Contribution of arbuscular mycorrhizal fungi to pearl millet [Pennisetum glaucum (L.) R. Br.] nutrition on Sahelian acid sandy soils at various levels of soil degradation

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ABSTRACT

Land degradation may cause nutrient deficiencies for plant growth. These deficiencies can be partly compensated through plant association with arbuscular mycorrhizal (AM) fungi under the condition that the degradation status does not affect the symbiosis. We therefore investigated P and K uptake by millet [Pennisetum glaucum (L.) R. Br.] roots when associated with AM fungi from an acid sandy soil of the Sahel at 3 different levels of soil degradation. Millet was grown in an eight-week greenhouse pot experiment. Nutrient uptake was quantified on the basis of nutrient depletion in P and K-enriched soil tubes accessible to roots and hyphae or solely to hyphae compared to tubes inaccessible to roots and hyphae. Neither total millet biomass nor root colonisation frequency differed between the weakly and the medium degraded soils. However, total millet biomass and root colonisation frequency were 61% and 40% lower, respectively, on the severely degraded soil compared to the other two degradation levels (weakly and medium). Irrespective of the soil degradation status, AM fungi alone depleted total soil P by 24 mg P kg⁻¹ soil but they had very little effect on exchangeable K⁺ levels. AM fungi maintained their potential to contribute to millet P nutrition, irrespective of the soil degradation status. On severely degraded soils, the mycorrhizal fungi's contribution to millet nutrition may be depressed to some extent but not sufficiently to impact P uptake by hyphae once they have access to P inaccessible to roots.

INTRODUCTION

In the Sahelian zone of West Africa, sandy arenosols constitute prime land for the cultivation of the main staple crop, millet, (Manu et al., 1991). In Niger, such soils occupy 80 % of the land. Because of their low organic matter, clay and weatherable mineral content, these soils have an intrinsically low chemical fertility (Bationo and Mokwunye, 1991). The near absence of external nutrient input in traditional agriculture, the gradual shortening of the fallow period and the rapid increase in cultivated land acreage have led to land degradation by nutrient mining (Smaling et al., 1993), wind and water erosion (Sterk et
Land degradation is defined by FAO (2002) as the loss of production capacity of land in terms of loss of soil fertility, soil biodiversity and degradation of natural resources.

Large yield increases can be achieved by the application of mineral fertilizer (Bationo and Mokwunye, 1991). However under these environmental conditions, mineral fertilizer application alone may cause lower base saturation and soil acidification increase in exchangeable aluminum (Al) and decline in crop yields (Bationo et al., 1987; Bielders et al., 2004; Bationo et al., 2006).

On degraded soil, acidification leads to large increases in exchangeable Al which may enhance P fixation (Wendt et al., 1993; Kretzschmar et al., 1991; Bielders et al., 2002) and further reduce the availability of this nutrient generally considered to be the main chemical constraint for crop growth on these sandy acid soils (Payne et al., 1991). Acidification increases the availability of metal in the soil solution to toxic levels which can persist for extremely long periods of time. The changes in soil properties could be toxic for soil microorganisms (Chaudri et al., 1993).

Elevated (Al) availability limits plant growth on acidic soils. Although this element is found naturally in soils, acidic conditions create an environment where Al solubility increases and toxic forms of Al impact plant function. Plant resistance to Al is often attributed to organic acid exudation from plant roots and the chelation of cationic Al in the rhizosphere (Katrina et al., 2009). The association of arbuscular mycorrhizal (AM) fungi with the roots of plants may alleviate Al toxicity by altering soil Al availability or plant exposure through the binding of Al to fungal structures or through the influence of fungi on exudation from roots. Diverse communities of AM fungi are found in soil ecosystems and research suggests that AM fungi exhibit functional diversity that may influence plant performance under varying edaphic environments.

Soil degradation and particularly desertification reduces the inoculum potential of mutualistic microbial symbionts that are key ecological factors in governing the cycles of major plant nutrients and hence in sustaining the vegetation cover in natural habitats. The most important symbionts are (i) mycorrhizal fungi, which enhance the ability of plants to establish and cope in stress situations (nutrient deficiency, drought, soil disturbance, etc.) (Barea et al., 1997), and (ii) N-fixing rhizobia, which enable leguminous plants to flourish in the absence of adequate fixed N source. Soil microorganisms are known to play a key role in the mobilization and immobilization of metal cations, thereby changing their availability to plants (Birch and Bachofen, 1990).

AM fungi can alleviate Al toxicity and improve water relations, especially under nutrient limitation (Rufyikiri et al., 2000; Klugh et al., 2009). The extra radical hyphae of AM fungi contribute to soil aggregation and structural stability. Therefore, mycorrhizas are multifunctional in (agro) ecosystems (Newsham et al., 1995; St John, 2005) and potentially improved physical soil quality (through the external hyphae), chemical soil quality (through enhanced nutrient uptake), and biological soil quality (through the soil food web).

AM fungi have been shown to stimulate crop growth through a range of different mechanisms, including indirect effects related to morphological or physiological changes in the host plant induced by the fungi (Berta et al., 1993; Requena et al., 2001; Gamalero et al., 2004;) particularly in low P soils (Thomson, 1990; Kothari et al., 1991; Rubio et al., 2003). They can also act as bioprotectants against pathogens and toxic stresses (Jeffries et al., 2003).

For soils severely degraded by wind erosion, water erosion or nutrient mining in which root development is severely restricted as a result of chemical deficiencies (Michels et al., 1998), the contribution of AM fungi to plant nutrition could nevertheless be more
important than on non degraded soil under the condition that the degradation status does not affect the symbiosis between AM fungi and the host plant. However, the dominant effect can generally be ascribed to enhanced nutrient uptake by the crop through extra-radical hyphae which act as an extension of the root system and help overcome the diffusion-limited transfer of low mobility nutrients from the soil to the roots (Griffiths et al., 1999; Arvieu et al., 2003). Mycorrhizal infection may affect the mineral nutrition of the host plant directly by enhancing plant growth through nutrient acquisition by the fungus, or indirectly by modifying transpiration rates and the composition of rhizosphere microflora (Marschner et al., 1994).

For the major crops of the Sahel such as millet, cowpea (Vigna unguiculata) and sorghum (Sorghum bicolor), root colonization by AM fungi and their favourable effect on crop nutrient uptake has been demonstrated (Hafner et al., 1993; Bagayoko et al., 2000). However, because millet develops an extensive root system with high root length densities, the relative impact of AM fungi on millet nutrient uptake is less than for leguminous crops or other semi-arid cereals (Subbarao et al., 1985; Isobe and Tsuboki, 1999; Bagayoko et al., 2000). But millet and corn seems to have the ability to induce multiplication of AM spores in the soil (Muok et al., 2009).

Phosphorus uptake by plants is determined not only by the solubility and mobility of P in soil, but also, by plant properties, for instance the total root length, reflecting the capacity of a plant to acquire nutrient (Jungk and Cloasen, 1989). This would be of particular relevance to P nutrition which has low mobility in most soils.

In soil solution, the concentration of phosphorus is very low and is transported to roots mainly via diffusion. However, the diffusion coefficient of P is very low and consequently P is easily depleted from the root zone. A mycorrhizal association can greatly increase a plant’s access to P sources in the soil (Nasim, 2005).

By extending beyond the depletion zone for phosphorus around the root, the external mycelium improves phosphorus absorption. Calculations have shown that a root associated with mycorrhizal fungi can transport phosphorus at a rate more than four times higher than that of a root not associated with mycorrhiza (Nasim, 2005).

Although K is seldom a limiting nutrient on the Sahel acid sandy soils, it was included in this study as it is nevertheless an essential element for plant growth and K reserves in these soils are generally very low (De Ridder and Van Keulen, 1990; Rebafka et al., 1994).

Millet is one of the major staple crops in the semi-arid tropics of Asia and Africa for Centuries. It is the principal source of energy, protein, vitamins and minerals for millions of poorest people in these regions (Codex Alimentarius Commission, 1990).

Unreliable rain fall and low nutrient availability in particular of P (Bationo et al., 1990) are the major constraints to pearl millet (Pennisetum glaucum L.).

The objective of this study was to evaluate the impact of the Sahel acid sandy soils' degradation level on: (i) yield (ii) indigenous AM fungi and parameters evolution ; (iii) the effects of indigenous AM fungi on millet plants growth and (iii) P and K uptake by millet, using a controlled pot trial to differentiate the contribution of roots and AM fungi to nutrient uptake by crops.

**MATERIALS AND METHODS**

**Site description**

**Field experiment**

The experiment was a randomized complete block design with three treatments replicated three times. The three treatments consisted in an annual surface application of 2 t millet stover ha\(^{-1}\), a one time application of synthetic mulch made of plastic tubing with a surface cover equivalent to 2 t ha\(^{-1}\) of millet stover, and a control without mulching. All treatments were planted annually with pearl millet (Pennisetum glaucum (L.) R. Br.) following a density of 10 000 hills ha\(^{-1}\) and...
were fertilized annually with 30 kg ha\(^{-1}\) of N and P\(_2\)O\(_5\). For further details on the experimental layout, the reader is referred to Buerkert and Lamers, 1999).

**Soil sampling**

Soil was sampled from selected treatments in an experimental field of the ICRISAT Sahelian Centre at Sadoré, Niger (13°15 N, 2°18 E). The site had been used from 1992 to 1994 for an experiment aimed at investigating mulch effects on soil erosion and pearl millet yields. The soil at the experimental site was classified as a psammentic paleustalf (West et al., 1984; Soil Survey Staff, 1990), or luvic arenosol (FAO, 1998).

In 1995 and 1996, the bare and millet stover mulched treatments were continued as described above. On the plots previously covered with the plastic mulch, 2 t ha\(^{-1}\) millet stover mulch was applied starting in 1995. This treatment will nevertheless be referred to as the 'plastic mulch treatment' hereafter. After 1994, no fertilizer was applied on any of these three treatments. All treatments were planted with pearl millet as previously.

**Pot experiment**

In order to study the contribution of indigenous AM fungi to P and K nutrition of millet, a greenhouse pot experiment was carried out using soil from the above-mentioned treatments.

The contribution of AM fungi to P and K uptake was evaluated using the method described by (George et al., 1996). PVC tubes of 50 mm diameter and 0.110 mm height were used. The bottom of these tubes were sealed and pierced with a set of 9 holes of 0.02 m diameter (total surface area per tube is 28 cm\(^2\)). For bulk soil tubes, the holes were covered by fixing around the tube a net with 0.45 µm mesh size membrane (Sartorius) which is not penetrable to roots or AM fungi hyphae. For “hyphal tubes” the net was replaced by a 30 µm mesh size penetrable to both roots and AM fungi ('Root + AM fungi tube).

Each tube was filled with 300 g air dry soil and placed in already made pot at planting. The soil used for the experience was excavated in air-dry condition at the end of the dry season on 16 May 1997 to a depth of 20 cm in all 3 replicates of the selected treatments. For each of the 9 plots, 2 plastic buckets were filled with 52.5 kg of air dry soil, for a total of 18 pots.

The soil was supplied with Nitrogen which was added as Calcium Ammonium Nitrate fertilizer (28% N content) at a rate of 27 mg N kg\(^{-1}\) soil (equivalent to approx. 60 kg N ha\(^{-1}\) for a depth of 20 cm and a bulk density of 1500 kg m\(^{-3}\)). No P or K fertilizer was added in the pots. Except that it was enriched in P and K in order to ease the detection of P and K depletion (George et al., 1996). P was added as Ca(HPO\(_4\))\(_2\) salt at a rate of 11.6 mg P kg\(^{-1}\) and K was added as K\(_2\)SO\(_4\) at a rate of 22 mg K\(_2\)O kg\(^{-1}\) soil, corresponding to a rate of 60 kg P\(_2\)O\(_5\) ha\(^{-1}\) and 60 kg K\(_2\)O ha\(^{-1}\), respectively. Each tube extended 10 mm above the soil surface. Care was taken to ensure good contact between the soil in the pots and the tubes.

Soil nutrient depletion in the different tubes was measured to compare nutrient depletion by roots versus hyphae.

The soil was wetted to a gravimetric water content of 10%, closed to field capacity. Prior to planting, the soil from the experimental plots was analysed for pH (1M KCl, 1:2.5 soil:water), exchangeable cations and Al\(^{3+}\) (Houba et al., 1995), plant available P (P-Bray 1) Olsen and Sommers (1982). At the beginning of the experiment, tubes were filled with the same moistened soil as the pot in which it was placed.

Fifteen seeds of a local landrace of millet, Sadoré Local, were sown in the middle of each pot 5 cm below the surface on 18 June 1997. Seedlings were thinned to three plants per pot 3 weeks after sowing. Water content of the pots was monitored gravimetrically, and
then using a three-pronged 0.2 m long TDR probe (Trase®) permanently installed in each pot, and was watering daily to bring the soil back to 10% gravimetric water content. Because of the constraints to monitor water content in the PVC tubes after installation and the need to avoid excess water conditions or leaching of nutrients through the meshes, the tubes were covered with a loose lid to minimize evaporative losses. The soil of the tubes was wetted only twice after starting the experiment, based on visual observations of the dryness status of the surface of the soil in the tubes.

Millet was harvested 8 weeks after planting on 14 August 1997. Roots from the pot were separated from the soil by sieving on a 2 mm mesh. Above and below ground dry matter was determined after oven drying at 60 °C. For the PVC tubes, roots were separated from the soil as described above and conserved in a refrigerator at 4 °C till further use. The soil from the tubes was then also analysed for pH (KCl), exchangeable potassium as described above, and for total P (Olsen and Sommers, 1982).

Roots’ observations

Root colonization by AM fungi was evaluated for each pot after trypan blue root coloring (Philips and Hayman, 1970). For each sample, 30 root segments of 1 cm length, were observed using an optical microscope and they were assessed for arbuscular mycorhizal fungi root colonization rate and frequency, and also for AMF content. Colonization frequency was calculated based on the percentage of root segments of a given sample colonized by AM fungi. The rate of colonization (%) refers to the proportion of the cortex colonised by AM fungi in the part of the root system that is colonized by the AM fungi, whereas AMF content refers to the proportion of the root cortex containing arbuscules (Trouvelot et al., 1986).

Statistical analysis

Statistical analysis was done using “Proc Anova” (Genstat 4.0 from Lawes Agricultural Trust, 1996) after log transforming yield data that were not normally distributed, in order to determine the statistical differences among the treatments. Specific pair-wise comparisons of treatments and years levels were done using the s.e.d test at P<5%.

RESULTS

Field experiment

Degradation levels and yield

With 486 and 544 mm respectively, 1995 and 1996 were years with slightly below or near the long-term average annual rainfall of 550 mm, without marked dry spells. On average over 1995 and 1996, total dry matter (TDM) yields on the continuously mulched plots reached 1521 kg ha⁻¹ yr⁻¹ (Table 1), which can be considered near average for the region. The continuously bare plots yielded 165 kg TDM ha⁻¹ yr⁻¹. At this level of productivity, farmers would normally abandon their field for more productive land. The plastic mulch plots yielded 753 kg TDM ha⁻¹ yr⁻¹. There was no significant treatment by year interaction for TDM (Table 1). The yield trends shown in Table 1 reveal an increasing degree of degradation from the plots continuously mulched with millet Stover (weakly degraded) to the continuously bare plots (strongly degraded), with intermediate productivity observed on the plastic mulch plots (medium degraded).

As a result of these treatments, millet total dry matter production continuously declined from about 2350 kg ha⁻¹ in 1992 to 290 kg ha⁻¹ in 1994 on bare plots, and from 3200 kg ha⁻¹ to 1100 kg ha⁻¹ on plots mulched with millet stover, with intermediate results for the plots covered by synthetic mulch.

Soil chemical properties

The soil chemical properties showed increasing levels of exchangeable Al³⁺ and decreasing levels of plant available P and soil pH as the degradation status went from weakly degraded to severely degraded (Table 2). For exchangeable K⁺, Ca²⁺ and Mg²⁺ only small differences existed between the weakly and medium degraded treatments, but larger
differences in nutrient content were observed between those two treatments and the severely degraded treatment.

**Pot experiment**

**Shoot and root dry matter**

Eight weeks after sowing, there was no significant effect of the soil degradation status on plant shoot and plant root dry matter (Figure 1). However, large differences were observed between the severely degraded treatment and the other two treatments. Shoot and root dry matter for the severely degraded treatment were, respectively, 68 and 56% lower than the weakly degraded treatment. The absence of significant effect of soil degradation status on plant growth largely reflects the large within treatment variability (CV = 27% and 41% for shoot and root dry matter, respectively). This variability is a typical characteristic of the Sahelian environment (e.g., Buerkert et al., 1995; Scott-Wendt, 1988), and agrees with the very high variability observed in the field plots.

**Nutrient uptake**

AM fungi significantly reduced total soil P levels in the absence of roots by 24 mg P kg\(^{-1}\) soil (s.e.d. = 10.6; P < 0.048), but only very little additional P was extracted in the presence of roots (Figure 2). There was no statistically significant difference between soil degradation levels with respect to the depletion of total P by AM fungi or roots, nor any significant degradation by tube type interaction. On average, AM fungi and the association roots+AM fungi reduced exchangeable K\(^+\) levels by 0.008 and 0.065 cmol kg\(^{-1}\), respectively (P < 0.001). There was a significant degradation by tube type interaction for exchangeable K\(^+\) levels (P < 0.026). Exchangeable K\(^+\) levels were reduced mostly in the combined presence of roots and hyphae, but this effect was stronger in the weakly and medium degraded soils than in the severely degraded soil (Figure 3). AM fungi alone had very little effect on exchangeable K\(^+\) levels, irrespective of soil degradation levels.

**AM infection**

Frequency was higher in weakly (93%) and medium (95%) degraded soils than in severe one (56%). The intensity of infection (% M) was higher in weakly degraded soil (24%) than in medium (14%) and severe (4%) degraded soils (Table 3).

The highest value for percentage arbuscules was found in weakly degraded soil (8.9%) and the lowest in severe degraded soil (0.6%).

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**Table 1:** Total dry matter yield for the three treatments (average over 1995 and 1996).

| Treatment               | Total dry matter\(^1\) |
|-------------------------|------------------------|
| Continuously mulched    | 3.182                  |
| Plastic mulch           | 2.877                  |
| Continuously bare       | 2.217                  |
| ANOVA                   |                        |
| Treatment *             |                        |
| Year ns                 |                        |
| Treatment x Year ns     |                        |
| s.e.d. (treatment effect)| 0.279                 |
| C.V. (%)                | 12                     |

\(^1\) Log-transformed data was used to correct for skewed distribution of untransformed data.
Table 2: Selected soil chemical properties of the experimental treatments in 1997 at the time of soil sampling immediately prior to the pot experiment.

| Degradation status | pH (KCl) | Exchangeable cations | P-Bray 1 |
|--------------------|----------|----------------------|----------|
|                     |          | K⁺ | Ca²⁺ | Mg²⁺ | Al³⁺ | cmol+ kg⁻¹ | mg kg⁻¹ |
| Weak               | 4.26     | 0.084 | 0.235 | 0.094 | 0.143 | 13.0 |
| Medium             | 4.16     | 0.088 | 0.247 | 0.075 | 0.280 | 12.1 |
| Severe             | 4.07     | 0.073 | 0.179 | 0.065 | 0.423 | 6.2  |

ANOVA

| F prob | ns | ns | ns | ns | * | * |
| s.e.d. | 0.06 | 0.008 | 0.031 | 0.019 | 0.063 | 1.7 |
| C.V. (%) | 1.8 | 12.4 | 17.1 | 30.5 | 27.5 | 20.3 |

(ns = insignificant; * = significant).

Table 3: Frequency, rate of root colonisation by AM fungi, and arbuscular content of millet roots in the Root+AM fungi tubes.

| Degradation level | Frequency | Rate | Arbuscular content |
|-------------------|-----------|------|--------------------|
|                   | %         | %    | %                  |
| Weak              | 93        | 24   | 8.9                |
| Medium            | 95        | 14   | 2.6                |
| Severe            | 56        | 4    | 0.6                |

ANOVA

| F probability | 0.04 | 0.14 | 0.44 |
| s.e.d.        | 10.3 | 8.0  | 5.99 |
| C.V. (%)      | 26   | 89   | 267  |

(AM = Arbuscular Mycorrhizal, CV = Coefficient of Variation)

Figure 1: Millet plant and root dry matter in pot experiment at harvest as affected by soil degradation status. Error bar = s.e.d.
Figure 2: Effect of AM fungi and millet roots on total P content in soil tubes inaccessible to roots and hyphae ('Control'), accessible to hyphae only ('Hyphae') or accessible to hyphae and millet roots ('Roots+Hyphae'). Average over all degradation levels (Error bar = s.e.d., P = Phosphorus).

Figure 3: Effect of AM fungi and millet roots on exchangeable K⁺ in soil tubes inaccessible. To roots and hyphae ('Control'), accessible to hyphae only ('Hyphae') or accessible to hyphae and millet roots ('Roots+Hyphae') for a) weakly, b) medium, and c) severely degraded soil (Error bar = s.e.d., Exch = exchangeable, K = Potassium).
DISCUSSION

Both the observed millet yields in 1995 and 1996 and the measured soil chemical properties clearly demonstrated the increasing levels of soil degradation from the continuously mulched plots (weakly degraded) to the continuously bare plots (strongly degraded; Tables 1 and 2). Plant available P was high on the weakly and medium degraded plots, reflecting past P fertilization. Although in principle well in excess of the soil P content requirement for optimal millet growth on these sandy soils (Bationo et al., 1991), plant available P content as determined by the Bray-1 method may not properly reflect P fixation by exchangeable Al and may therefore overestimate plant available P on acidified soils such as in the case of the medium and strongly degraded treatments. The lower P content of the strongly degraded plot likely reflects P losses following soil erosion by wind and water (Buerkert and Lamers, 1999). It has been shown on the basis of a controlled pot experiment that N and P were the primary limiting chemical elements on the weakly and severely degraded plots, respectively (Michels et al., 1998).

Differences in millet growth in the pot experiment were only apparent between the weakly and medium degraded treatments vs. the severely degraded treatments (Figure 2).

The P and K enrichment of the soil in the AM fungi and roots+AM fungi tubes may have contributed to this situation by providing a readily available source of P once the tubes were colonized by AM fungi or roots. Plant growth in the pot experiment may therefore not properly reflect the soil degradation status.

We used in this experiment the indigenous arbuscular fungi, because some studies showed that the use of an exotic and not indigenous strains of mycorrhizal fungus shows some time absence of plant response (Plenchette et al., 2000).

It is important to note that millet as other grasses has a low mycorrhizal dependency although increases in plant response were obtained (Subba Rao et al., 1985). These increases change the base on millet genotypes (Krishna et al., 1985) and mycorrhizal strains used (Krishna and Darf, 1985).

The large difference in root colonization frequency in the root+AM fungi tubes between the strongly degraded treatment and the two less degraded treatments may reflect lower levels of AM fungi propagules or reduced mycorrhizal symbiosis in the severely degraded soil. Other studies in the tropics have shown, however, that bare land may support few propagules, possibly as a result of lack of roots to produce propagules (Cuenca et al., 1998; Fischer et al., 1994). Similarly, Roldan et al. (1997) observed under semi-arid Mediterranean conditions that the number of spores as well as the percentage of root length colonized by AM fungi increased with the duration of recovery of abandoned cultivated land, suggesting that cultivation and degradation resulting from cropping, negatively affected AM fungi spore numbers and root colonization Kabir (2005).

Alternatively, it may also reflect the shorter exposure time of roots to AM fungi in the root+AM fungi tubes of the strongly degraded soil, as explained above. Bagayoko et al. (2000) reported that P application at rates similar to the one used here had no negative impact on root colonization rate by AM fungi on similar soils. P addition in the tubes therefore does not explain the lower root colonization frequency. Once colonized, the degradation status of the soil clearly did not impact the rate of mycorrhization or arbuscular content.

The main mechanisms for acidification in the soil are the loss of nutrients by leaching, application of acidifying mineral fertilizers containing ammonium, and excess uptake of cations by the crop compared to anions. The process can be enhanced by loss of buffering capacity as could result from a decline in soil organic matter content. In the present experiment, leaching was prevented because of the controlled water supply, and fertilizer additions were identical for all treatments. In addition, organic carbon content was not
significantly different among degradation levels.

AM fungi alone significantly reduced total P content, irrespective of the degradation level (Figure 3). This demonstrates that AM fungi have the potential to contribute substantially to P nutrition of millet, especially from P sources that would be inaccessible to roots such as inside compacted layers or dense aggregates. The small additional P depletion observed in the presence of roots does not necessarily imply that roots do not contribute to P uptake but rather that total P uptake was limited irrespective of the source (root or hyphae). The potential of AM fungi to increase P uptake by many different crops is well documented (Barea, 1991). Although, Bagayoko et al. (2000) did not observe a significant impact of AM fungi on plant P uptake for unfertilized and P-fertilized acid sandy soil from Western Niger. George et al. (1996) reported P depletion in hyphal tubes of sterilized soils, which they attributed to P uptake by root hairs that may have extended several millimeters into the hyphal tubes and to P diffusion from the enriched soil in the tubes to the non enriched bulk soil in the pots. In the present experiment, these mechanisms are expected to have a much lower impact on P depletion in AM fungi tubes than in the study of (George et al., 1996) given the much larger diameter of the tubes in the present experiment (50 mm diam. vs. 18 mm diam).

In addition, the very low K depletion in the hyphal tubes further indicates that nutrient diffusion and uptake by root hairs in hyphal tubes was minimal. Given the lower solubility of P vs. K, the contribution of diffusion to P depletion in the hyphal tubes can therefore also be assumed to be small.

The absence of degradation effect on P depletion by AM fungi appears to indicate that nutrient uptake by AM fungi was not affected by the degradation level of the soil, despite the lower colonization rate. At nearly 60%, the colonization rate in the severely degraded soil may have been sufficient to ensure ample transfer of P to the crop. This is reasonably close to the 80% root colonization rate reported by Pande and Tarafdar (1999) to be optimal for millet. The present experiment clearly demonstrates that AM fungi may contribute substantially to P nutrition of millet. However, although root colonization rates may be somewhat reduced as the degradation level increases. It appears that the results of the present experiment assess only that the degradation level did not reduce the potential of AM fungi to contribute to P nutrition if P sources occluded from roots are available.

As opposed to P, K uptake occurred mostly through roots, the contribution of AM fungi being insignificant (Figure 4). This concurs with previous studies (Barea, 1991; George et al., 1999; Bagayoko et al., 2000) and may be related to the higher mobility of K in these sandy soils.

The difficulty was to assess the actual contribution of this association to plant nutrient uptake under field conditions. Mycorrhizal association is ubiquitous. In field, the lack of non mycorrhizal “control” individuals precludes in the quantification of relative benefits or drawbacks of mycorrhizal colonization in these situations (George et al., 1995).

To this end, it seems interesting to focus our researches on the investigation of our cultural practices that will enhance soil biological activity (the development of indigenous arbuscular mycorrhizal fungus and improvement of their efficiency on the plant development) and optimize nutrient cycling.

Various tillage practices used in the management of soil for maximum crop production may negatively impact the survival of AM fungal propagules (Kabir, 2005).

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REFERENCES
Arvieu J-C, Leprince F, Plassard C. 2003. Release of oxalate and protons by ectomycorrhizal fungi in response to P-deficiency and calcium carbonate in nutrient solution. Annals of Forest Science, 60: 815–821
Bagayoko M, George E, Römheld V, Buerkert A. 2000a. Effects of mycorrhizae and phosphorus on growth and nutrient uptake of millet, cowpea and sorghum on a West African soil. J. Agric. Sci., 135: 399-407.
Barea JM, Azcón-Aguilar C, Azcón R. 1997. Interactions between mycorrhizal fungi and rhizosphere microorganisms within the context of sustainable soil-plant systems. In Multitrophic Interactions in Terrestrial Systems. Backwell Science, Gange AC, Brown VK (eds). Cambridge: United Kingdom; 65-77.
Barea JM. 1991. Vesicular-arbuscular mycorrhizae as modifiers of soil fertility. In Advances in Soil Science, Stewart BA (ed). Springer Verlag: New York, USA; 1-40.
Bationo A, Christion, CB, Mokwunye AU. 1987. Soil fertility management of the Millet –producing in the sandy Soils of sahelian West Africa: the Niger Experience. Paper presented at the workshop on Soil and Crop management System for Rained Agriculture in the Sudan- sahelian zone, International Crops Resarch Institute for the Semi-Arid Tropics (ICRISAT), Niamey, Niger.
Bationo A, Christianson CB, Baethgen WE. 1990. Plant density and nitrogen effects on pearl millet production in Niger. Agronomy Journal, 82: 290-294.
Bationo A, Baethgen WE, Christianson CB, Mokwunye AU. 1991. Comparison of five soil testing methods to establish phosphorus sufficiency levels in soil fertilized with water-soluble and sparingly soluble-P sources. Fert. Res., 28: 271-279.
Bationo A, Mokwunye AU. 1991. Alleviating soil fertility constraints to increased crop production in West Africa: The experience in the Sahel. Fert. Res., 29: 95-115.
Bationo A, Hartemink A, Lungu O, Naimi M, OkothP, Smaling E, Thombiano L. 2006. African soils: Their Productivity and Profitability of Fertilizer Use. Africa fertilizet Summit. 9-13 June 2006 Abuja, Nigeria.
Berta G, Fusconi A, Trotta A. 1993. VA mycorrhizal infection and the morphology and function of root systems. Environ. Exp. Bot. 33: 159-173.
Bielders CL, Michels K, Bationo A. 2002. On-farm evaluation of ridging and residue management options in a Sahelian millet-cowpea intercrop. I. Soil quality changes. Soil Use Manage, 18: 216-222.
Bielders CL, Michels K, Rajot JL. 2000. On-farm evaluation of ridging and residue management practices to reduce wind erosion in Niger. Soil Sci. Soc. Am. J., 64: 1776-1785.
Bielders C, Rajot J-L., Karlheinz M. 2004. L’érosion éolienne dans le Sahel nigérien: influence des pratiques culturales actuelles et méthodes de lutte, Sécheresse, 15(1): 19-32.
Birch LD, Bachofen R. 1990. Effects of microorganisms on the environmental mobility of radionucleides. In Soil biochemistry (vol. 6), Bollang. JM, Slozky G (eds). New York: New York.
Bonfante P, Perotto S. 1995. Strategies of arbuscular mycorrhizal fungi when infecting host plants. New phytologist, 130(1): 3.
Buerkert A, Lamers JPA. 1999. Soil erosion and deposition effects on surface characteristics and pearl millet growth in

934
the West African Sahel. *Plant Soil*, 215: 239-253.

Buerkert A, Bationo A, Dossa K. 2000. Mechanisms of residue mulch-induced cereal growth increases in West Africa. *Soil Sci. Soc. Am. J.*, 64: 346-358.

Buerkert A, Stern RD, Marschner H. 1995. Post stratification clarifies treatment effects on pearl millet growth in the Sahel. *Agron. J.*, 87(4): 752-761.

Carpenter FL, Mayorga SP, Quintero EG, Schroeder M. 2001. Land-use and erosion of a Costa Rican Ultisol affect soil chemistry, mycorrhizal fungi and early regeneration. *Forest Ecol. Manag.*, 144: 1-17.

Chaudri AM, McGrath SP, Giller KE, Rietz E, Sauerbeck D. 1993. Enumeration of indigenous *Rhizobium leguminosarum* biovar trifolii in soils previously treated with metal sewage sludge. *Soil Biol. Biochem.*, 25: 301-309.

Codex Alimentarius Commission. 1990. Codex standards for cereals, pulses, legumes and derived products. *FAO/WHO, Rome.*

Cuenca G, De Andrade Z, Escalante G. 1998. Diversity of Glomalean spores from natural, disturbed and revegetated communities growing on nutrient-poor tropical soils. *Soil Biol. Biochem.*, 30: 711-719.

De Ridder N, Van Keulen H. 1990. Some aspects of the role of organic matter in sustainable intensified arable farming systems in West African semi-arid tropics (SAT). *Fert. Res.*, 26: 299-310.

Del Val C, Barea JM, Azcon-Aguilar. 1998. Diversity of *Arbuscular mycorrhizal* fungus populations in heavy-metal-contaminated soils: *Appl. Environ. Microbiol.*, 65(2): 718-723.

European Commission - DG ENV. 2010. Soil biodiversity: functions, threats and tools for policy makers.

FAO. 1998. World reference base for soil resources. ISSS/ISRIC/FAO: Rome, Italy.

FAO. 2002. *Land Degradation Assessment in Drylands*. Rome: Italy; 18.

Fischer CR, Janos DP, Perry DA, Linderman RG, Sollins P. 1994. Mycorrhiza inoculum potentials in tropical secondary succession. *Biotropica*, 26: 369-377.

Gamalero E, Trotta A, Massa N, Copetta A, Martinotti MG, Berta G. 2004. Impact of two fluorescent pseudomonads and an arbuscular mycorrhizal fungus on tomato plant growth, root architecture and P acquisition. *Mycorrhiza*, 14: 185-192.

George E, Gorgus E, Schmeisser A, Marschner H. 1996. A method to measure nutrient uptake from soil by mycorrhizal hyphae. In *Mycorrhizas in Integrated Systems from Genes to Plant Development* Azcon-Aguilar C, Barea JM (eds). Office for Official Publications of the European Community: Luxembourg; 535-538.

George E, Haussler KU, Vetterlein D, Gorgus E, Marschner H. 1999. Water and nutrient translocation by hyphae of Glomus-Mosseeae. *Can. J. Bot.*, 70(11): 2130-2137.

George E, Häussler K, Kothari SKLiXL, Marschner H. 1992. Contribution of mycorrhizal hyphae to nutrient and water uptake by plants. In *Mycorrhizae in Ecosystems*, Read DJ (ed).

George E, Marshner H. Jacobsen. 1995. Critical reviews. *Biotechnology*, 15(3/4): 257-270.

Griffiths BS, Bonkowski M, Dobson G, Caul S. 1999. Changes in soil microbial community structure in the presence of microbial-feeding nematodes and protozoa. *Pedobiologia*, 43: 297-304.

Hafner H, George E, Bationo A, Marschner H. 1993. Effect of crop residues on root growth and phosphorus acquisition of...
pearl millet on an acid sandy soil in Niger. *Plant Soil*, **150**: 117-127.

Houba VJG, Van der Lee JJ, Novozamski I. 1995. Soil analysis procedures, other procedures. Dept. *Soil Sci. and Plant Nutr.,* Wageningen University: Wageningen, The Netherlands.

Isobe K, Tsuboki Y. 1999. The relationship between growth promotion by arbuscular mycorrhizal fungi and root morphology and phosphorus absorption in gramineous and leguminous crops. *Jpn J Crop Sci*, **67**: 347-352.

Jasper DA, Abbott L, Robson AD. 1991. The effect of soil disturbance on vesicular arbuscular mycorrhizal fungi in soils from different vegetation types. *New Phytol.*, **118**: 471-476.

Jeffries P, Gianinazzi S, Perotto S, Turnau K, Barrea JM. 2003. The contribution of arbuscular mycorrhizal fungi in sustainable maintenance of plant health and soil fertility. *Biol. Fert. Soils*, **37**: 1-16.

Jung K, Claassen N. 1986. Availability of phosphate and potassium as the result of interactions between root and soil in the rhizosphere. *Z. Pflanzenernähr. Boden Kd.*, **149**: 411-427.

Kabir Z. 2005. Tillage or no-tillage: Impact on mycorrhizae. *Canadian Journal of Plant Science*, **85**(1): 23-29.

Klugh-Stewart K, Cumming R. 2009. Organic acid exudation by mycorrhizal *Andropogon virginicus* L. (broomsedge) roots in response to aluminum. *Soil Biol. Biochem.*, **41**: 367-373.

Koomen I, McGrath SP, Giller K. 1990. Mycorrhizal infection of clover is delayed in soils contaminated with heavy metals from past sewage sludge applications. *Soil Biol. Biochem.*, **22**: 871-873.

Khothari SK, Marschner H, Römheld V. 1991. Contribution of the VA Mycorrhizal hyphae in acquisition of phosphorus and zinc by maize grown in a calcareous soil. *Plant and soil*, **131**: 177-185.

Kretzschmar RM, Hafner H, Bationo A, Marschner H. 1991. Long- and short-term effects of crop residues on aluminum toxicity, phosphorus availability and growth of pearl millet in an acid sandy soil. *Plant Soil*, **136**: 215-223.

Krishna KR, Shetty KG, Dart PJ, Andrews DJ. 1985. Genotype dependent variation in mycorrhizal colonization and response to inoculation of pearl millet. *Plant and soil*, **86**: 113-125.

Krishna KR, Dart PJ. 1984. Effect of mycorrhizal inoculation and soluble phosphorus fertilizer on growth and phosphorus uptake of pearl millet. *Plant and soil*, **81**: 247-256.

Lawes. 1996. *Agricultural Trust: Genstat 5, Release 3.2.* Oxford Science Publications, Clarendon Press: Oxford, UK; 796.

Loth C. 1996. Abundance of arbuscular mycorrhizal fungi spores at different native sites in dependence of sludge applications. *Bodenkultur*, **47**: 89-96.

Manu A, Bationo A, Geiger SC. 1991. Fertility status of selected millet producing soils of West Africa with emphasis on phosphorus. *Soil Science*, **152**: 315-320.

Marschner H, Dell B. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant Soil*, **159**: 89-102.

Michels K, Bielders CL, Mühlig-Versen B, Malher F. 1998. Rehabilitation of degraded land in the Sahel: an example from Niger. In *Towards Sustainable Land Use: Furthering cooperation between people and institutions,* Blume HP, Eger H, Fleischhauer E, Hebel, Reij AC, Steiner KG (eds). Catena Verlag GMBH: Reiskirchen, Germany; 1287-1293

Muok BO, Matsumura A, Ishii T, Odee DW. 2009. The effect of intercropping
Sclerocarya birrea (A. Rich.) Hochst., millet and corn in the presence of arbuscular mycorrhizal fungi. *African Journal of Biotechnology*, 8(5): 807–812.

Nasim G. 2005. The role of symbiotic soil fungi in controlling roadside erosion and the establishment of plant communities. *Caderno de Pesquisa serie Biologia*, 17(1): 119-136.

Newsham KK, Fitter AH, Watkinson AR. 1995. Multi-fonctionality and biodiversity in arbuscular mycorrhizas trends. *Ecol. Evol.*, 10: 407-411.

Requena N, Perez-Solis E, Azcón-Aguilar C, Jeffries P, Barea JM. 2001. Management of indigenous plant-microbe symbioses aids restoration of desertified ecosystems. *Applied and Environmental Microbiology*, 6(2): 495-498.

Olsen SR, Sommers LE. 1982. Phosphorus. In *Methods of Soil Analysis. Part II. Chemical and Microbiological Properties*, Page AL, Miller RH, Keeney DR (eds). ASA and SSSA: Madison, WI, USA; 403-430.

Pande M, Tarafdar JC. 1999. Critical level of VAM fungal propagules in different arid crops. *Agrochimica*, 43: 187-192.

Payne WA, Lascano RJ, Hossner LR, Wendt CW, Onken AB. 1991. Pearl millet growth as affected by phosphorus and water. *Agron. J.*, 83: 942-948.

Philips JM, Hayman DS. 1970. Improved procedure for cleaning roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Br. Mycol. Soc.*, 55: 158-161.

Plenchette C, Bois JF, Dupponnais R, Cadet P. 2000. La mycorhization (Glomus aggregatum) du mil (pennisetum glaucum). *Etude et gestion du sol*, 7(4): 379-384.

Rebakfa FP, Hebel A, Batiano A, Stahr K, Marschner H. 1994. Short- and long-term effects of crop residues and of phosphorus fertilization on pearl millet on an acid sandy soil in Niger, West Africa. *Field Crop Res.*, 36: 113-124.

Roldan A, Garcia C, Albaladejo J. 1997. AM fungal abundance and activity in a chronosequence of abandoned fields in a semi-arid Mediterranean site. *Arid Soil Res. Rehab.*, 11: 211-220.

Rubio R, Borie F, Schalchli C, Castillo C, AZcon R. 2003. Occurrence and effect of arbuscular mycorrhizal propagules in wheat as affected by the source and amount of phosphorus fertilizer and fungal inoculation. *Appl. Soil Ecol.*, 23: 245-255.

Rufyikiri G, Declerck S, Dufey JE, Delvaux B. 2000. Arbuscular mycorrhizal fungi might alleviate aluminium toxicity in banana plants. *New phytol.*, 148: 343-352.

Smaling EMA, Stoorvogel JJ, Windmeijer PN. 1993. Calculating soil nutrient balances in Africa at different scales. 2. District scale. *Fert. Res.*, 35(3): 237-250.

St. John T. 2005. The Instant Expert Guide to Mycorrhiza. The Connection for Functional Ecosystems. www.mycorrhiza.org/EXPERTflat.PDF.

Subba Rao NS, Tilak KVBR, Singh CS. 1985. Effect of combined inoculation of *Azospirillum brasilense* and vesicular arbuscular mycorrhiza on pearl millet. *Plant and Soil*, 84: 283-286.

Sureshkumar Singh IS, Tiwarii SC, Dkhar MS. 2003. Species diversity of vesicular-arbuscular mycorrhizal (VAM) fungi in jhum fallow and natural forest soils of Arunachal Pradesh, north eastern India. *Tropical Ecology*, 44(2): 207-215.
Sterk G, Herrmann L, Bationo A. 1996. Wind-blown nutrient transport and soil productivity changes in Southwest Niger. *Land Degrad. Develop.*, 7: 325-335.
Thompson P. 1990. Soil sterilization methods to show VA mycorrhizae aid P and zinc nutrition of wheat in vertisols. *Soil Biol. Biochem.*, 22: 229-240.
Trouvelot A, Kough JL, Gianinazzi-Pearson V. 1986. Mesure du taux de mycorrhization VA. d'un système radiculaire. Recherche de méthode d'estimation ayant une signification fonctionelle. In *Physiological and Genetic Aspects of Mycorrhiza*, Gianninazzi-Pearson V, Gianninazzi S (eds). INRA: Paris; 217-221.
Wendt JW, Berrada A, Gaoh MG, Schulze DG. 1993. Phosphorus sorption characteristics of productive and unproductive Niger soils. *Soil Sci. Soc. Am. J.*, 57: 766-773.
West LT, Wilding LP, Landeck JK, Calhoun FG. 1984. Soil survey of the ICRISAT Sahelian center, Niger, West Africa. Texas A&M University / ICRISAT: College Station, Texas, USA, p. 66.