



## Cereal/legume rotation effects on cereal growth in Sudano-Sahelian West Africa: soil mineral nitrogen, mycorrhizae and nematodes

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### Abstract

Yield increases of cereals following legumes in rotation have been previously reported for West Africa, but little progress has been made to explain the mechanisms involved. At four sites in Niger and Burkina Faso, field trials with pearl millet (*Pennisetum glaucum* (L.) R. Br.), cowpea (*Vigna unguiculata* (L.) Walp), sorghum (*Sorghum bicolor* (L.) Moench) and groundnut (*Arachis hypogaea* L.) were conducted from 1996 to 1998 to investigate the role of soil mineral nitrogen (N<sub>min</sub>), native arbuscular mycorrhizae (AM) and nematodes in cereal/legume rotations. Grain and total dry matter yields of cereals at harvest were increased by legume/cereal rotations at all sites. Soil N<sub>min</sub> levels in the topsoil were consistently higher in cereal plots previously sown with legumes (rotation cereals) compared with plots under continuous cereal cultivation. However, these rotation effects on N<sub>min</sub> were much larger with groundnut than with cowpea. Roots of rotation cereals also had higher early AM infection rates compared to continuous cereals. The dominant plant-parasitic nematodes found in all experiment fields were *Helicotylenchus* sp., *Rotylenchus* sp. and *Pratylenchus* sp. In sorghum/groundnut cropping systems, nematode densities were consistently lower in rotation sorghum compared to continuous sorghum. Continuous groundnut had the lowest nematode densities indicating that groundnut was a poor host for the three nematode groups. In millet/cowpea cropping systems with inherently high nematode densities, crop rotations barely affected nematode densities indicating that both crops were good hosts. These results suggest that on the nutrient poor Sudano-Sahelian soils of our study, total dry matter increases of rotation cereals compared with continuous cereals can be explained by higher N<sub>min</sub> and AM infection levels early in the season. The site-specific magnitude of these effects may be related to the efficiency of the legume species to suppress nematode populations and increase plant available N through N<sub>2</sub>-fixation.

### Introduction

Cereal/legume rotation effects on cereal yields have been frequently reported for the semi-arid regions of West Africa (Bagayoko et al., 1996; Bationo et al., 1998; Nicou, 1978; Stoop and Van Stavern, 1981). A generally proposed cause for such effects is an increased N availability for the cereal crop from symbiotic N<sub>2</sub>-fixation of the preceding legume which can

lead to significant increases in the available soil N pool (Baldock et al., 1981; Pierce and Rice, 1988). Under Sahelian conditions, however, the few available data from fertiliser trials show similarly large rotation effects for millet and sorghum with increasing levels of applied N (Bationo et al., 1998). Cereal yield increases after legumes were also reported without significant legume effects on the levels of total soil N (Bagayoko et al., 1996). In this context, some workers have suggested that rotation-related increases in cereal yields may be due to changes in microbial activities (Shipton, 1977; Turco et al., 1990), and research conducted

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in temperate climates suggest that vesicular arbuscular mycorrhizae (AM) may also be involved in these effects (Johnson et al., 1992).

Compared with insect pests and fungal diseases, very little is known about the role of nematodes in cereal/legume systems of West Africa. Crop rotation has been reported as a tool to control nematode densities in many part of the world (Johnson, 1982; McSorley et al., 1994). A variety of crops such as cotton (*Gossypium hirsutum*), soybean (*Glycine max*), sorghum (*Sorghum bicolor*) and sorghum sudangrass (*S. bicolor* × *S. sudanense*) hybrids have been successfully used in rotation trials to suppress root knot nematodes (McSorley and Gallaher, 1991; Rodríguez-Kábana et al., 1991). Given the lack of reliable data on soil mineral nitrogen levels, AM infection rates and nematode population densities in cereal/legume rotations of West Africa, this research was conducted to investigate their role in explaining rotation effects on the acid nutrient deficient soils of this region.

## Materials and methods

### *Site description and experimental design*

In Niger, at the onset of the rainy season in May 1995, rotation trials with millet and cowpea were established in the Sahelian zone at Sadoré (13° 14' N, 2° 17' E; 560 mm average annual rainfall) and at Goberi (12° 58' N, 2° 50' E; 600 mm) and in the Sudanian zone at Gaya (11° 59' N, 3° 32'; 800 mm). The same trial was also conducted with sorghum and groundnut in the Sudanian zone of Burkina Faso at Kouaré (11° 59' N, 0° 19' N; 850 mm). The soils had a  $\text{pH}_{KCl}$  between 4.1 and 5.4, P-Bray levels between 1.3 and 2.8 mg  $\text{kg}^{-1}$  soil, N min between 3 and 9 mg  $\text{kg}^{-1}$ , organic C between 1.6 to 5.2 g  $\text{kg}^{-1}$  and cation exchange capacities between 0.8 and 2.8 cmol  $\text{kg}^{-1}$  (Buerkert et al., 2000). The experiment was a split-plot design with main-plot treatments being factorial combinations of phosphorus (P) applied annually as broadcast single superphosphate (SSP) at 0 and 13 kg P  $\text{ha}^{-1}$  and Tahoua rockphosphate (TRP) at 39 kg P  $\text{ha}^{-1}$ , cereal crop residues (CR) applied as surface mulch at 500 and 2000 kg  $\text{ha}^{-1}$  and calcium ammonium nitrate (CAN) broadcast at 0 and 60 kg N  $\text{ha}^{-1}$  and split into three applications: 25% at 10 days after sowing (DAS), 25% at thinning and 50% at booting.

The four subplot treatments were: continuous cereal, continuous legume and both phases of the cereal/legume rotation. Crop residues were applied to the

soil surface of the respective treatments plots in the middle of the dry season (from November to May) and uniformly redistributed before planting. Single superphosphate was broadcast in early May at the start of the rainy season. The main-plot treatments were completely randomised and replicated twice before the four subplot treatments were randomly attributed to each main-plot. Mainplot size was 10 m × 10 m and subplot size 5 m × 5 m. Over all, the design allowed the estimation of rotation main effects with 24 replicates. In millet/cowpea cropping systems, millet was planted with the first major rain at the end of May or early June, 15 days before cowpea was sown. For sorghum/groundnut cropping systems, both crops were planted simultaneously in June of each year. The planting geometry was 1 m × 1 m for millet, 1 m × 0.25 m for cowpea, 0.6 × 0.5 m for sorghum and 0.6 × 0.3 m for groundnut. At sowing, 25–30 viable seeds of cereals (millet and sorghum), 5–10 seeds of cowpea and 2–5 seeds of groundnut were placed at 30 mm depth in the soil. At thinning, about 25 days after sowing (DAS), seedlings were reduced to three plants per pocket (planting hole) for millet and sorghum, two plants per pocket for cowpea and a single plant per pocket for groundnut.

### *Soil and plant sampling*

#### *Soil mineral N*

To determine rotation effects on soil mineral N (N<sub>min</sub>), bulked samples from three cores per subplot were collected in 1997 and 1998 according to Table 1. In 1997, the samples were taken at 0–0.3 and 0.3–0.6 m in continuous and rotated cereal. In 1998, continuous cereal, continuous legume and both rotation plots were sampled at 0–0.15 m and 0.15–0.30 m depth. Immediately after sampling, all samples were air-dried and sieved to pass a 2 mm screen. After sieving, they were transferred into plastic bags and stored in a dry and shaded place until analysis.

#### *Mycorrhizal spores*

Samples from Sadoré and Gaya taken before planting (May of 1997 and 1998) for mineral N determination were also used for spore counts. About 100 g soil per sample was washed repeatedly through a set of sieves with 500  $\mu\text{m}$ , 250  $\mu\text{m}$ , 125  $\mu\text{m}$  and 40  $\mu\text{m}$  mesh size. Then the contents of the two first sieves (125  $\mu\text{m}$  and 40  $\mu\text{m}$ ) were transferred into a 50% sucrose solution centrifuged at 3000 rpm (1408 g) for five min and the supernatant washed through a 40  $\mu\text{m}$  sieve to remove

Table 1. Sampling dates for soil mineral nitrogen, mycorrhizae and nematodes

Sites	Soil mineral N					Mycorrhizae				Nematodes				
	May	June	July	Aug	Sept	July	Aug	Sept	Oct	May	June	July	Aug	Sept
1996														
Sadoré	–	–	–	–	–	–	–	–	10	–	–	–	–	–
Goberi	–	–	–	–	–	–	–	–	13	–	–	–	–	–
Gaya	–	–	–	–	–	–	–	–	14	–	–	–	–	–
1997														
Sadoré	–	–	–	–	–	9	–	3	–	–	–	–	–	–
Goberi	16	17	–	–	4	17	–	4	–	16	17	–	–	4
Gaya	17	–	30	–	3	30	–	3	–	17	–	30	–	3
Kouaré	29	–	22	–	9	–	–	–	–	29	–	22	–	9
1998														
Goberi	24	23	–	7, 25	–	–	7, 25	–	–	24	23	–	7, 25	–
Gaya	22	24	–	8, 27	–	–	8, 27	–	–	22	24	–	8, 27	–
Kouaré	29	31	31	–	3	31	–	3	–	29	31	31	–	3

the spores. Subsequently, spores were placed into Petri dishes with a small amount of water and counted under a dissecting microscope.

#### Root sampling for AM infection

To determine root colonisation by AM, composite samples (roots and soil) from eight holes per subplot were taken in the vicinity of plants within the central three planting rows from 0–0.3 m in 1996 and 1997 and from 0–0.15, 0.15–0.30, 0.30–0.45 and 0.45–0.60 m in 1998. In 1996, samples were taken at crop harvest in October. The sampling dates (Table 1) corresponded to 35 and 75 DAS at Sadoré, 45 and 75 DAS at Goberi and 50 and 85 DAS at Gaya in 1997 and to 45, 65 and 85 DAS at Goberi, 45, 65 and 85 DAS at Gaya and 45, 65 and 85 DAS at Kouaré in 1998. After carefully washing the samples, the roots were cut into small segments, transferred into staining tubes and cleared with 10% KOH for 1 h at 60 °C. Then KOH was removed and the roots were washed three times with demineralised water and acidified with 2 N HCl for 30 min. After removal of the acid, roots were stained with 0.05% trypan blue in lactoglycerol and destained in lactic acid. The percent mycorrhizal colonisation was measured with the line intersection method of Kormanik and McGraw (1984). Initially, some samples had been examined under a compound microscope to verify that the stained fungal material was indeed from AM.

#### Soil and root sampling for nematodes

Bulked samples from three cores per subplot were collected at 0–0.3 m depth in 1997 and 1998. In 1997, treatments sampled were continuous and rotated cereal plots at 500 and 2000 kg CR ha<sup>-1</sup>, 0, 13 and 39 kg P ha<sup>-1</sup> and at 0 and 60 kg N ha<sup>-1</sup>. In 1998, treatments sampled were continuous cereal, continuous legume and both rotation plots at 500 and 2000 kg CR ha<sup>-1</sup> and at 0 and 13 kg P ha<sup>-1</sup>. Sampling dates are shown in Table 1. Nematodes were extracted from sub-samples of 100 g soil and 50 g fresh roots with a modified Baerman Funnel method as described by Hooper (1984).

#### Yield data and statistical analysis

Young plants were sampled at thinning, 25 DAS, to determine their dry matter. At maturity, grain yield and total dry matter (TDM) were determined from the three central rows of each sub-plot without border pockets at both ends of each row. The fresh weights of heads, pods and straw were recorded in the field and sub-samples were taken and oven dried to constant weight at 65 °C. Heads were threshed to separate grain from straw. Subsequently, all dry matter data were subjected to analysis of variance with GENSTAT release 3.2 (Lawes Agricultural Trust, 1995).

Table 2. Millet and sorghum dry matter at thinning and grain and total dry matter yield at harvest as influenced by millet/cowpea cropping systems at Gaya, Goberi and Sadoré (Niger) and sorghum/groundnut cropping systems at Kouaré (Burkina Faso)

Sites and Cropping system	Thinning		Harvest					
	TDM		Gain yield			TDM <sup>b</sup>		
	1996	1998	1996	1997	1998	1996	1997	1998
	kg ha <sup>-1</sup>							
Sadoré								
Continuous millet	4	6	937	321	1557	4227	2219	6992
Millet after cowpea	5	7	1255	340	1904	5785	2832	8613
<i>P&gt;F<sup>a</sup></i>	<0.001	0.059	<0.001	0.344	<0.001	<0.001	<0.001	<0.001
Goberi								
Continuous millet	13	8	–	779	956	2328	3444	4220
Millet after cowpea	16	9	–	827	1151	2579	3743	4800
<i>P&gt;F</i>	<0.001	0.063	–	0.145	<0.001	<0.001	0.019	<0.001
Gaya								
Continuous millet	13	13	794	378	645	2601	2469	2598
Millet after cowpea	15	11	889	466	636	2823	2684	2510
<i>P&gt;F</i>	0.001	0.014	0.085	<0.001	0.801	0.025	0.069	0.353
Kouaré								
Continuous sorghum	30	26	397	786	238	3056	4505	2689
Sorghum after cowpea	36	25	553	884	357	4191	5316	3633
<i>P&gt;F</i>	<0.001	0.352	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

<sup>a</sup> Probability of a treatment effect (significance level).

<sup>b</sup> Total dry matter.

## Results

### Total dry matter and grain yields at thinning and harvest

Compared to those of continuous cereals in 1996, cereal TDM yields following legumes were at thinning 15% higher at Gaya, 23% higher at Goberi, 25% higher at Sadoré and 20% higher at Kouaré (Table 2). Similar increases were observed in 1997. In 1998 at thinning, millet TDM from rotation plots was 12% and 17% higher compared with the respective data of continuous millet at Sadoré and Goberi.

Throughout the three years of the experiment, grain and rotation cereal TDM yields at harvest were higher than yields from continuous cereal plots, but these TDM differences strongly varied with site and year (Table 2). Effects of cropping systems on legume yields, however, were negligible. Therefore, only data related to cereal plots are reported. At Sadoré, relative increases in cereal TDM due to rotation varied from 37% in 1996 to 23% in 1998. At Goberi, millet

TDM increases with rotation were 22% in 1998, 8% in 1997 and 14% in 1998 compared with grain yield increases between 6% and 20%. At Gaya, rotation increased millet TDM by 9% compared with continuous millet in 1996, but differences were negligible in 1998. Compared with continuous cereal plots, millet grain from rotation plots was 12% and 24% higher in 1996 and 1997 but similar in 1998. In general, the highest rotation effects in millet/cowpea systems were observed at Sadoré and the lowest at Gaya. In the sorghum/groundnut cropping systems in Burkina Faso, particularly large sorghum TDM increases due to rotation with groundnut were observed with 37% in 1996, 12% in 1997 and 35% in 1998. This corresponded to grain yield increases of 39% in 1996, 12% in 1997 and 50% in 1998 (Table 2).

### Soil mineral N

At planting time in May 1997, Nmin levels in rotation cereal plots were 12% higher at Goberi, 24% higher at Gaya and 89% higher at Kouaré ( $P = 0.10$ )

Table 3. Effects of cereal-legume cropping systems on soil mineral N (Nmin =  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N) and  $\text{NO}_3^-$ -N in May, June and September 1997 and 1998 at Gaya, Goberi and Kouaré. Sampling depth was 0 – 0.3 m

Time	Goberi		Gaya		Kouaré	
	Millet/cowpea				Sorghum/groundnut	
	Nmin	$\text{NO}_3^-$ -N	Nmin	$\text{NO}_3^-$ -N	Nmin	$\text{NO}_3^-$ -N
Cropping system	mg N kg <sup>-1</sup> soil					
1997						
May						
Continuous	3.1	1.3	8.9	4.7	12.1	8.3
Rotation	3.5	1.2	11.0	6.0	23.1	18.6
<i>P</i> > <i>F</i> <sup>a</sup>	0.448	0.587	0.045	0.025	0.050	0.008
June–July						
Continuous	5.2	3.4	9.6	5.6	14.4	11.2
Rotation	5.2	3.2	12.1	7.9	20.0	15.9
<i>P</i> > <i>F</i>	0.675	0.706	0.055	<0.001	0.025	0.016
September						
Continuous	1.2	0.2	6.5	3.3	10.6	6.6
Rotation	1.6	0.2	4.9	1.8	17.9	13.8
<i>P</i> > <i>F</i>	0.626	0.803	0.706	0.035	0.021	0.002
1998						
May						
Continuous	8.6	5.2	10.3	6.7	8.3	6.5
Rotation	6.5	5.4	11.5	7.5	15.4	13.9
<i>P</i> > <i>F</i>	0.316	0.406	0.406	0.446	0.332	0.063
June						
Continuous	4.0	1.4	5.4	3.1	14.9	9.8
Rotation	3.8	0.9	5.7	3.1	15.2	10.3
<i>P</i> > <i>F</i>	0.440	0.421	0.589	0.700	0.979	0.647
July						
Continuous	5.5	3.8	12.4	7.5	8.5	4.9
Rotation	4.6	3.3	11.0	7.2	7.7	4.6
<i>P</i> > <i>F</i>	0.876	0.427	0.765	0.814	0.430	0.059
August–September						
Continuous	3.8	1.7	5.4	2.7	6.8	4.3
Rotation	3.8	1.8	5.7	3.0	7.7	5.0
<i>P</i> > <i>F</i>	0.650	0.955	0.359	0.502	0.606	0.144

<sup>a</sup> Probability of a treatment effect (significance level).

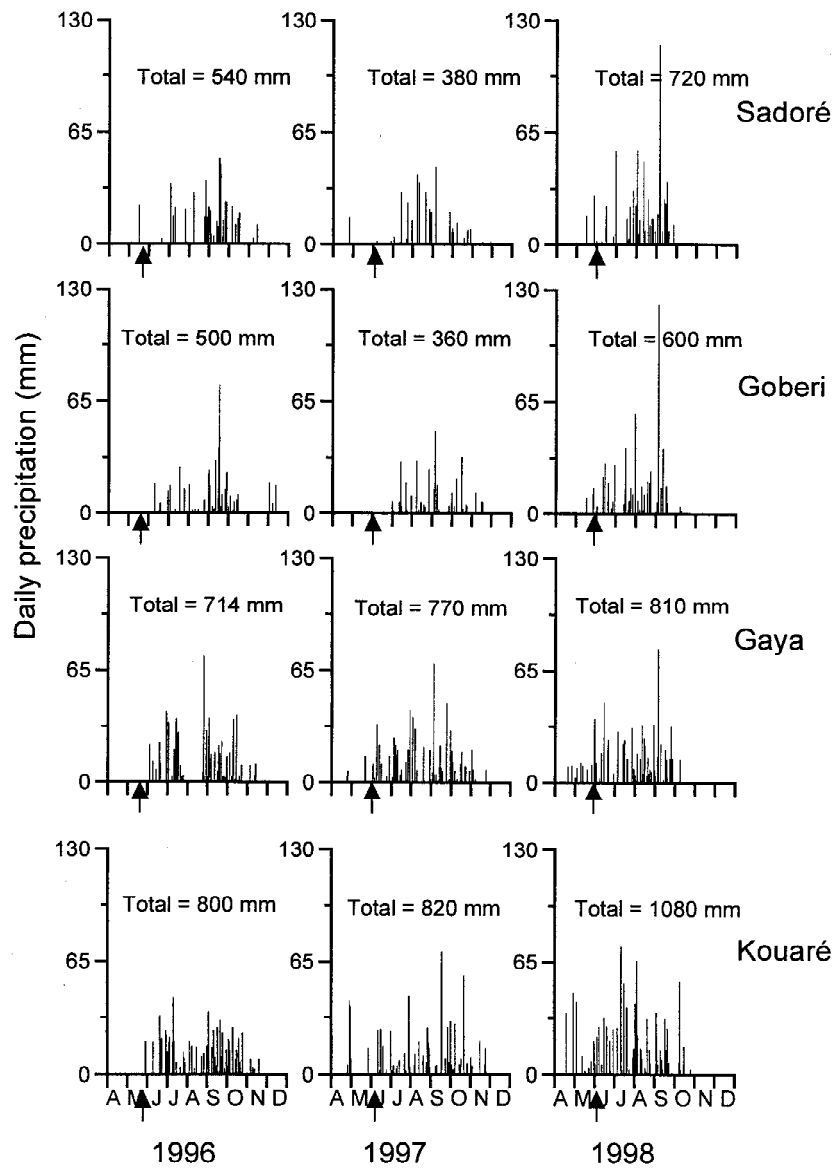


Figure 1. Daily precipitation in 1996, 1997 and 1998 at Sadoré, Goberi and Gaya in Niger and at Kouaré in Burkina Faso from April (A) to December (D) of each year. The arrows indicate the time of sowing of the cereal crop at each site.

than continuous cereal plots (Table 3). In July of the same year, even after considerable rainfall had occurred (Figure 1), cereal plots grown previously to legumes still had 26% more Nmin at Gaya and 39% more Nmin at Kouaré in their topsoil than continuous cereal plots. In September, differences were reversed at Gaya with 25% lower Nmin concentrations in rotation cereal plots compared to plots with continuous cereal.

At planting time in May 1998, rotation cereal plots at Gaya and Kouaré had higher Nmin levels in the top-

soil than continuous cereal plots, but differences were statistically significant only at Kouaré. From June to September 1998, no significant differences in Nmin between cropping systems were observed at any location. For the sites in the Sahelian zone at Sadoré (data not shown) and Goberi (Table 3), however, no rotation effects on soil Nmin levels in the topsoil were found for any sampling time.

Table 4. Root infection by mycorrhizae (AM) in millet (0–0.3 m) as affected by cropping systems at Sadoré, Goberi and Gaya

Cropping systems	1996		1997				
	Goberi	Gaya	Sadoré		Goberi	Gaya	
	120 DAS <sup>b</sup>		35 DAS	75 DAS	45 DAS	75 DAS	50 DAS
AM infection (% of roots)							
Continuous millet	35	31	23	44	27	48	11
Millet after cowpea	39	33	32	50	48	64	31
$P > F^a$	0.280	0.325	<0.001	0.109	<0.001	<0.001	<0.001

<sup>a</sup> Probability of a treatment effect (significance level).

<sup>b</sup> Days after sowing (DAS).

### Spore numbers and mycorrhizal infection

Although the number of spores in soils of rotation cereal plots were higher than those from continuous cereal plots, these differences were not statistically significant, with a high variation between the individual spore counts leading to CVs between 75 and 122%.

At harvest in 1996, millet root infection by AM at Sadoré, Goberi and Gaya (Table 4) was similar for all cropping systems. However, early sampling in 1997 showed increases in AM infection rates of millet roots from rotation plots of 9% at 35 DAS at Sadoré, 21% at 45 DAS at Goberi and 20% at 50 DAS at Gaya (Table 4). These differences between cropping systems sharply decreased later in the season.

The 1998 data from 35 to 85 DAS at different soil depths at Gaya confirmed the results of 1997 (Figure 2). At 0.15 m depth, root infection rates of rotation millet were 14% higher than those of continuous millet at 45 and 65 DAS. At 85 DAS, the differences between cropping systems were small and not significant. For all sampling periods, these differences were significant at 0.3 and 0.45 m, but not at 0.6 m.

In the sorghum/groundnut cropping systems at Kouaré (Figure 3), significant differences of AM infection rates between cropping system were found at 45 DAS with an increase of 7% in rotation sorghum compared with continuous sorghum. Rotation effects on AM infection rates appeared to be larger in cereals than in legumes (Figures 2 and 3).

### Nematode populations in millet/cowpea cropping systems

Nematodes extracted from soil and root samples in millet/cowpea rotations generally belonged to the groups of *Helicotylenchus* sp., *Rotylenchus* sp. and

*Pratylenchus* sp. *Helicotylenchus* was more abundant at Gaya, while *Rotylenchus* was most frequently encountered at Goberi. In 1997, no significant differences were observed between cropping systems at Sadoré (Table 5). However, at 65 DAS there were 70% more plant-parasitic nematodes in rotation millet compared with continuous millet at Goberi ( $P = 0.028$ ). At Gaya, nematodes extracted from soil 45 and 90 DAS did not show differences between rotation millet and continuous millet (Figure 4) but roots of rotation cowpea at harvest had 79 and 81% more nematodes compared with roots of continuous millet and rotation millet (Table 5). In 1998, no differences were observed between cropping systems throughout the growing season at Gaya (Figure 4) nor at any other millet/cowpea growing site.

Table 5. Total plant-parasitic nematode numbers 65, 95 and 105 days after sowing (DAS) as affected by millet/cowpea rotation in 1997 at Sadoré, Goberi and Gaya

Cropping Systems	Sadoré	Goberi	Gaya
	95 DAS		
	105 DAS (maturity)		
Nematode numbers			
100 g <sup>-1</sup> soil		100 g <sup>-1</sup> fresh roots	
Continuous millet	102	270	3180
Millet after cowpea	81	460	3140
Cowpea after millet	108	200	5680
LSD <sup>a</sup>	45	137	2720
$P > F^b$	0.541	0.028	0.071
CV <sup>c</sup> (%)	90	99	69

<sup>a</sup> Least significant difference (LSD) of means at  $P = 0.05$ .

<sup>b</sup> Probability of a treatment effect (significance level).

<sup>c</sup> Coefficient of variation.

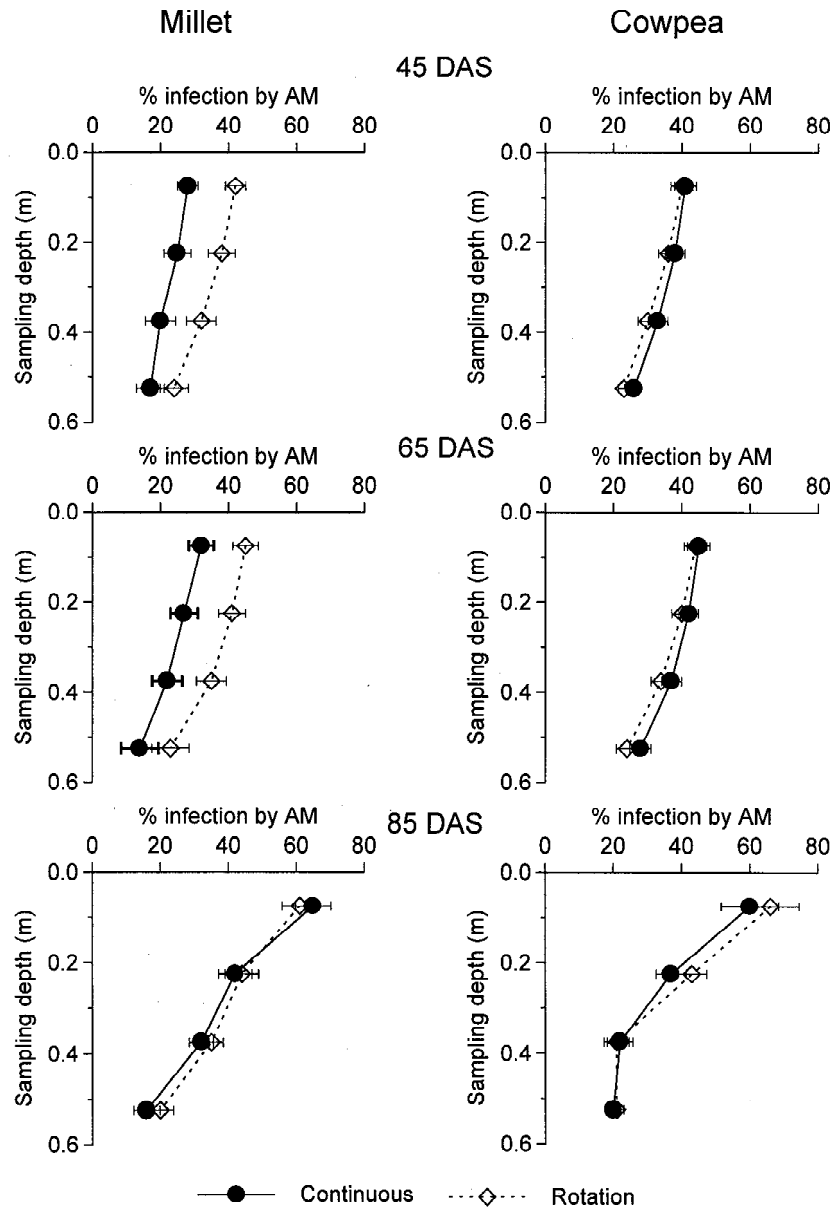


Figure 2. Infection rates of millet and cowpea roots by vesicular arbuscular mycorrhizae (AM) at 45, 65 and 85 days after sowing (DAS) as influenced by millet/cowpea rotations and rooting depth in 1998 at Gaya. Horizontal lines across data points indicate  $\pm$  one standard error of the mean.

*Nematode populations in sorghum/groundnut cropping systems*

In general, *Ditylenchus* sp. was found only in 5% of the samples extracted from soil and roots at Kouaré, whereas 90% of the samples contained *Pratylenchus* sp. 40% *Helicotylenchus* sp. and 20% *Rotylenchus* sp. In 1997 at 45 DAS, averaged over fertilisation treatments, continuous sorghum soil had six-fold more

nematodes than rotation sorghum and nine-fold more than rotation groundnut (Figure 5). Roots at 95 DAS (data not shown) had seven- to ten-fold more nematodes in continuous sorghum than in either rotation sorghum or rotation cowpea. Throughout the growing season of 1998, continuous sorghum soil had four- to eleven-fold more nematodes than rotation sorghum. In general, no statistical differences were observed between continuous and rotation groundnut, but the



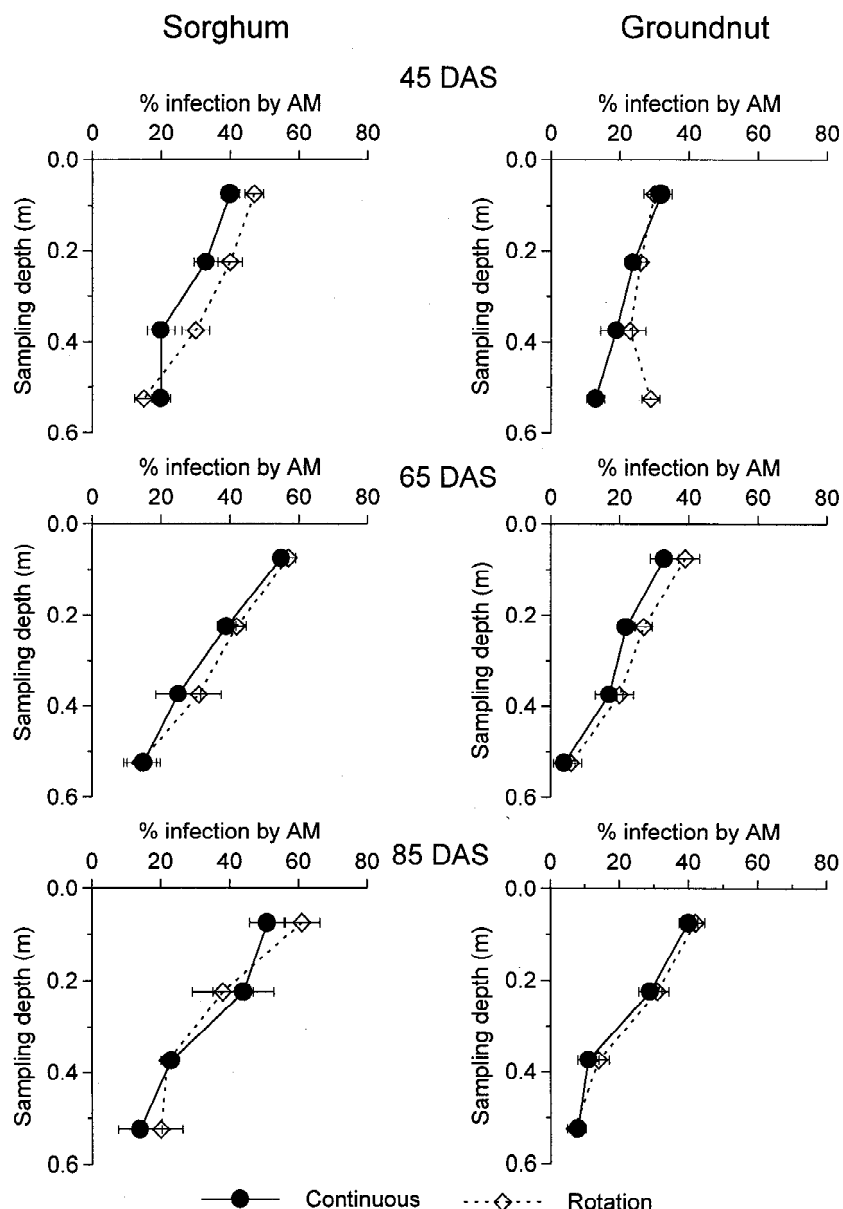


Figure 3. Infection rates of sorghum and groundnut roots by vesicular arbuscular mycorrhizae (AM) at 45, 65 and 85 days after sowing (DAS) as influenced by sorghum/groundnut rotations and rooting depth in 1998 at Kouaré. Horizontal lines across data points indicate  $\pm$  one standard error of the mean.

lowest absolute numbers of nematodes were detected in continuous groundnut.

### Discussion

Plant stands in many parts of semi-arid West Africa are characterised by high spatial-variability over short distances (Buerkert et al., 1995; Chase et al., 1989).

This makes it rather difficult to clearly demonstrate rotation effects on crop growth in small field plots and even more challenging to investigate their biochemical causes such as differences in Nmin levels, AM infection rates or nematode densities. In a pot experiment with a West African soil, it has been shown recently that AM infection can play an important role for growth and nutrient uptake of cereals and legumes

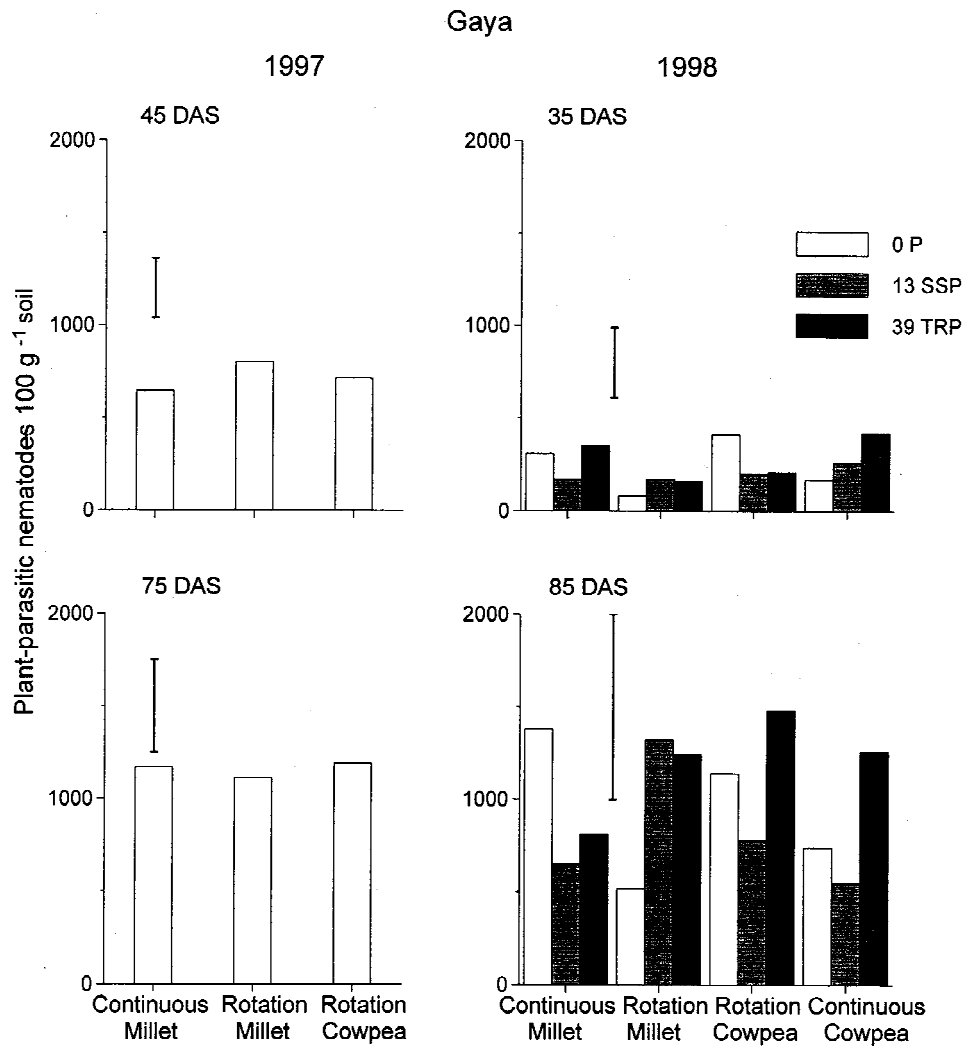


Figure 4. Plant-parasitic nematode numbers as affected by millet/cowpea rotations and phosphorus (P) application in 1997 and 1998 at Gaya. Phosphorus was applied as single superphosphate at 13 kg P ha<sup>-1</sup> (13 SSP) and Tahoua rock phosphate at 39 kg P ha<sup>-1</sup> (39 TRP). Vertical lines across data points indicate least significant differences (LSD<sub>0.05</sub>) of means.

(Bagayoko, unpublished data). To our knowledge, this is the first report indicating the role of AM for rotation effects in field experiments of Sudano-Sahelian West Africa.

The consistently higher N<sub>min</sub> levels in rotation cereal compared to continuous cereal and the observed higher early dry matter production at thinning also suggest that differences in soil mineral N at the beginning of the growing season may play, at least initially, a primary role in rotation effects on cereal growth. With higher soil N<sub>min</sub> concentrations after germination, millet and sorghum in rotation had better growth conditions than continuous cereals leading to higher

shoot biomass (Table 2) and larger root length density (data not recorded) at thinning. This caused a subsequent increase in early AM infection (Table 4, Figures 2 and 3). Early AM infection in turn may then have further stimulated plant growth through higher nutrient uptake (Bagayoko, unpublished data). In the severely nutrient deficient soils of West Africa, even small absolute differences in soil available nutrients, particularly in N and P, by the time when the seed reserves are exhausted may be decisive in promoting growth during the time of major stresses such as sand storms and high rainfall intensity (Sivakumar, 1989).

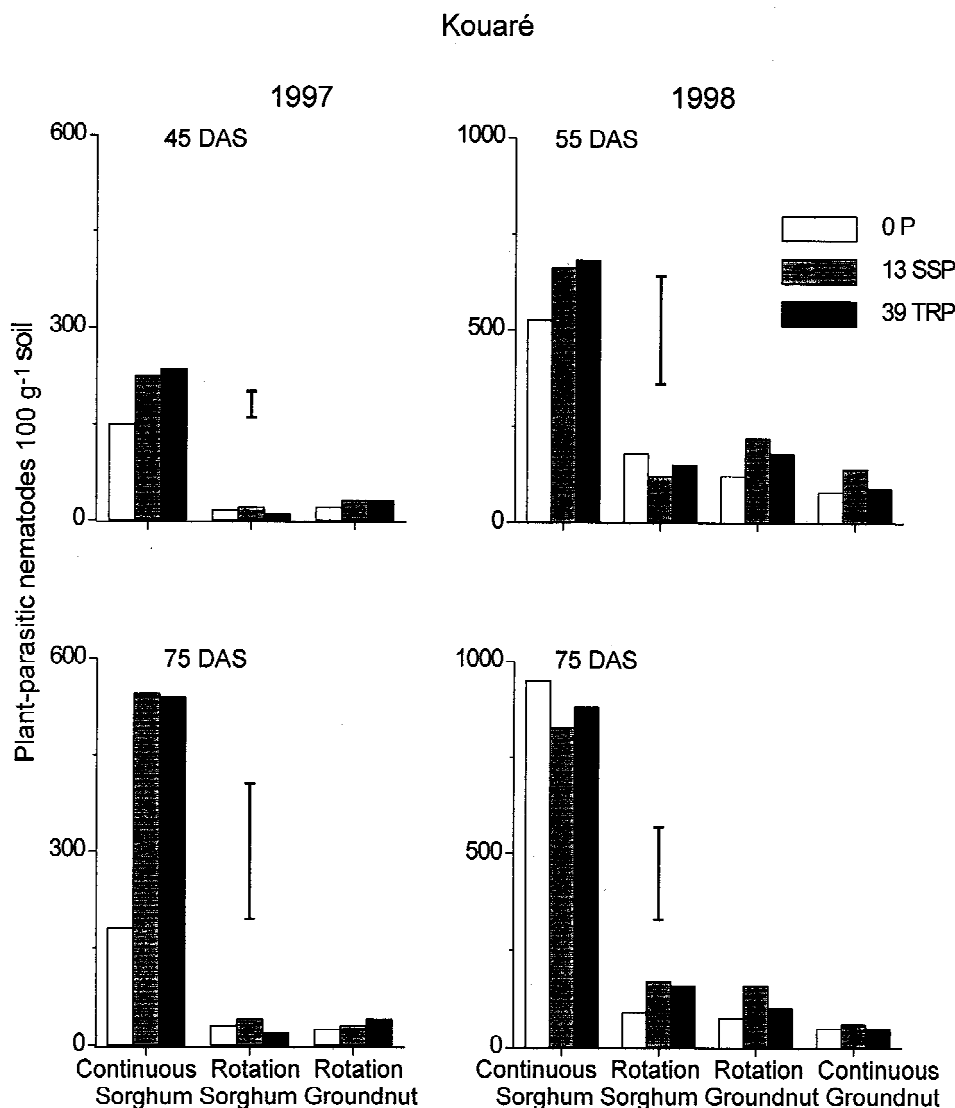


Figure 5. Plant-parasitic nematode numbers as affected by sorghum/groundnut rotations and phosphorus (P) application in 1997 and 1998 at Kouaré. Phosphorus was applied as single superphosphate at 13 kg P ha<sup>-1</sup> (13 SSP) and Tahoua rock phosphate at 39 kg P ha<sup>-1</sup> (39 TRP). Vertical lines across data points indicate least significant differences (LSD<sub>0.05</sub>) of means.

Plant-parasitic nematodes have been reported to cause world-wide yield losses of 11.8% in millet, 12% in groundnut and 7% in sorghum (Sharma and McDonald, 1990). Given the difficulty to visually distinguish the effects of low soil fertility and the effects of nematodes on crop growth under field conditions and the absence of a nematode free treatment in our experiments, the direct importance of nematodes on crop yields was hard to assess. Nevertheless, despite the higher rainfall at Gaya where plant-parasitic nematode numbers were particularly large, the yield levels there were much lower than at the other sites. On the

sandy infertile soils which cover most of the millet and cowpea growing zone of Niger, even low numbers of plant-parasitic nematodes may cause substantial damages to a plant's root system and thus have large effects on nutrient uptake and subsequent crop growth.

The three important nematode groups found in our soils (*Helicotylenchus*, *Pratylenchus* and *Rotylenchus*) are all parasites of both cereals and legumes. The lack of suppressive effects of millet/cowpea rotations on these plant nematodes is, therefore, predictable as both crop species are hosts. While there is no data on nematode-induced damages for millet and cowpea

in Niger, *Helicotylenchus* sp. *Pratylenchus* sp., and *Rotylenchus* sp. have been reported to cause major yield losses for both crops in India (Jain, 1983), in the United States (Johnson and Fassuliotis, 1991), in Australia (Thompson et al., 1994; Wildermuth et al., 1997) and in Zimbabwe (Sharma and McDonald, 1990). This was in sharp contrast to the strong suppressive effects of sorghum/groundnut rotation on *Pratylenchus* and *Helicotylenchus* densities at Kouaré (Figure 5). *Pratylenchus* and *Helicotylenchus* were found to be commonly associated with sorghum in Colombia (Trevathan et al., 1985). A survey conducted on 16 sorghum genotypes in Brazil indicated that *Helicotylenchus* and *Pratylenchus* were present in all samples with an average of 70 nematodes per 100 g soil for *Helicotylenchus dihystra* and 95 nematodes per 100 g soil for *Pratylenchus brachyurus* (Sharma and Medeiros, 1982). Much less is known about *Helicotylenchus* or *Pratylenchus* in groundnut. Osseni (1985) reported from the Ivory Coast that both groundnut and maize were poor hosts for *Pratylenchus brachyurus*, whereas the same species has also been reported to occasionally cause severe yield losses in peanut in the United States (Dickson, 1998). It is possible that differences in groundnut genotype and *Pratylenchus* species may explain this contradicting evidence.

The mechanisms of site-specific differences in yield responses to crop rotation in the semi-arid regions of West Africa are poorly understood. The results of this study showed that sites with low plant-parasitic nematode densities such as Sadoré had large rotation effects in contrast to sites with high numbers of total plant-parasitic nematodes such as Gaya. At Kouaré, the significantly higher nematode numbers in continuous sorghum compared with rotation are presumably one reason for the observed large rotation effects at this site.

Based on the results of this study, a conceptual model is proposed to explain rotation effects in Sudano-Sahelian West Africa (Figure 6). 1. Symbiotic N<sub>2</sub> fixation, although poorly quantified under Sahelian conditions, seems to be a primary driving force in cereal/legume rotation effects on cereal growth. Compared to continuous cereal, increased levels of N<sub>min</sub> from decomposing legumes roots and nodules will lead to an increase in early root and shoot growth of rotation cereals. 2. Vigorous early root development leads to increases in AM infection rates as it is well known that the establishment and maintenance of mycorrhizal symbiosis requires a flow of carbon from the

host plant to the fungus (Todd et al., 1984). Nitrogen-driven differences in AM infection rates were largest early in the growing season. Thus, late sampling may fail to detect differences between cropping systems as even a poorly growing continuous cereal crop becomes more infected with AM as plants get older. 3. A secondary driving force of rotation effects may thus be the increased P uptake through early AM infection. In the Sudano-Sahelian zone of West Africa, P deficiency is so acute that crop growth remains low without the application of P fertilisers (Bationo et al., 1990). Under these conditions, an early root infection by AM alone or in combination with a starter application of P can improve and maintain plant growth, particularly under the harsh climatic conditions early in the season and as a consequence throughout the growing cycle enhance the uptake of P and other micro nutrients such as copper (Cu) and zinc (Zn; George et al., 1994, 1996; Ortas et al., 1996). Similar effects of early VA infection on early growth of sorghum and other cereals on acid-infertile soils have been reported previously (Dodd and Jeffries, 1986; Dodd et al., 1990). 4. A third factor likely contributing to cereal/legume rotation effects on cereal growth which requires further investigation may be a better control of soil born parasites, such as nematodes, in such systems compared to continuous cereal cropping. The influence of nematodes in crop rotations, however, will largely depend on the nematode species present in the field, their infestation levels and the choice of rotation crops (Thompson et al., 1994; Wildermuth et al., 1997). When both crops in a rotation are hosts, the nematode levels may steadily increase because nematodes will be able to propagate continuously (Wildermuth et al., 1997). In such a case, differences between rotation and continuous cereal TDM yields may be small as it was probably the case in millet/cowpea rotations at Gaya. Rotating a host crop with a non-host crop will reduce the nematode population densities and lead to large rotation effects, such as in the sorghum/groundnut rotation at Kouaré. In this study, sorghum/groundnut rotations appeared much more effective in controlling nematode densities than millet/cowpea rotations.

## Conclusions

The results provide evidence that higher early N availability at planting time and higher early mycorrhizal infection contribute to the often observed increases in the TDM of cereal grown in rotation with legumes

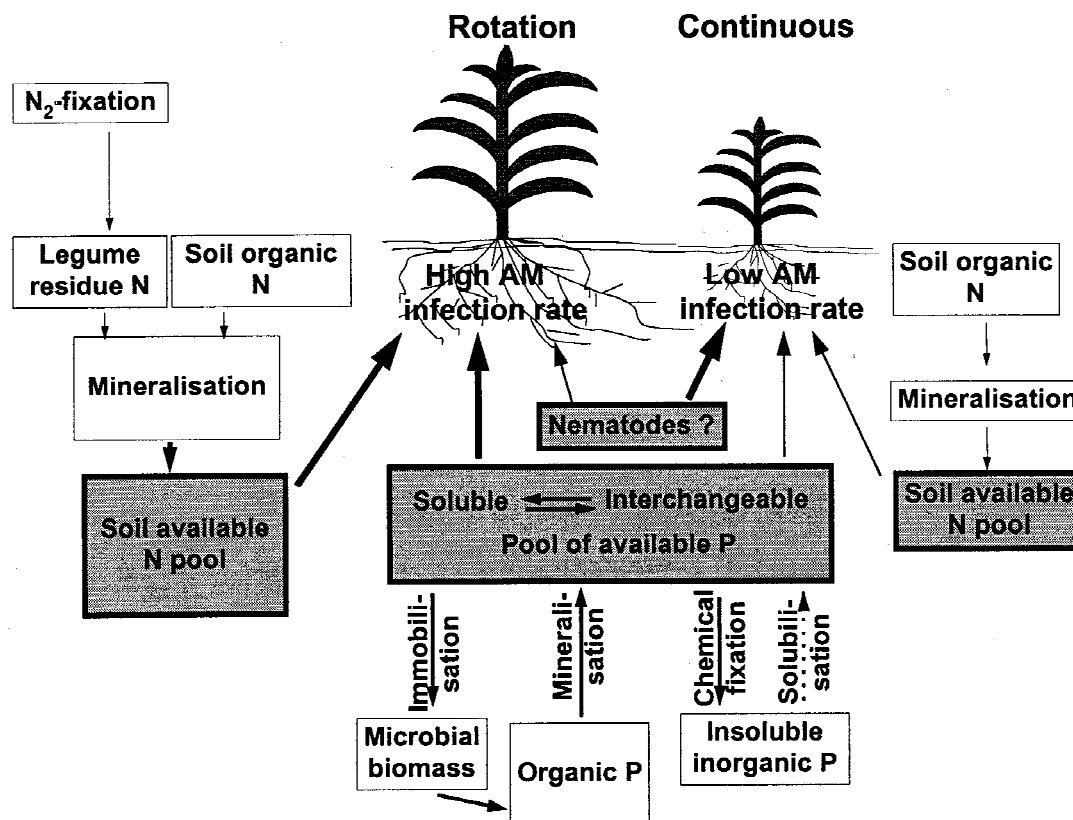


Figure 6. A conceptual model to explain rotation effects in the Sudano-Sahelian zone of West Africa.

on nutrient-poor acid sandy soils of the West African Sudano-Sahelian zone. This would also explain the often observed phenomenon that rotation effects on cereal TDM are unaffected by even high rates of applied mineral N and P fertilisers. From the farmers' point of view, the role of legumes in the agro-pastoral cropping systems of Sudano-Sahelian West Africa is expected to increase wherever advantageous product prices for legume grain or shoot material can be obtained. If so, the right choice of the crop species should help to stabilise cereal yields.

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