm. Maize seeds were planted 30 cm apart, with a distance between rows of 75 cm. To ensure uniform plant stands, two to three seeds were planted per hole and then thinned to one seedling 10 days after emergence. Due to poor emergence of lablab beans, those plots were reseeded between 10 and 16 January 2001. All plants were grown with or without P (0 or 20 kg P ha^{-1} as triple super phosphate containing 21% P) in a randomized complete block design with four replications. Each plot (containing a single plant species) was 4×5 m in size, and there was a 0.5-m separation between plots. Plots were clean weeded by hand at the beginning of January and again in February 2001. A small (4×5 m) adjacent area per block was left unattended during the growing season to determine the effect of natural fallows on the subsequent AMF abundance.

Final harvests were conducted in May 2001, 5 months after planting. All plants were cut at the soil surface, and the fresh shoot weight for the plot was recorded (excluding the border rows). Shoots of four randomly selected plants were chosen from each plot and oven dried at 65°C to constant weight. The root systems of these four plants were excavated carefully, and percent mycorrhizal colonization on fine roots (<2-mm diameter) collected from the upper 15 cm was determined from a pooled sample from each plot using the gridline intersect method on cleared roots stained in trypan blue (Brundrett et al. 1996). Even though pigeonpea and maize can develop deep roots in these soils, the majority of fine roots that harbor AM fungi was found in the upper 15 cm (personal observation).

Year 2 Following a 6-month fallow, the soil was manually hoed to a depth of about 15 cm to prepare a seed bed on 11, 20, and 23 November 2001 in the granitic sand, fine sand, and black clay, respectively. Due to the small size of the plots, the common tillage practice of animal draft plowing was not employed due to the risk of cross contamination of AMF between plots. Maize seeds (var. SC 513) were planted 40 cm apart within a row and 75 cm between rows immediately after preparing the seed bed. Ten days after emergence, four maize seedlings were randomly selected from each plot. Seedling roots were carefully excavated from the upper 15 cm and pooled within plots, and early mycorrhizal colonization (measuring primary colonization units) on these roots was used as a proxy for AMF abundance.

Percent mycorrhizal colonization was analyzed in Minitab Release 11 (Minitab Inc., State College, PA, USA) as a four-factor analysis of variance with soil, crop species, P fertilization, and block as the four factors. Correlations were conducted in Minitab Release 11.

Experiment 2—effect of winter tillage and dry-season fallow period

Year 1 Areas within the black clay, fine sand, and granitic sand where no fertilizers had been applied the previous year were plowed to a depth of approximately 15 cm using animal-drawn moldboard plows between 27 November and 1 December 2001 to prepare a seed bed. We opted to use animal-drawn plows on the granitic sand in favor of a tractor-drawn disc plow, the normal practice at this site, as tillage was a treatment in this experiment, and we wanted to simulate small-scale farmer practices. The experiment utilized a split-plot design (with four replications) with winter tillage as the main plot and dry-season fallow period as the sub-plot. Main plots were 6×26 m, and sub-plots were 6×8 m in size, with 1 m between sub-plots to facilitate animal-drawn tillage and reduce the possibility of cross contamination between plots during the second phase of the experiment.

Two maize varieties that mature in either 4 (var. ZS 257) or 5 months (var. C2H99044) or a perennial pigeonpea variety (ICRISAT var. ICEAP 0004) were utilized to generate a fallow period between growing seasons Year 1 and Year 2 of 8.5 months (for the 4-month-duration maize, termed 8.5F), 7.5 months (for the 5-month-duration maize, 7.5F), and 1 month (for the long-duration pigeonpea, 1F). All plots were seeded between 27 November and 4 December 2001, with a between-row distance of 90 cm and a within-row distance of 40 cm and clean weeded by hand twice during the growing season. Unexpected events (discussed below) prevented us harvesting and measuring the biomass of the maize and pigeonpea grown on the black clay and fine sand. In the granitic sand, however, the 4-month-duration maize was harvested on 3 April, the 5-month-duration on 5 May, and the pigeonpea on 13 November 2002. At harvest, all the shoots were cut at the soil surface, and the fresh weight was recorded (net plot size of 36 m^2 excluding the guard rows). A sub-sample was taken from each plot, brought to the ICRISAT research station, dried in 65°C until constant weight, and dry weight recorded. All remaining biomass was removed from the plots. Winter tillage was conducted on half of all plots (TILL) at the end of the rainy season between 10 and 17 May 2002 on all three sites. The remaining main plots were left undisturbed (NO-TILL). Thus, the experiment consisted of five treatment combinations: 8.5F:TILL, 8.5F:NO-TILL, 7.5F:TILL, 7.5F:NO-TILL, and 1F:NO-TILL. The treatment combination 1F:TILL was not possible because the winter tillage would have destroyed the long-duration pigeonpea crop, and thus, the experiment was unbalanced.

Unexpected events at the black clay and fine sand changed the experimental set-up slightly. Farm animals entered these fields and consumed all the aboveground biomass of the two maize varieties in February 2002. By August 2002, farm animals had eaten or trampled 50% of the pigeonpea stands in both fields, and by November 2002, only about 10% of pigeonpea plants remained. Due to this, the planned 7.5- and 8.5-month fallow treatment from the two maize varieties became a 10-month fallow treatment, and no data regarding shoot weight was recorded. Furthermore, the previously designated 1-month fallow with the pigeonpea became a 4-month fallow. Thus, we were left with only three treatment combinations in the black clay and fine sand; 10F:TILL, 10F:NO-TILL, and 4F:NO-TILL.

Year 2 Weed samples were collected from three randomly selected 1-m^2 quadrats per plot between 13 and 14 November 2002 from all three sites. Biomass measurements, weed identification, and estimation of mycorrhizal colonization were conducted on pooled weed samples from each plot. All plots, including NO-TILL plots, were then tilled using animal-drawn moldboard plows between 15 and 19 November in the fine sand and black clay and on 13 December in the granitic sand. Early mycorrhizal colonization of lablab (var Rongai) was used to evaluate the effects of winter tillage and fallow period on AMF abundance. Planting was conducted on 12 and 13 December in the fine sand and black clay and on 19 December 2002 in the granitic sand. Only fifty lablab plants were planted per plot in the black clay and fine sand, and the remaining plot was seeded with maize (var. SC 401) due to the strong wish expressed by the farmers to have the staple crop grown on their fields. The same row and seed distance was used as in Year 1 for both crops. Five lablab seedlings per plot were harvested 20 days after emergence in the black clay and granitic sand, but five maize seedlings were harvested per plot in the fine sand due to poor emergence of lablab bean in that soil. For clarity, the timing of the various treatments in this experiment is outlined in Fig. 1.

Treatment effects on mycorrhizal colonization were analyzed as a split-plot design, with winter tillage as the main plot and fallow period as the sub-plot in SAS (SAS Institute Inc., Cary, NC, USA). The error term for the winter tillage effect was the block × tillage treatment interaction, whereas the error mean square was used to test the effect of fallow period as is appropriate for split-plot designs (Zar 1999). Mean separations were accomplished using the least significant difference method and were considered significant if $p \leq 0.05$.

Results

Experiment 1—effect of crop species and P fertilization on subsequent AMF abundance

Overall AMF abundance, as represented by mycorrhizal colonization of maize 10 days after emergence, differed significantly between sites ($p<0.001$). It was higher in the two subsistence farmers' fields (fine sand: 47.6%±2.2, mean ± SE; black clay: 42.8%±2.5), compared with the ICRISAT research fields at Lucydale (granitic sand: 23.1%±1.6), which may, at least partly, be due to the more intense disturbance during seed preparation Year 1 in the granitic sand. Application of P in Year 1 resulted in a slight but non-significant ($p=0.079$; no significant site × P application interaction) decrease in AM colonization in

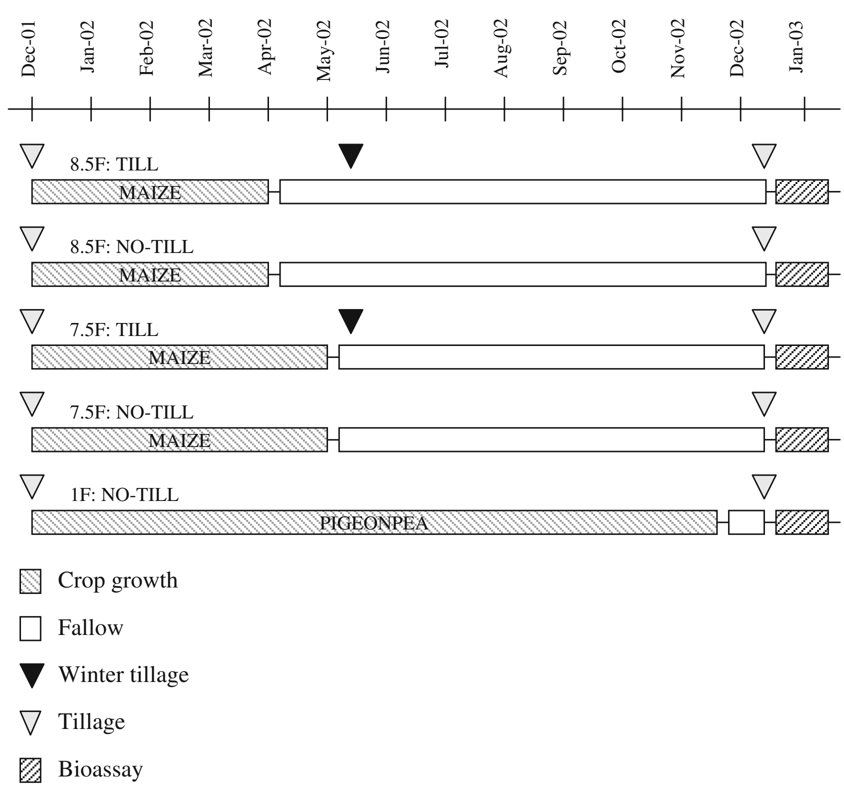

Fig. 1 Outline of Experiment 2 in the granitic sand showing the various treatments, as well as the timing of their applications

all three sites ranging from 1.3% in the granitic sand to 7.8% in the black clay. When controlling for differences between sites and P applications, crops grown in Year 1 differentially affected the AMF abundance in Year 2 ($p<0.001$, with no significant site × crop interaction). Overall, subsequent AMF abundance was significantly higher after lablab (45.3±3.0, means ± SE, pooled over the three sites and two P treatments), pigeonpea (39.5±4.1), and maize (37.0±2.8) compared with groundnut (29.5±2.5). Mycorrhizal colonization of plants in Year 1 was not correlated with mycorrhizal colonization in Year 2 ($r=0.20$, $p=0.11$). However, there were significant positive correlations between aboveground dry weight in Year 1 and AMF abundance in Year 2 for lablab, pigeonpea, and maize but not for groundnut (Fig. 2). Mycorrhizal colonization Year 2 in adjacent plots that were under a natural fallow and covered in weeds Year 1 did not differ statistically from maize, lablab, and pigeonpea but was significantly higher than groundnut (data not shown). There were no other significant two- and three-way interactions.

Experiment 2—effect of winter tillage and dry-season fallow period on AMF abundance and weed biomass

Both maize and pigeonpea roots were heavily colonized (>50%) at all three sites at the end of the growing season in May Year 1. Thus, both crops appeared to be good host plants for AMF. Contrary to expectation, neither winter tillage nor fallow period significantly affected AMF abundance at any site Year 2 (Table 2). Winter tillage did, however, significantly reduce weed densities in the 8.5F and 7.5F treatments in the granitic sand ($p=0.014$) from 909.1 g plot^{-1} (±147, SE) to 147.2 g plot^{-1} (±57.1). The

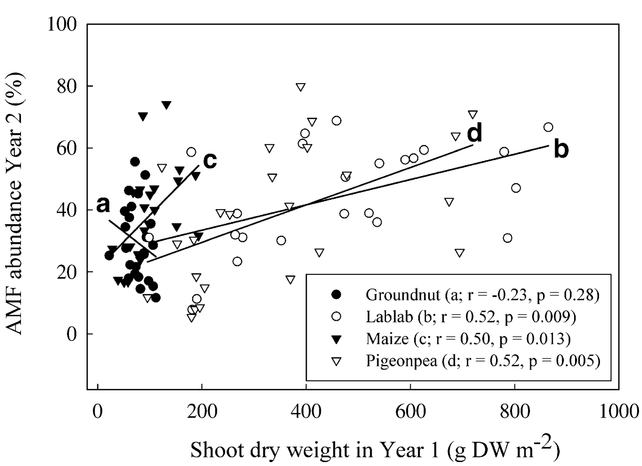

Fig. 2 Correlation between shoot dry weight of groundnut (*a*), lablab (*b*), maize (*c*), and pigeonpea (*d*) in Year 1 and AMF abundance Year 2 as assessed by mycorrhizal colonization of maize 10 days after emergence from the granitic sand, fine sand, and black clay in Experiment 1

Table 2 Effect of fallow period and winter tillage on subsequent AMF abundance as assessed by percent mycorrhizal colonization 20 days after emergence on lablab in the granite sand and black clay and maize in the fine sand in Experiment 2

Site	Fallow period (months)	AM (%; mean ± SE)	
		No tillage	Tillage
Granitic sand	1	40.5 (3.1)	
	7.5	42.0 (3.5)	39.0 (2.4)
	8.5	43.3 (3.6)	36.0 (3.7)
Fine sand	4	64.7 (2.2)	
	10	66.2 (2.8)	62.7 (2.6)
Black clay	4	60.6 (6.1)	
	10	53.7 (4.6)	58.8 (4.5)

There were no significant main plot (tillage treatment) or sub-plot (fallow period) treatment effects or interactions at any of the 3 sites, $n=4$. Not all treatment combinations were possible due to the nature of the experiment and unexpected events (see "Materials and methods" section)

dominant weeds at this site included three forbs [*Conyza sumatrensis* (Retz.)E. Walker, *Schkuhria pinnata* (Lam.) Kuntze ex Thell, and *Tagetes minuta* (L.)] and two grasses [*Eleusine indica* (L.) Gaertn and *Eragrostis viscosa* (Retz.) Trin.], but mycorrhizal colonization was low in all samples (<10%), and thus, these weeds may not be important for maintaining AMF abundances between growing seasons. Winter tillage reduced weed biomass by more than half in the fine sand as well, but this difference was not statistically significant ($p=0.28$), most likely due to the low number of replicates and the great variability between replicates. At this site, a perennial, rhizomonous grass (*Cynodon dactylon* (L.) Pers.) was the dominant weed with a mycorrhizal colonization of about 30%. In the black clay, all weeds consisted of less than 2-week-old broad leaf annuals. Due to their young age, they were not considered important for maintaining AMF abundance and thus, mycorrhizal colonization and shoot dry weight were not determined at this site.

Discussion

This work demonstrates that agricultural management practices differentially affect AMF abundance in these low-input cropping systems in the semi-arid tropics of Zimbabwe. In accordance with previous research in West Africa (Bagayoko et al. 2000), South America (Dodd et al. 1990; Sieverding and Leihner 1984), and India (Harinikumar and Bagyaraj 1988), subsistence crops differed in their effect on the subsequent AMF abundance. However, the underlying mechanisms remain uncertain. In the current study, there was no correlation between mycorrhizal colonization Year 1 and AMF abundance in Year 2, suggesting that a high mycorrhizal colonization by itself is not sufficient to increase AMF abundance. Instead, AMF abundance in Year 2 was positively correlated with plant biomass in Year 1 for three out of the four crops (Fig. 2). This positive relationship has been recorded previously by Osunde et al. (2003) working with promiscuous soybean (*Glycine max* (L.) Merrill) in West Africa. Thus, mycorrhizal crops that produce high biomass, and therefore in most cases possess a large root system that harbors AMF, could be important in building or maintaining a high AMF abundance in these cropping systems. In all three sites, the subsequent AMF abundance of the adjacent natural fallow Year 1 did not differ from AMF abundance observed after maize, pigeonpea, and lablab but was higher than the low-biomass-producing groundnut (data not shown). Contrary to some previous research (e.g. Howeler et al. 1987), natural fallows in these systems may not negatively impact AMF abundance as long as they are good hosts for AMF and produce a substantial amount of biomass.

Moderate P applications to these low-P soils tended to decrease AMF abundance slightly but not significantly. Unfortunately, available soil P levels were never measured after fertilization Year 1, but it is possible that they were still below inhibitory levels for mycorrhizal formation. In fact, Sieverding and Howeler (1985) showed that P applications up to 50 kg per ha actually increased root colonization in a Colombian agroecosystem, presumably due to an improved plant vigor.

Contrary to expectations, fallow period and winter tillage had no apparent effect on AMF abundance. Previous research in North America has shown that fallow periods and tillage can have substantial negative effects on AMF abundance (Kabir and Koide 2002; Kabir et al. 1997; McGonigle and Miller 1993). For example, growing a winter cover crop in Pennsylvania, USA increased the subsequent mycorrhizal colonization fourfold of the following crop compared with fallow (Boswell et al. 1998). The obligate nature of AMF makes it intuitive that fallow periods and disturbance would be harmful to the fungi irrespective of climate. Indeed, a 40% decline in viable AMF propagules was observed after a 3-month-long fallow period under warm and moist conditions (Harinikumar and Bagyaraj 1988). Nonetheless, a difference in fallow by up to 7.5 months in the current study did not result in any significant difference in subsequent AMF abundance (Table 2). There are several possible explanations for the lack of treatment effects seen here. First, higher soil water contents during fallows in mesic climates could be more harmful to AMF survival than the dry conditions in the semi-arid tropics. Indeed, results from pot studies have shown that AMF viability remains high for long periods under dry conditions (Tommertup and Abbott 1981; Brundrett et al. 1987; Pattison and McGee 1997; but see Jasper et al. 1989), possibly due to both lower fungal respiration and reduced activity of hyphal and spore grazing soil biota (Bakhtiar et al. 2001). However, the existence of the so-called long fallow disorder reported in Australia (Thompson 1987) indicates that fungal viability can decline during long fallow periods (exceeding 1 year) even in the semi-arid tropics. Second, spores can provide an important source of inoculum in the semi-arid tropics (Veenendaal et al. 1992), and they are less likely to be negatively affected by fallow periods and disturbance than external mycelia (Evans and Miller 1990) due to their large carbon reserve. The source of inoculum in the current study is unknown. However, the high early mycorrhizal colonization in both experiments is unlikely to be generated from spores alone because spore germination usually result in delayed colonization compared with colonization from root and hyphal fragments (Klironomos and Hart 2002). Third, it is possible that low-input systems support a higher overall abundance of AMF (Mäder et al. 2000), which could mask any treatment effects because root colonization is maximized in all treatments (McGonigle and Miller 2000). It is unlikely that this is the sole explanation for the result from this study, however, because no significant treatment effects were detected in the granitic sand in spite of overall lower mycorrhizal colonization. Furthermore, significant effects were detected when different crops were grown, indicating that AMF abundances can indeed be altered in these systems. Unfortunately, there was no way to alter fallow periods using the same crop in Experiment 2. It is possible, therefore, that the results from the fallow experiment were confounded by the different crop species used. However, maize and pigeonpea did not generate significantly different AMF abundances in Experiment 1 (Table 2) and were therefore viewed as essentially equivalent hosts here. Finally, we cannot exclude that the lack of tillage effect seen here is due to the lesser disturbance resulting from the animal-drawn plow compared to the tractor, which has been used in most previous studies where tillage effects have been documented.

Weeds can have both positive and negative effects in these cropping systems. On the one hand, they can maintain AMF activity if they themselves are good hosts and produce sufficient biomass as shown by Sieverding and Leihner (1984). On the other hand, they consume water (Twomlow and Bruneau 2000), which is often a limiting resource in these cropping systems. Winter tillage did significantly reduce weed biomass in the granitic sand, but this did not result in any reduction of subsequent AMF abundance, most likely due to a combined effect of low weed biomass production during the dry season and low mycorrhizal colonization (<10%). Weed-mediated survival of AMF between growing seasons, therefore, did not appear to be important at this site. However, weed production during the growing season appeared to be beneficial to AMF abundance because natural fallows resulted in higher AMF abundance than that observed from groundnut plots. Generalizations regarding the impact of weeds, therefore, appear to be difficult as they are both site and seasonal specific.

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