Plant and Soil **231:** 45–54, 2001.

Cereal/legume rotations affect chemical properties and biological activities in two West African soils

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Key words: millet, mycorrhizae, nematodes, nitrogen, phosphatase activity, phosphorus

Abstract

A more widespread use of cereal/legume rotations has been suggested as a means to sustainably meet increasing food demands in sub-Saharan West Africa. Enhanced cereal yields following legumes have been attributed to chemical and biological factors such as higher levels of mineral nitrogen (N_{min}) and arbuscular mycorrhizae (AM) but also to lower amounts of plant parasitic nematodes. This study was conducted under controlled conditions to examine the relative contribution of AM, plant parasitic nematodes and increased nitrogen (N) and phosphorus (P) availability to cereal/legume rotation effects on two West African soils. Sample soils were taken from field experiments at Gaya (Niger) and Fada (Burkina Faso) supporting continuous cereal and cereal/legume rotation systems and analysed for chemical and biological parameters. Average increases in cereal shoot dry matter (DM) of rotation cereals compared with continuous cereals were 490% at Gaya and 550% at Fada. Shoot P concentration of rotation millet was significantly higher than in continuous millet and P uptake in rotation cereals was on average 62.5-fold higher than in continuous cereals. Rotation rhizosphere soils also had higher pH at both sites. For the Fada soil, large increases in Bray1-P and organic P were observed in bulk and rhizosphere soils. Plant parasitic nematodes in roots of continuous cereals were 60–80-fold higher than in those of rotation cereals. In both cropping systems mycorrhizal infection rates were similar at 37 days after sowing (DAS) but at 57 DAS AM infection was 10–15% higher in rotation sorghum than in continuous sorghum. This study provides strong evidence that cereal/legume rotations can enhance P nutrition of cereals through improved soil chemical P availability and microbiologically increased P uptake.

Introduction

In the past, the productivity of the prevailing subsistence-oriented agro-pastoral land use systems of sub-Saharan West Africa based on pearl millet (*Pennisetum glaucum* L.), sorghum (*Sorghum bicolor* L. Moench), cowpea (*Vigna unguiculata* L.) and groundnut (*Arachis hypogaea* L.) relied on extended fallow periods. These allowed to restore phosphorus (P) and nitrogen (N) availability on the predominantly acid sandy soils where P was found to be a major constraint to crop growth (Bationo et al., 1992). In view of a population growth-induced scarcity of suitable farm land cereal/legume rotations have been suggested as an effective means to increase soil productivity without, however, a thorough understanding of their effects on soil fertility. Many crop rotation studies have focused on rotation-induced differences in the availability of N (Pierce and Rice, 1988). In the Sahelian zone, however, rotation effects on P availability may be more important, as P appeares to be the most growth limiting factor. Rotation-induced changes in the pH of the bulk or the rhizosphere soil of legumes, e.g. through the exudation of organic acids or ligand exchange on the root epidermal cell surfaces may enhance P availability (Ae and Otani, 1997; Ohwaki and Hirata, 1992). On the poorly buffered acid sandy soils of the Sahel such pH effects on P availability can be very im-

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portant as shown recently by Powell and Ikpe (1998) and Buerkert et al. (2000). In addition, changes in pH are widely known to affect the growth and activity of microorganisms (Madigan et al., 1997) many of which are important components of diseases and nutrient cycling processes.

So far little research has been conducted in sub-Saharan West Africa to examine the role of organic P (P_o) for crop growth and how this P pool may be affected by cereal/legume rotations. Bacteria, fungi, mycorrhizae and plant roots have all been reported to produce acid phosphatase (Dinkelaker and Marschner, 1992; Tarafdar and Claassen, 1988). Bacteria have also been found to produce alkaline phosphatase (Tabatabai and Bremner, 1969). Acid phosphatases secreted by roots have been shown to hydrolyse organic P compounds and release orthophosphate in the rhizosphere. In P deficient soils, the release of acid phosphatases may therefore be an adaptive mechanism of plants, to contribute to the replenishment of soil solution P (Bieleski, 1973; Li et al. 1997; Tadano and Sakai 1991). Crop rotation may also affect mycorrhizal infection and parasitic nematode populations that influence the effectiveness of roots to take up nutrients. This is of particular importance in soils with low P availability (Lambert et al., 1979; George et al., 1994).

Field experiments at several sites in West Africa have shown cereal yield increases in cereal/legume rotations between 15 and 79% compared with continuous cereal systems. However, the degree to which N was involved as a driving force in these effects remained unclear (Bagayoko et al., 2000b; Bationo et al., 1998). Observed legume/rotation effects on cereal plots included site-specific increases in mineral N, mycorrhizal infection and a decrease in nematode infestation (Bagayoko et al., 2000b).

As crop growth in the Sahel was reported to be highly variable over space and time (Brouwer et al., 1993; Buerkert et al., 1995) further investigations under controlled conditions are needed to identify the mechanisms of the observed rotation-induced increases in cereal yields in West African soils. This research focused on the P and N components of the cause-effect model proposed by Bagayoko et al. (2000b) as affected by microbial and plant acid phosphatase production as well as P_o and Bray1-P (P_b; Bray and Kurtz, 1945) in the bulk and rhizosphere soil. Plant parasitic nematodes and mycorrhizal infection rates were also determined to investigate their contribution to the soil nutrient dynamics in cereal/legume rotation systems of Sudano-Sahelian West Africa.

Materials and methods

Experimental setup

For the studies under controlled conditions surface soil (0–0.2 m) was collected in December 1998 from cereal/legume rotation experiments established during 1995 in the Sudanian zone of Niger on an Arenic Kandiustalf at Gaya (11°59'N, 3°32'E; 800 mm annual average precipitation) and of Burkina Faso on a Haplustalf at Fada (11°59'N, 0°19'E; 850 mm). The chemical properties of the surface soils before cultivation, at Gaya and Fada respectively, were as follows: pH (KCl) 4.2 and 5.4; 3.3 and 5.2 mg kg^{-1} organic carbon; 2.5 and 1.3 mg kg^{-1} P_b; 1.3 and 2.8 cmol kg^{-1} cation exchange capacity; 66 and 99% base saturation; 9 and 3 g kg^{-1} mineral N; and 13 and 15 g kg^{-1} clay. The plots chosen had been cropped for four years either continuously to cereals (millet at Gaya and sorghum at Kouare) or to legumes (cowpea at Gaya and groundnut at Fada) rotated with cereals. The air-dry soils were passed through a 2-mm sieve before they were packed in polyethylene bags and shipped to Germany for the subsequently described two independent two-factorial experiments with six replicates each.

Fada soil, planted to sorghum, was placed in 36 root boxes of 60 × 180 × 600 mm with a removable PVC face plate at a rate of 7 kg per pot. The first treatment factor referred to the cropping system (soil type) and thus half of the boxes were filled with continuous cereal soil and the other half with legume rotation soil. Each of the two soil types was then amended with mineral N creating the following treatments: (i) no amendment (control), (ii) 10 mg N kg^{-1} soil as NO_3^-; and (iii) 10 mg N kg^{-1} soil as NH_4^+ to examine the effects of the applied N form on plant growth, nutrient concentrations, nutrient uptake and soil pH. At 37 and at 57 days after sowing (DAS) pots were harvested in triplicate for all treatments except NH_4^+ application. To stimulate root growth along the face plate, the boxes were placed at an angle of 60°. During the course of the experiment day temperature (14 h) in the greenhouse ranged from 36 to 44°C and night temperature from 22 to 24°C. The photon flux density during the day was about 480 μE m^{-2} s^{-1}. Similarly Gaya soil, planted to millet, was placed in 36 pots at a

rate of 3.5 kg per pot and placed in a growth chamber. Day (14 h) temperatures were 38°C and night temperatures 24°C. Soil treatments were identical to those of the Fada soil. As plant growth was very poor on this soil, all millet was harvested at 31 DAS. Root and shoot dry matter (DM) was determined after drying all plant material to constant weight at 65°C.

Measurements of soil pH and phosphatase activity

An antimony microelectrode (Häussling et al., 1985) was used for in situ measurements of soil pH in the rhizosphere and bulk soil upon removal of the face plate in each root box of the Fada soil prior to harvest at 37 DAS and in the rhizoplane, rhizophere and bulk soil in each remaining box at 57 DAS. Subsequently, plants were carefully removed from root boxes to avoid damage to the roots. To determine phosphatase activities, root systems were shaken to remove loosely adhering soil and subsequently rinsed by repeated submersion in 10 ml of deionised water for 5–10 sec thereby creating a rhizosphere soil suspension. Small samples of fresh roots sized 10–20 mm were placed into 1.5 ml Eppendorf tubes and soaked in deionised water for 1 h followed by three rinses in deionised water to remove leached acid phosphatases (APase) from wounded cells. Bulk soil suspensions of 4:1 dilution in deionised water were also prepared. Alkaline and acid phosphatase activity was determined as described by Tabatabai and Bremner (1969) using 0.5 ml of soil suspension or root samples as described above. Given the poor growth of millet on the Gaya soil, these measurements were only conducted for the Fada soil. After analysis the dry weight of soil or root material in the tubes was determined to report phosphatase activities per mass unit.

Mycorrhizae, nematodes and total bacterial counts

Washed roots from all Fada boxes were cut into segments of 10–20 mm and cleared with 10% KOH at 60° C for 1 h. After clearing, roots were rinsed three times in deionised water and acidified for 30 min in 2 N HCl. Subsequently, roots were stained with 0.05% trypan blue in lactic acid over night followed by destaining in lactic acid. The percent mycorrhizal colonisation of roots was determined by the line intersect method (Kormanik and McGraw, 1982). A modified Baerman Funnel method as described by Hooper (1984) was used for the extraction of nematodes from soil and root samples. Total nematodes were counted under a dissecting microscope and differentiated into plant parasitic and non-plant parasitic. The number of total bacteria was estimated by plating on Tryptone Soy Agar for bacterial counts (Difco, Detroit, MI, USA).

Plant nutrients

All plant samples were analysed for N using a Macro-N-analyser (Heraeus; Bremen, Germany), for P with a Hitachi U-3300 spectrophotometer according to the colorimetric procedure of vanado-molybdate (Gericke and Kurmies, 1952) and for K by flame-emission photometry (Eppendorf, Elex 6361; Ismaning, Germany) after ashing of samples for 4 h at 500°C in a muffle furnace and dissolution of the ash in 1:30 (v/v) diluted HCl.

Soil phosphorus

Levels of P_o, P_b and total extractable (P_t) were determined for the Fada bulk soil prior to planting and for rhizosphere and bulk soil at 57 DAS. To this end suspensions of rhizosphere and bulk soil were dried at 60°C and analysed for P_o with the ignition extraction method of Saunders and Williams (1955) and for P_b according to Olsen and Sommers (1982). Phosphorus concentrations of the various extracts were measured colorimetrically using the ascorbic-acid–molybdenum blue method (Murphy and Riley, 1962). Phosphorus in the soil solution was determined from retrieval of porewater by centrifugation of 100 g soil, for 20 min at 8000 × g, 25°C and subsequent direct analysis as described above.

Data analysis

All data were subjected to analysis of variance using SAS version 6.06 (SAS, 1991). Results were reported with their respective *F*-values. To examine the relative importance of treatment-induced root effects on shoot growth on the Fada soil, analyses of covariance on millet shoot DM at 57 DAS were conducted using pH measurements in the rhizoplane, rhizosphere and bulk soil as well as log-transformed mycorrhizal infection and nematode count data as individual covariates (Steel and Torrie, 1980).

Results

Plant dry matter

The analysis of covariance revealed highly significant

Table 1. Effects of cropping system and nitrogen application (as NO_3^- or NH_4^+) on root and shoot dry matter and on root/shoot ratio (R/S) of sorghum on the Fada soil at 37 and 57 days after sowing (DAS).

Treatment	37 DAS			57 DAS		
	Shoot (g)	Root (g)	R/S	Shoot (g)	Root (g)	R/S
Continuous	0.52	0.086	0.16	3.4	1.5	0.45
Rotation	4.23	0.456	0.14	15.3	7.5	0.54
Continuous + NO_3^-	0.41	0.056	0.14	4.5	1.8	0.36
Rotation + NO_3^-	2.04	0.281	0.15	17.6	12.4	0.70
Continuous + NH_4^+	nd[a]	nd	nd	5.2	1.2	0.24
Rotation + NH_4^+	nd	nd	nd	15.3	8.6	0.58
SED[b]	0.759	0.0565	0.138	0.90	1.55	0.130
P>F[c]						
System	0.015	0.002	0.871	<0.001	<0.001	0.071
Nitrogen	0.056	0.008	0.935	0.260	0.378	0.741
System × Nitrogen	0.266	0.248	0.666	0.539	0.488	0.676

[a] No data available.
[b] Standard error of the difference.
[c] Probability of a treatment effect (significance level).

($p < 0.001$) effects of all measured root parameters on shoot growth. *F*-values amounted to 98, 100 and 60 for pH in the rhizoplane, rhizosphere and bulk soil, respectively and to 65 and 44 for mycorrhizal and nematode infection.

Depending on the level and form of applied N, the shoot DM of rotation sorghum at Fada was 5- to 8-times higher than that of continuous sorghum at 37 DAS and 3- to 5-times higher at 57 DAS (Table 1). Similarly, relative increases in the early shoot DM of rotation millet with Gaya soil were between 4- and 6-times higher on rotation soils (Table 2). In sorghum at 37 DAS the root/shoot (R/S) ratio was virtually identical for all treatments but at 57 DAS this ratio tended to be higher in rotation than in continuous sorghum. Effects of N addition on either shoot or root DM or on R/S were small and not significant (Table 1). On the Gaya soil the R/S of rotation millet ranged from 0.1 to 0.4, whereas the R/S for continuous millet was 0.2 (data not shown). Compared with unfertilised control treatments, the addition of NO_3^- nearly doubled the millet shoot DM on rotation soil, whereas an increase of 21% was observed in continuous millet (Table 2).

Plant nutrients

Shoot N concentration in rotation sorghum was significantly higher than in continuous sorghum at both harvests but was not affected by application of different N forms (Table 3). Regardless of N application sorghum shoots in rotation soil were also significantly higher in P than in continuous sorghum soil, particularly at 57 DAS. However, cropping system effects were negligible for K. Total N uptake in sorghum was 3–9-fold higher and P uptake 3–9-fold higher with rotation than with continuous soil (Table 3). In millet shoot N concentrations were similar for all treatments, whereas shoot P concentrations were 5–16-fold higher on rotation soils than in continuous millet (Table 2). Total P uptake was thus 19–106-fold higher in rotation than in continuous cereal.

pH

In the Fada soil regardless of N application, bulk soil pH values at 37 DAS and 57 DAS were significantly higher ($p < 0.001$) in rotation compared with continuous cereal but differences decreased over time (Fig. 1). In contrast, bulk soil pH at Gaya was similar for both cropping systems but a 0.7 pH unit increase was observed in the rhizosphere of rotation millet compared with continuous millet (data not shown). Over the duration of the Fada soil experiment, NO_3^- fertilisation at all distances from the root surface and across cropping systems, led to soil pH increases and NH_4^+ fertilisation to soil pH decreases. However, in all treatments pH levels in rotation soils were higher than in continuous cereal soils (Fig. 1).

Table 2. Effects of cropping system and nitrogen application (as NO_3^-) on the concentration and total uptake of millet shoot dry matter (DM) on the Gaya soil at 31 days after sowing.

Treatment	Dry matter (mg)	Concentration (mg g^{-1})			Total uptake (mg $plant^{-1}$)		
		N	P	K	N	P	K
Continuous	57	23.3[a]	0.19	49.1	1.33	0.011	2.80
Rotation	230	23.2	0.93	62.9	5.34	0.213	14.50
Continuous + NO_3^-	69	25.6	0.05	50.0	1.77	0.003	3.45
Rotation + NO_3^-	403	24.3	0.79	62.0	9.79	0.318	25.00
SED[b]	44						
$P>F$[c]							
System	0.001						
Nitrogen	0.253						
System × Nitrogen	0.280						

[a] Due to the low dry matter obtained the concentration values represent a single pooled sample of six replicates. The uptake data is based on this average concentration multiplied by the average DM of the six replicate samples.
[b] Standard error of the difference.
[c] Probability of a treatment effect (significance level).

Phosphatase activity

At 37 DAS acid phosphatase activity at the root surface of unfertilised continuous sorghum was over threefold ($p < 0.004$) higher than in rotation soil. With NO_3^- application total activities were lower than in unfertilised soil but acid phosphatase activity still was over two-fold higer in continuous sorghum than in rotation sorghum (Fig. 2). However, in the rhizosphere of sorghum acid phosphatase activity was 74% higher in rotation than in continuous soil ($p < 0.001$). Again, with NO_3^- application activities were lower but differences between cropping systems were similar. Although total activity of alkaline phosphatases was significantly lower compared with acid phosphatase, alkaline phosphatase activity in the rhizosphere of non-fertilised rotation sorghum was nearly 2-fold higher ($p < 0.002$) than in continuous sorghum (Fig. 2).

Irrespective of N application, at 57 DAS acid phosphatase activity at the root surface of continuous sorghum was 15–20% higher than in the respective rotation treatment (data not shown). At the same time acid phosphatase activity in the rhizosphere of non-fertilised rotation sorghum was nearly 2- fold higher ($p < 0.001$) than in the respective continuous cereal soils. The addition of N in either form increased the acid phosphatase activity in the rhizosphere of the continuous soil grown plants, however, the activity in rotation sorghum remained always higher (data not shown).

Soil phosphorus

For Fada soils prior to planting P_o, P_b and P_t were 18, 29 and 16%, respectively, higher in rotation than in continuous soil. In the rhizosphere at 57 DAS, P_b levels were twice as high in rotation compared with continuous soil, even P_o was significantly increased in rotation compared with continuous cereal soil ($p < 0.001$). In the bulk soil of rotation plots levels of P_b were 25% higher than those of continuous plots (Table 4). In all investigated soil samples, porewater P was below the detection limit of 0.05 mg l^{-1}.

Nematodes, mycorrhizae and total bacterial counts

At 57 DAS the number of plant parasitic nematodes in the continuous sorghum soil at Fada were over 10-fold higher than in the rotation soil. Plant parasitic nematodes in continuous soil grown roots were 60–80-fold higher than in rotation soil grown roots (Fig. 3). Mycorrhizal infection rates were not affected by cropping system at 37 DAS but at 57 DAS they were 10–15% higher in rotation sorghum than in continuous sorghum (data not shown). VA infection rates for millet in Gaya soils did not show any significant treatment effect. Across sites total bacterial numbers were 10-fold higher in rhizosphere versus bulk soils but there were no significant differences between continuous and rotation soils regardless of the level of N application.

Table 3. Effects of cropping system and nitrogen application (as NO_3^- or NH_4^+) on the concentration and total nutrient uptake of sorghum shoot dry matter on the Fada soil at 37 and 57 days after sowing (DAS).

Treatment	37 DAS						57 DAS					
	Concentration (mg g^{-1})			Total uptake (mg $plant^{-1}$)			Concentration (mg g^{-1})			Total uptake (mg $plant^{-1}$)		
	N	P	K	N	P	K	N	P	K	N	P	K
Continuous	33.5	1.60	34.8	17.4	0.83	18.1	13.0	0.76	26.7	44	2.3	91
Rotation	34.4	1.73	38.3	145.5	7.31	162.0	25.4	0.93	28.1	388	14.2	429
Continuous + NO_3^-	32.5	1.49	35.8	13.3	0.61	14.7	14.9	0.68	27.7	67	3.1	124
Rotation + NO_3^-	39.7	2.17	40.2	81.0	4.43	82.0	22.6	0.80	28.3	397	14.1	498
Continuous + NH_4^+	nd[a]	nd	nd	nd	nd	nd	19.8	0.87	30.8	103	4.5	160
Rotation + NH_4^+	nd	nd	nd	nd	nd	nd	23.9	0.93	30.2	365	14.2	462
SED[b]	1.27	0.121	1.99	30.7	1.39	34.6	1.35	0.032	1.31	17.2	0.78	28.3
$P>F$[c]												
System	0.018	0.002	0.101	0.017	0.012	0.020	<0.001	0.004	0.624	<0.001	<0.001	<0.001
Nitrogen	0.126	0.022	0.512	0.062	0.054	0.061	0.177	0.005	0.150	0.473	0.562	0.224
System × Nitrogen	0.102	0.036	0.909	0.406	0.485	0.333	0.087	0.420	0.803	0.234	0.669	0.708

[a] No data available
[b] Standard error of the difference.
[c] Probability of a treatment effect (significance level).

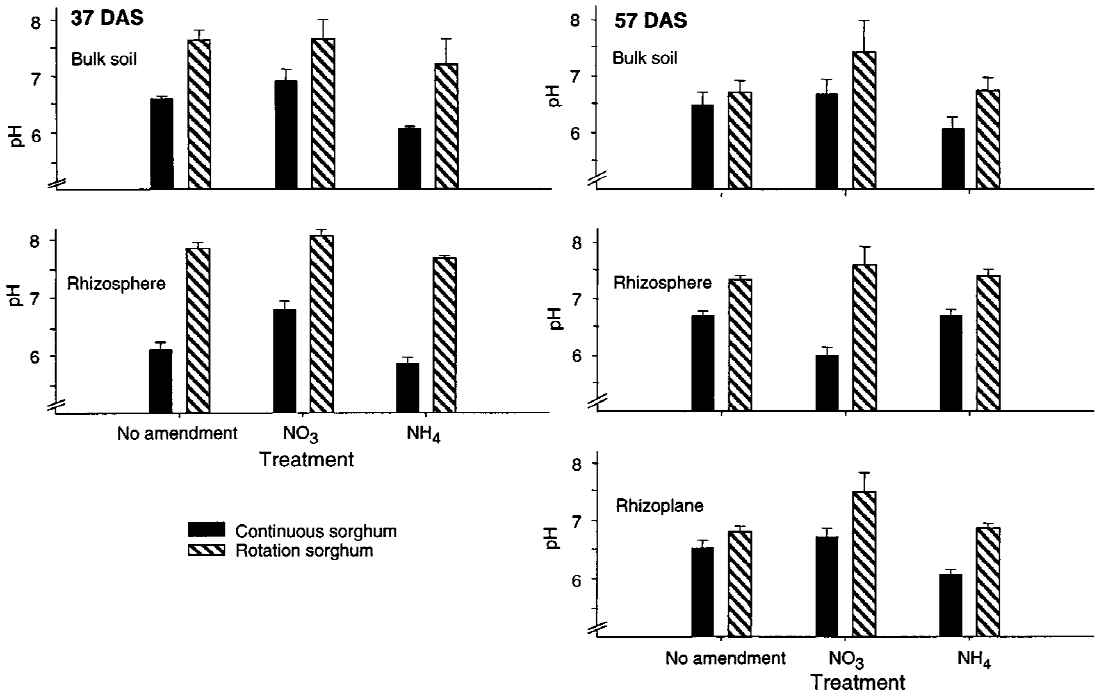

Figure 1. Bulk, rhizosphere and rhizoplane pH of rotation and continuous sorghum soil from Fada 37 and 57 days after sowing (DAS).

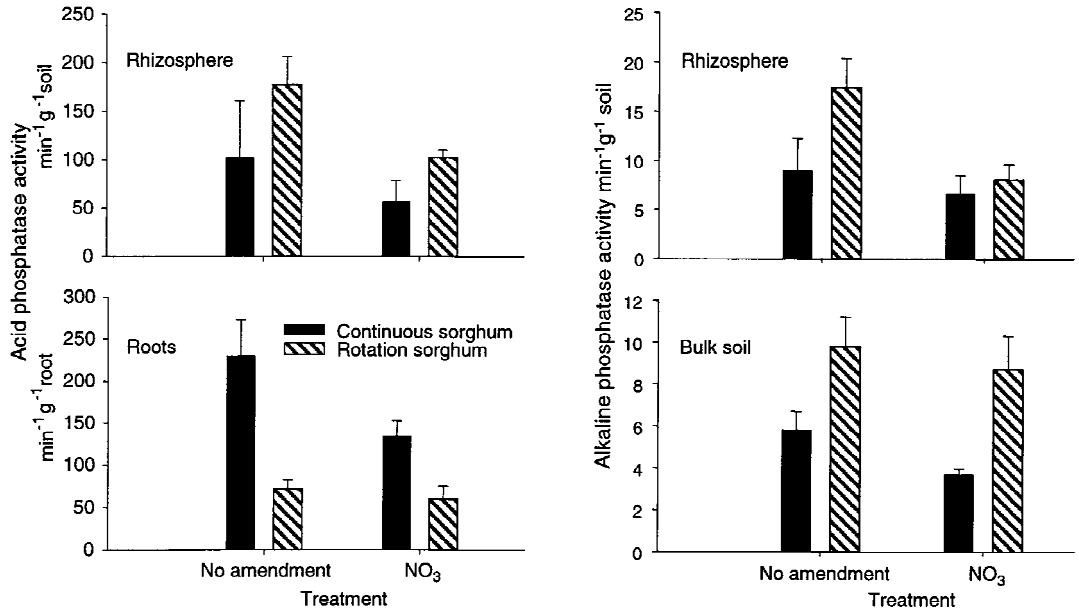

Figure 2. Acid and alkaline phosphatase activity in the rhizosphere and root surface of rotation and continuous sorghum soil from Fada 37 days after sowing.

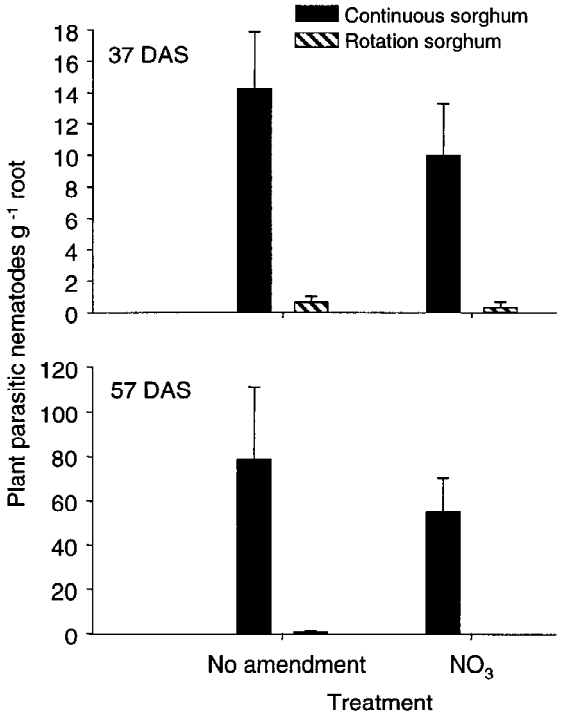

Figure 3. Plant parasitic nematodes in roots of continuous and rotation sorghum 37 and 57 days after sowing (DAS) in soil from Fada.

Discussion

The rotation-induced cereal DM increases of up to 810% for the Fada soil and of up to 580% for the Gaya soil found under the controlled conditions of this study were much larger than respective field data showing DM increases of 40 and 9% at maturity (Bagayoko et al., 2000b). These differences could be due to the limited soil volume, associated with a higher root length density, higher root zone temperatures and the shorter duration of the experiments in the pot trials. These factors may have induced an artefact in the controlled experimental system, particularly with respect to the intensity of rhizosphere processes and the effects of nematodes on plant growth whose contribution to differences in shoot growth was evidenced by the analyses of covariance. Given that both soils were dry when sampled in West Africa and stored for less than 6 months at between 20 and 25°C prior to use for the experiments of this study, it seems unlikely that there were major alterations in their biological properties affecting the measured parameters. The poor growth of plants in the Gaya soil precluded a second havest and only allowed a reduced set of measurements. However, under field conditions poor millet growth at Gaya has been described previously (Bationo et al., 1995) and was attributed to the very high levels of

Table 4. Phosphorus availability in bulk and rhizosphere soils of continuous sorghum and rotation sorghum soils from Fada without N application at 57 days after sowing.

Soil type	Phosphorus fraction			
	Total (P_t)	H_2SO_4	Organic (P_o)	Bray (P_b)
	(mg P kg^{-1} soil)			
Rotation without plant	44.1	19.7	24.7	6.3
Continuous without plant	37.0	16.0	21.0	4.9
Rotation rhizosphere	45.0	15.3	29.7	5.8
Rotation bulk soil	37.8	15.2	22.7	3.9
Continuous rhizosphere	38.8	13.8	25.0	2.7
Continuous bulk soil	33.8	12.7	21.2	2.9
SED[a]	1.08	1.12	1.42	0.31
$P>F$[b]				
System	0.009	0.390	<0.001	<0.001
Location	0.001	0.296	0.029	0.015
System × Location	0.378	0.512	0.871	0.004

[a] Standard error of the difference.
[b] Probability of a treatment effect (significance level).

plant parasitic nematodes at this site (Bagayoko et al., 2000b).

The analysis of various parameters with a putative impact on plant growth (e.g. P and N nutritional status of the plants, P and N availability, rhizosphere processes, AM colonisation, infection with parasitic nematodes), which was conducted in this study suggests that beneficial growth effects in the rotation system may be attributable to the combined effects of different factors. The small expression or even the absence of responses in shoot N content and DM production (Tables 1–3) to the application of N fertilisers in both cropping systems, with the exception of Gaya rotation with NO_3^- application, indicates that N was not a limiting nutrient at least during the first 31 days of plant growth. However, the higher N concentration in plants grown on Fada rotation soil compared with those on continuous soil (Table 3) could be due to increased N availability from the previous groundnut crop in the rotation soil. Bagayoko et al. (2000b) found large legume-specific increases in mineral N in a number of West African rotation soils suggesting synergistic effects of N and P as a cause for rotation-induced increases in cereal growth.

On both soils, P concentration and DM production of plants grown on rotation soils was higher than in the continuous system (Tables 2 and 3) indicating that P was a major growth limiting factor. This conclusion is supported by the large increase of acid phosphatase activity at the root surface of plants grown on soils from the continuous system. Since root secretion of acid phosphatase increases under P starvation (Tadano and Sakai, 1991), the data suggest that continuous sorghum at Fada was more P deficient than rotation sorghum (Fig. 1).

In the rhizosphere soil, however, activities of both acid phosphatase and alkaline phosphatase increased in the soil obtained from the rotation system. This increase might be rather attributable to microbial activity than to root-borne phosphatases and may indicate a higher rate of P mineralisation in the rhizosphere soil of the rotation system. Accordingly, the rhizosphere levels of plant-available inorganic P (P_b) increased in the rotation soil, associated also with elevated levels of P_o, which probably originated from the increased microbial biomass. Accumulation of inorganic P in the rhizosphere in response to P_o hydrolysis has been previously reported (Häusling and Marschner, 1989). This may be explained as a result of intense P mineralisation in the rhizosphere, which exceeded the P uptake capacity in distinct root zones (e.g., with older root parts). Moreover, a highly significant, rotation-induced increase in the level of P_b and P_o in the bulk soil of our pot experiments (Table 4) probably contributed to the improved P supply of the plants grown on rotation soils particularly during early growth. Higher P_o has been repeatedly shown to play an important role in P cycling and plant nutrition in tropical soils and

could have contributed to the plant available P pool through mineralisation (Acquaye, 1963; Adepetu and Corey, 1976).

The higher soil pH in rotation bulk soil (Fada only) and rhizosphere soil (Fada and Gaya) compared with the continuous cereal soils was likely due to the much higher NO_3^- uptake of the more vigorously growing plants and compensatory exudation of OH^-. Imai (1991) measured the pH in soybean- and mungbean-based rotation systems for 10 years and found rotation-induced pH changes of up to 1 pH unit. Powell and Ikpe (1992) reported from a similar soil of the region that a near neutral pH resulted in maximum dissolution of P from iron and aluminium complexes.

In the acid sandy soils of this study the measured rise in pH could have made a major contribution to the large observed rotation-induced increases in P availability by influencing P solubility and equilibrium concentrations. However, recent studies with Sudano-Sahelian sandy soils failed to demonstrate a direct impact of pH on P solubility. Thus, increased P availability was rather attributed to indirect effects, such as pH-dependent stimulation of P mineralising bacteria (Bagayoko et al., 2000a). Furthermore, a rotation-induced pH increase may contribute to reduced Al concentrations and enhanced availability of Mg and Ca, which are other important growth limiting factors on acid mineral soils (Bagayoko et al., 2000a).

Rotation-induced increases in AM colonisation were with 10–15% only small and appeared late during the growing period (57 DAS). The fact that even in the presence of higher levels of P_b AM infection was higher in rotation soil than in continuous soil may be explained by the still low absolute levels of available P (< 5 mg P kg^{-1}). Under such conditions even small additions of fertiliser P have been reported to stimulate early root growth and AM infection (Bolan et al., 1984). Abbott et al. (1984) reported an increased length of external fungal hyphae with low levels of added P. Tarafdar and Marschner (1993) reported for wheat that phosphatase activities were distinctly higher in the presence of mycorrhizae and that they were strongly correlated with hyphal length. However, this could not be verified in this study as no measurements of hyphal length were made.

One of the most striking effects observed in the present study was the drastic reduction of plant parasitic nematodes associated with roots grown in rotation soil. This may be attributed to accumulation of root-borne secondary metabolites such as nematocidal or nematostatic flavonoids in the rotation soil, released as root exudates or from root residues particularly in leguminous plants (Rao, 1990). A lower infection rate with pathogenic nematodes may enable better root growth associated with improved spatial acquisition of nutrients and stimulation of rhizosphere processes.

Thus, the combination of higher P_o, P_b, AM infection rate, rhizosphere phosphatase activity and decreased parasitic nematode populations likely explain the improved P nutrition of rotation soil plants compared with continuous soil plants. They indicate the likely interaction between chemical and biological factors involved in rotation effects on poorly buffered West African soils. A more detailed analysis of mutual interactions and temporal sequences of the various plant-growth promoting factors would require additional experiments considering earlier stages of plant development.

The data of our experiments from controlled conditions also seem to indicate that rotation effects on cereal growth are rather triggered by improved P than N availability. Nevertheless, it is the combination of improved availability of both nutrients that seems responsible for the overall increase in final total dry matter and grain yield.

Acknowledgements

The authors are grateful to M. Bachir, A. Thiombiano, B. Leick and B. Renz for their technical help at sampling and to H. Traoré (INERA, Burkina Faso) and A. Bationo (IFDC at ICRISAT Sahelian Centre) for their collaboration. This research was partly funded by the Deutsche Forschungsgemeinschaft (DFG) as part of the SFB 308.

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Section editor: F.R. Minchin