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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.

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Keywords: Land degradation status, indigenous arbuscular mycorrhizal, nutrient uptake, millet, acid sandy soil

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

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al., 1996; Buerkert and Lamers, 1999; Biielders, 2000) ; Bationo *et al.*, 2006).

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; Biielders *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; Biielders *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 (iiii) 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 P₂O₅. 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 luvisol 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 m 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 cm²). 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 membrane (Zürich Bolting cloth Mfg¹.) penetrable to

hyphae but not to roots. For "roots tubes" the net was replaced by a 2 mm 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(HPO₄)₂ salt at a rate of 11.6 mg P kg⁻¹ and K was added as K₂SO₄ at a rate of 22 mg K₂O kg⁻¹ soil, corresponding to a rate of 60 kg P₂O₅ ha⁻¹ and 60 kg K₂O 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 Al³⁺ (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 mycorrhizal 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 2c\350 kg ha⁻¹ in 1992 to 290 kg ha⁻¹ in 1994 on bare plots, and from 3 200 kg ha⁻¹ to 1 100 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⁺, Ca⁺⁺ and Mg⁺⁺ 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%).

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	F prob
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 ⁺	Ca ⁺⁺	Mg ⁺⁺	Al ⁺⁺⁺	
		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)

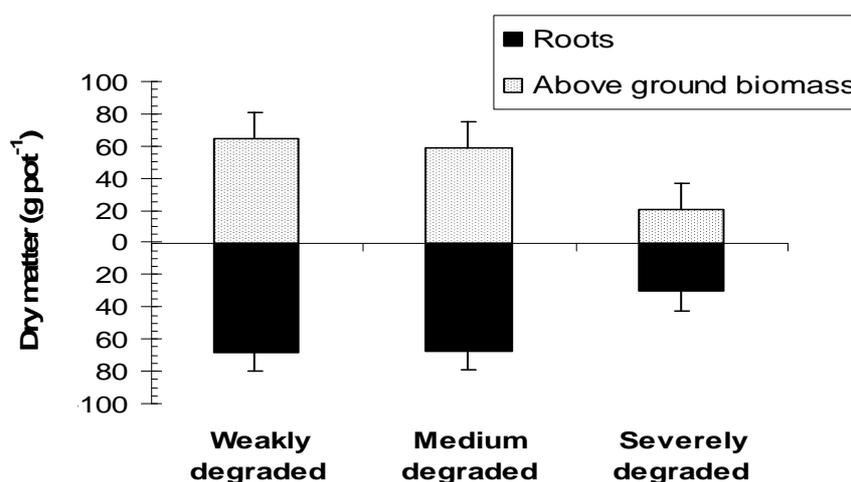


Figure 1: Millet plant and root dry matter in pot experiment at harvest as affected by soil degradation status. Error bar = s.e.d.

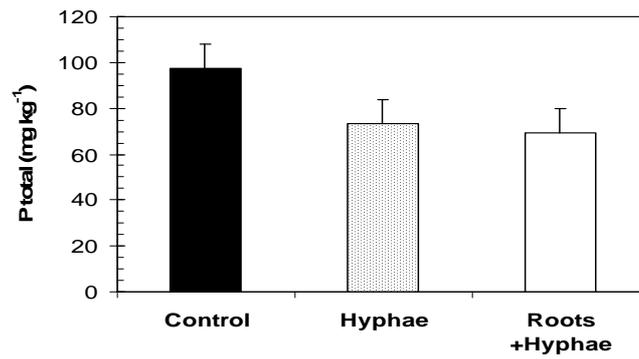


Figure 2: Effect of AM fungi and millet roots on total P content in soil tubes inaccessible to roots and hyphae ('Control'), accessible to hyphae only ('Hyphae') or accessible to hyphae and millet roots ('Roots+Hyphae'). Average over all degradation levels (Error bar = s.e.d., P = Phosphorus).

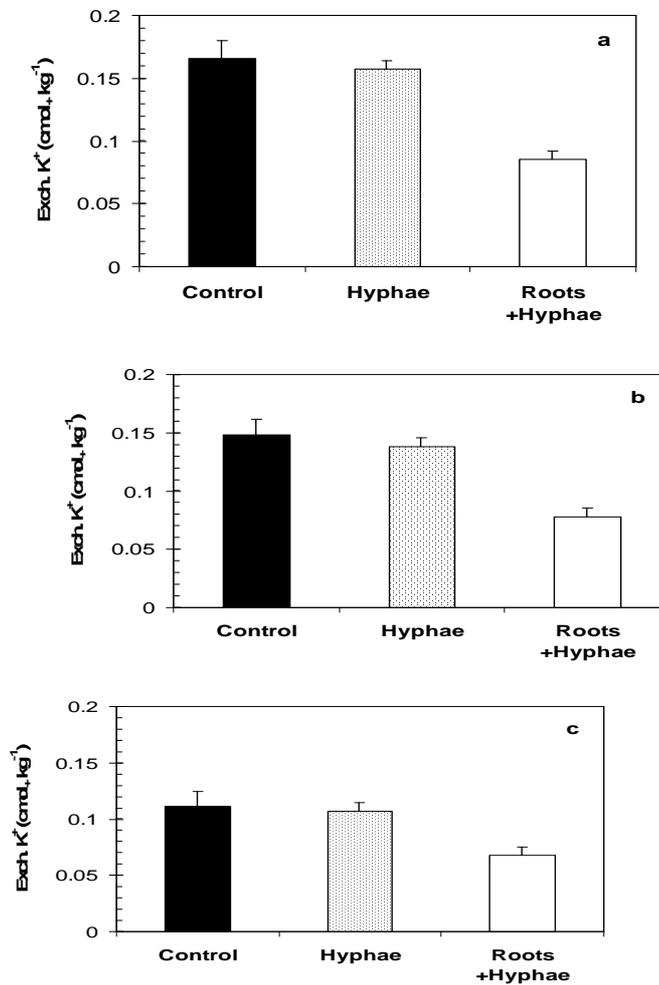


Figure 3: Effect of AM fungi and millet roots on exchangeable K⁺ in soil tubes inaccessible to roots and hyphae ('Control'), accessible to hyphae only ('Hyphae') or accessible to hyphae and millet roots ('Roots+Hyphae') for a) weakly, b) medium, and c) severely degraded soil (Error bar = s.e.d., Exch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