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## Relationships between abiotic and biotic soil properties during fallow periods in the sudanian zone of Senegal

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### Abstract

Relationships between soil characteristics, various forms of soil organic matter, microbial biomass and the structure of phytoparasitic nematode populations were investigated in six fallow fields aged from 1 to 26 years in the West African Savanna (WAS) belt in southern Senegal. Soil sampling was performed along two transects in each field. Herbaceous biomass and soil physical, chemical and biological characteristics were studied with principal component analysis (PCA) and the relationships between the parameters were extracted with co-inertia analysis.

Soil properties (mainly calcium, magnesium and total carbon contents, and cation exchange capacity) slightly improved in the upper soil layer (0–5 cm) during the succession of vegetation. In contrast, in the 0–10 cm soil layer, microbial biomass and total soil organic carbon content showed no clear pattern of change over time, while highest charcoal stocks were found in older fallows where bush fires are frequent. In the 0–40 cm layer, living root biomass increased and herbaceous biomass decreased through the chronosequence. Evidence is presented here for particular relationships between some of the carbon components and the structure of the nematode community. *Pratylenchus* and *Ditylenchus* species were associated with the grass vegetation of the youngest fallows. In contrast *Helicotylenchus* and *Scutellonema* were present in old fallows. The multiplication of the latter appeared closely related to the presence of woody fine roots, whereas, that of the former seemed to be favoured by the presence of the coarsest roots of trees.

*Xiphinema* had a higher density in soils with higher bulk density. Microbial biomass was not affected by fallow duration and was not correlated with the abundance of non-phytoparasitic nematodes. These results suggested that the management of crop pests such as nematodes in the soils of the WAS could be exerted through stump protection and tree plantation (improved fallow, agroforestry) during the crop-fallow cycle. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Co-inertia analysis; Fallow field; Nematodes; Organic matter; Soil abiotic factors; Sudanian area

### 1. Introduction

Chemical fertility and physical stability of sandy soils in West Africa are low (Sanchez and Logan, 1992). Coarse texture, low activity clays, and harsh climatic conditions are the main reasons for nutrient leaching, erosion and low organic status of soils. Consequently, biota plays a crucial role in the fertility of

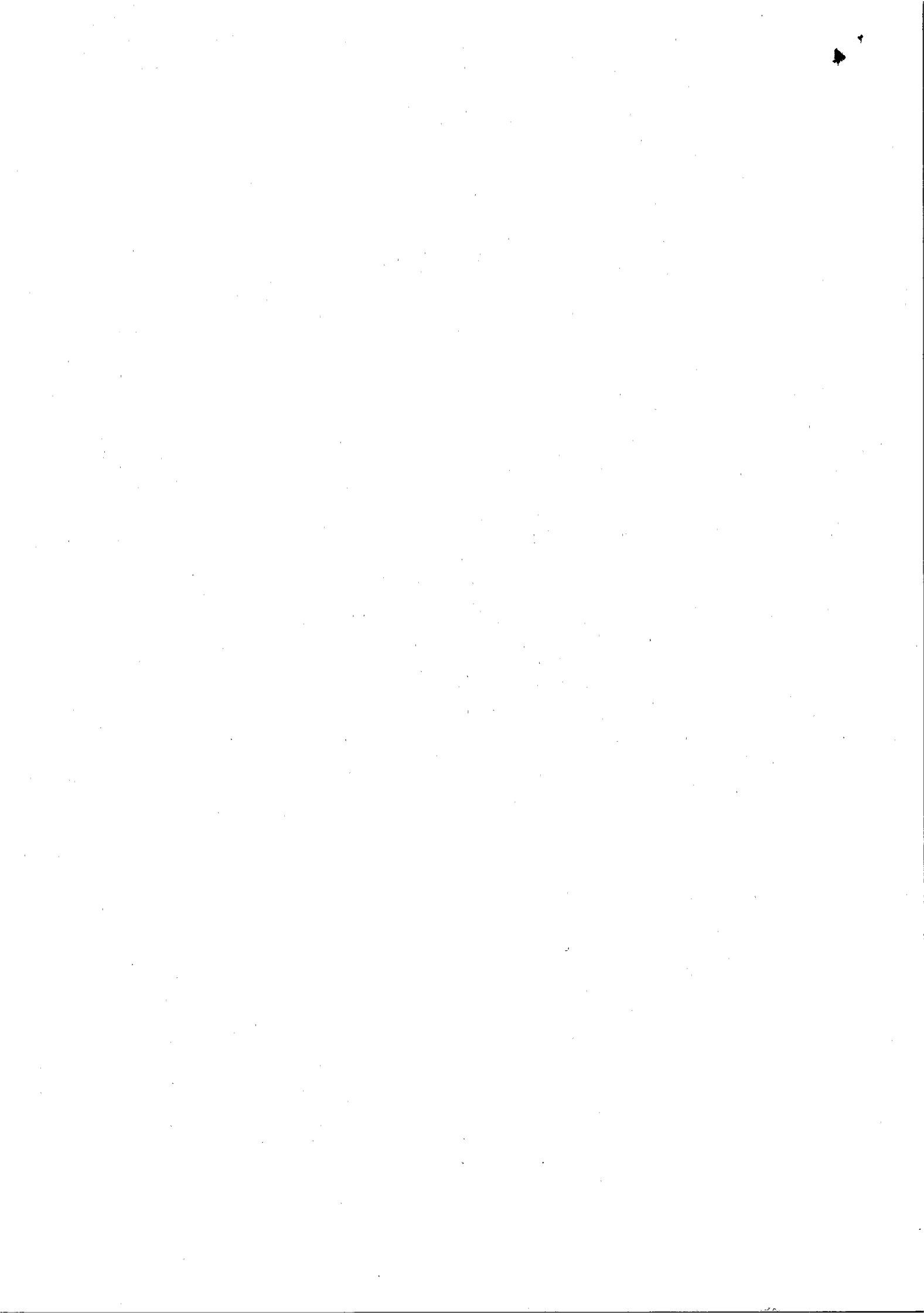
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these soils (Chotte et al., 1995; Lavelle, 1997). Mechanisms commonly put forward for the beneficial impact of biota on soil properties are the improvement of physical properties (aggregate stability and porosity) due to root dynamics, macrofaunal activity, and the conservation of nutrients in the plant biomass (Abbadie et al., 1992).

In the West African Savanna (WAS) zone, the sustainability of farming systems relies very much on practices meant to promote biological activity and diversity in soils. Fallowing and manure amendment are thought to be the most popular means. The latter aims at preserving the activity of soil biota, whereas fallowing stimulates the development of soil organism communities, resulting in a more intense activity and a greater biological diversity (Feller et al., 1990; Pate, 1997). However, as a result of demographic pressure and local land tenure policy, fallows have nearly disappeared in the WAS (Ruthenberg, 1980; Floret et al., 1993). Therefore, traditional farming systems known for preserving soil health and quality have in fact shifted to 'mining' agriculture; their duration depends only on the depletion rates of assimilable nutrients (Van Der Pol, 1992). Thus, alternatives for the improvement, or substitution of fallowing should take into account the traditional functions of fallow, such as biomass production and soil biological fertility enhancement.

In this study fertility was defined as the ability of the whole below-ground ecosystem to enable steady plant productivity. The aim of our work was to describe the process of fertility replenishment during the fallow period by investigating the interactions between living, functional groups (mainly roots, microflora and nematode communities) and abiotic soil properties during the fallow period in the semi-arid zone of Senegal. We hypothesised that the sustainability of ecosystems of WAS relies largely on the relationships between the status of soil biota (fauna, mesofauna, micro-organisms) and soil carbon quantity and quality (Menaut et al., 1985; Perry et al., 1989; Lavelle, 1997). Therefore, this study focused on the relationships between:

- Root biomass and soil organic matter (SOM) content. Roots are the main source of carbon to the soils in agro-ecosystems including those frequently exposed to fire, such as those encountered in the WAS (Menaut et al., 1985; Young, 1989)

- Nematodes, microbial biomass and SOM. The energy required for the metabolism of heterotrophic organisms is contained in the SOM and also represents the main source of nitrogen assimilable by plants. Carbon can be stored under biologically very active (living biomass) or more inert forms (litter, humus).

## 2. Methods

### 2.1. Field site

The study was conducted in the Region of Kolda, in Casamance, southern Senegal (12°49'N–14°53'W). The climate is dry tropical and rainfall occurs between June and October, averaging 960 mm per annum from 1978 to 1997. Mixed farming systems dominate. The main crops are millet, rice, sorghum, groundnut and cotton, and there is extensive management of livestock on rangeland. The soil was described as sandy, ferruginous by Baldensperger et al. (1967) and belongs to the order of Lixisols (FAO, 1998).

The up-slope plateau, on which slash-and-burn agriculture is practised, is still covered with vast areas of 'woodlands with a well developed tree stratum and shrubby undergrowth' (DeWolf, 1998), savanna and old fallows. Resprouting Combretaceae (mostly *Combretum geitonophyllum* Diels, *C. glutinosum* Perr. and *Terminalia macroptera* G. et Perr.) are the major component of the woody vegetation. Bush fields at the edge of the plateau are devoted to the cropping of groundnut (*Arachis hypogaea* L.) mostly in short rotation with fallow, and sometime in biennial rotation with millet if manured.

### 2.2. Locations

In 1996, six fallows, aged from 1 to 25 years, were selected, the older being the farthest from the village (Table 1). The size of the plots ranged from 0.3 to 9.3 ha. Field plots were located where secondary dry forest and savanna mix with cropped fields due to slash-and-burn practices. A synchronic approach was adopted (Sanchez, 1987). A selection was made of fallow fields of different age of abandonment but with similar farming practice history and equivalent soil features. The age of the fallows was estimated from

Table 1  
Description of the sampled plots

Fallow field plot number	Date of abandonment	Age of fallow (years)	Description of the vegetation
1	1994	1 and 2	Herbaceous fallow in biennial rotation with groundnut.
2	1992	3 and 4	Grass layer: <i>Andropogon pseudapricus</i> Stapf. ( <i>A.p.</i> ), <i>Tephrosia pedicellata</i> Bak., <i>Pennisetum pedicellatum</i> Trin. ( <i>P.p.</i> ) Woody layer: a few resprouting thickets of <i>Terminalia macroptera</i> G. et Perr. ( <i>T.m.</i> ), <i>Combretum glutinosum</i> Perr. ( <i>C.glu.</i> )
3	1989	6 and 7	Bush fallow
4	1983	12 and 13	Grass layer: <i>A.p.</i> , <i>P.p.</i> Woody layer: <i>T.m.</i> , <i>Dichrostachys glomerata</i> (Forsk.) Chiov. ( <i>D.g.</i> ), <i>C.glu.</i> , <i>Combretum geitonophyllum</i> Diels ( <i>C.gei.</i> )
5	1978	17 and 18	Woody fallow
6	1971	25 and 26	Grass layer: <i>P.p.</i> Woody layer: <i>C.gei.</i> , <i>T.m.</i> , <i>C.glu.</i> , <i>Combretum nigricans</i> Lepr., <i>Piliostigma thonningii</i> (Sch.) Miln.-Redh, <i>D.g.</i>

local enquiries among peasants and confirmed by ring counts of cross-sections of woody species.

### 2.3. Sampling schemes

In each plot, two representative transects (TA and TB) were laid out 1 m apart.

For TA, 16 cores, 1.5 m apart, were taken from the topsoil layer (0–5 cm) for chemical and textural analysis. Each sample contained approximately 300 g of soil. For TB, 20 soil samples (each weighing around 750 g), 1 m apart, were taken from the 0–10 cm layer for microbial biomass, carbon content, and nematode analyses. Fine root biomass and charcoal stock were sampled from the same spot in 10 cm increments to 40 cm depth using a 5.6 cm diameter core auger. Herbaceous and litter biomass were measured from a 1×0.5 m rectangle. Within this area soil was removed to 40 cm depth and coarse roots and stumps recovered. A detailed description of the abbreviations of the variables can be found in Table 2.

Soils were sampled at the beginning of the dry season. Subsamples for chemical analyses were air-dried, sieved to <2 mm and stored at room temperature prior to analysis. Soils for biological determinations (microbial biomass and nematodes) were kept at field conditions and analysed the day after collection.

### 2.4. Analyses

All soil subsamples used for physical, chemical and biological analyses were individual samples taken from intact TA/TB cores; no composite was made from these cores.

#### 2.4.1. Physical and chemical properties

Mineral particles of the clay (Cla), fine (Fsi) and coarse (Csi) silt, and fine (Fsa) and coarse (Csa) sand fractions were collected by mechanical analysis after the destruction of organic matter by hydrogen peroxide and the total dispersion of 10 g of soil in a NH<sub>4</sub>Cl solution (1 M final concentration). Bulk density (Dens) was calculated from the weight of intact soil contained in a 100 cm<sup>3</sup> cylinder pushed in the ground, on an oven-dry basis (105°C). The cation exchange capacity (CEC) was measured on 5 g of soil with ammonium acetate at pH 7 (Page et al., 1989). The main exchangeable cations, calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K) were titrated with a flame spectrometer after exchange with ammonium acetate. The saturation percentage (Sat) is the ratio of the CEC and the sum of the cations. Assimilable phosphorus (P) was determined on 2 g of soil after Olsen modified by Dabin (1967). Volumetric water content (WpF4) was determined on approximately 10 g of soil at a suction equivalent to pF 4.2–(1.6 MPa) (Klute, 1986).

Table 2  
Variable codes for the 'organic matter' data

Variable	Description	Unit	Depth (cm)	Code
Total carbon rate		g kg <sup>-1</sup>	0–10	C
Total nitrogen rate		g kg <sup>-1</sup>	0–10	N
Carbon:nitrogen ratio			0–10	C/N
Bulk density		g cm <sup>-3</sup>	0–10	Dens
Fine elements	Weight contribution of the 0–50 µm fraction	g 100 g <sup>-1</sup> of soil	0–10	Frac1
Organic debris of the soil fraction	2 mm diameter, minus charcoals and roots floating fraction collected on a 1 mm sieve quick sieving followed by hand sorting	t ha <sup>-1</sup>	0–10	Deb1
			10–20	Deb2
			20–30	Deb3
			30–40	Deb4
Charcoal	Floating fraction collected on a 1 mm sieve quick sieving followed by hand sorting	t ha <sup>-1</sup>	0–10	Char1
			10–20	Char2
			20–30	Char3
			30–40	Char4
Fine roots	Diameter: (0–2) mm collected on a 1 mm sieve	t ha <sup>-1</sup>	0–10	FRo1
			10–20	FRo2
			20–30	FRo3
			30–40	FRo4
Coarse roots	Diameter: (2–5) mm hand sorted on field Diameter: (5–10) mm hand sorted on field Diameter: >10 mm hand sorted on field Diameter: non measurable (root debris) hand sorted on field	t ha <sup>-1</sup>	0–40	CRo1
				CRo2
				CRo3
				Crodeb
Stump	Living biomass hand sorted on field Dead biomass hand sorted on field	t ha <sup>-1</sup>	0–40	LSt
				DSt
Litter	Free organic fraction with diameter >2 mm excludes dead wood	t ha <sup>-1</sup>	Surface	Lit
Dead wood		t ha <sup>-1</sup>	Surface	DWo
Herbaceous biomass		t ha <sup>-1</sup>	Surface	Herb
Soil humidity	Measured at the sampling date	g 100 g <sup>-1</sup> of soil		Water
Microbial biomass		µg 100 g <sup>-1</sup> of soil		MiB

#### 2.4.2. Forms of organic matter

The litter collected at the surface comprised organic debris free of mineral soil particles (sieved to >2 mm). It was manually separated into two fractions: dead wood (Dwo) and litter (Lit). Core samples were elutriated under a water stream (Webb, 1995). The organic fraction collected on a 1 mm sieve was then separated by hand into three fractions: fine roots <2 mm (FRo), particles of charcoal (Char) and organic residues (ORes). Coarse roots (>2 mm) (CRo) and stumps (dead and living) (DSt, LSt) were manually sorted in the field, washed and as for grass, litter and fine root biomass, oven-dried at 60°C. Roots were classified into three diameter categories: 2–5, 5–10 and >10 mm (Cro1, Cro2

and Cro3, respectively), those which could not be so classified are referred to as root debris (Rdeb) (Table 2).

Soil samples were fractionated using a method adapted from Gavinelli et al. (1995) allowing the soil to be entirely dispersed without any alteration of organic components. Soil was sieved to <50 µm under water and the fractions (0–50) and (50–2000) µm weighed.

#### 2.4.3. Organic carbon and nitrogen

Total carbon (C) and nitrogen (N) contents of the samples (equivalent to 1 g of oven-dried soil) were determined by the Walkley and Black, and Kjeldhal methods, respectively (Bremner, 1965).

#### 2.4.4. Microbial biomass

Microbial biomass of soil subsamples (equivalent to 50 g of oven-dried soil) was estimated by the fumigation–extraction method, using the gain in ninhydrin-reactive N after fumigation, multiplied by 21 (Amato and Ladd, 1988). The results were expressed as  $\mu\text{g C } 100 \text{ g}^{-1}$  soil (MiB) (see Table 2).

#### 2.4.5. Nematodes

Nematodes were collected from soil samples (equivalent to 250 g oven-dried soil) by the Seinhorst's method (Seinhorst, 1962). For phytoparasitic species, only those which were present in at least 5% of the soil samples, were used for statistics: *Helicotylenchus dihystera* (Helico), *Scutellonema cavenessi* (Scut), *Rotylenchulus reniformis* (Rotyl), *Gracilacus parvula* (Gracil), *Criconemella curvata* (Crico), *Hemicycliophora belemnis* (Hemi), *Tylenchorhynchus gladiolatus* (Tylen), *Xiphinema parasetariae* (Xiphi), *Pratylenchus pseudopratensis* (Praty), *Ditylenchus myceliophagus* (Dity). Free-living species were pooled in a single group (Sapro). Results were expressed as individuals per  $\text{dm}^3$  and transformed  $[\log(x+1)]$  prior to analysis.

#### 2.5. Statistics

Statistical analyses were performed on three data sets: (a) the pedological data, with 96 rows (six plots, with 16 sampling points per plot) and 15 columns (15 physical-chemical variables); (b) the soil organic and microbial biomass data, with 120 rows (six plots,

with 20 sampling points per plot) and 28 columns (27 variables describing the organic matter, plus the microbial biomass); (c) the faunistic data, with 120 rows (six plots, with 20 sampling points per plot) and 11 columns (10 plant parasitic nematode species plus the free-living nematode group). Each table of data sets was analysed using Principal Component Analysis (PCA). PCA was based on a correlation matrix for the pedological and organic matter tables, and on a covariance matrix for the nematode table (since there is no reason to standardise the nematode species numbers). The relationships between the nematode table and the organic matter table were analysed with Co-inertia Analysis (Chessel and Mercier, 1993; Dolédec and Chessel, 1994). The permutation test was done by permutating the rows of one of the tables, and recomputing the total inertia (sum of the variances of all variables) of the co-inertia analysis. The distribution of this criterion (total inertia) is then plotted as a histogram for 1000 permutations and the observed value (not permutated) is placed on the histogram to evaluate its position among the permutated values. Computations and graphical displays were performed with the ADE-4 software (Thioulouse et al., 1997).

### 3. Results

#### 3.1. Trends in soil properties

Fig. 1A shows the PCA correlation circle for the pedological variables. Most variables had positive

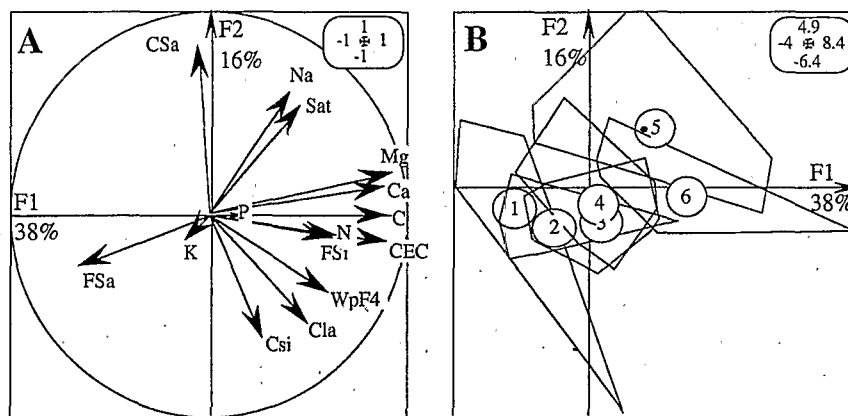


Fig. 1. PCA of soil properties of the 0–5 cm layer. (A) correlation circle of the variables; (B) factorial plan of the sampling spots.

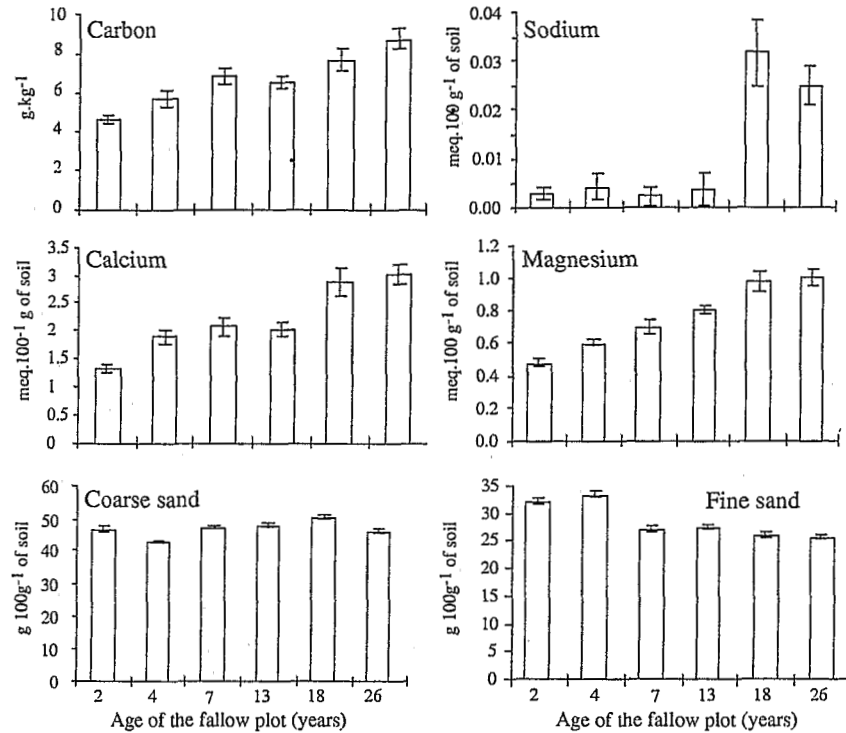


Fig. 2. Plot means and standard errors for selected soil properties of the 0–5 cm layer.

co-ordinates on the first factor (F1). Only coarse sand (Csa), exchangeable potassium (K) and in particular, fine sand (Fsa) had negative co-ordinates. However, Factor 1 was not strictly a particle-size gradient but rather a global size factor causally related to organic carbon (C), and nitrogen (N), cation exchange capacity (CEC), exchangeable calcium (Ca), and magnesium (Mg), water content (WpF4), clay (Cla), and fine silt (Fsi) particles, with all these variables being correlated and varying in the same manner. On the second factor (F2), the variables Csa, sodium (Na) and saturation percentage (Sat) had high positive co-ordinates, in contrast to the fine particles (Cla, Fsi).

Fig. 1B shows the PCA factor map for the 96 sampling points, with convex hulls around the 16 points of each fallow age. These convex hulls are partly superimposed, as a result of high soil spatial heterogeneity encountered at micro-local scale. Their centers (numbers 1–6) are well separated and ordered along the first axis, from younger (negative co-ordinates) to older fallows (positive co-ordinates). Similarly, the means

of the variables C, N, CEC, Ca, Mg, PF4, Cla, and FSi increased with the age of fallows. Fig. 2 clearly shows such increases for C, Ca, and Mg, and the contrasting, relative decrease for FSa. Points of Plots 5 and 6 (18 and 26 year-old fallow) had higher positive co-ordinates on F2 (Fig. 1B) due to high levels of Na (Fig. 2).

### 3.2. Analysis of the forms of soil organic matter and associated microbial biomass

Fig. 3A shows the PCA correlation circle of the organic matter and microbial biomass variables. The F1 axis is restricted to living plant components: the herbaceous biomass is opposed to several kinds of root biomass (coarse, fine, debris). The F2 axis is mainly characterised by biologically inert variables, such as litter (Lit), carbon (C), stumps (Dst), dead wood (Dwo), which are opposed to soil density (Dens) and charcoal (Char1). Microbial biomass (MIB) has a similar magnitude and direction to litter, carbon,

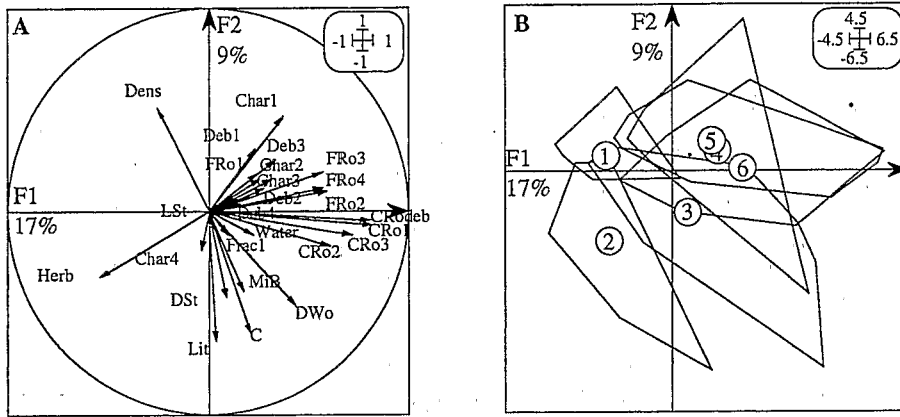


Fig. 3. PCA of the organic matter status variables (A) factorial plan of the variables; (B) factorial map of samples grouped per age of fallow.

stumps, and dead wood, but the correlation with these variables remained weak (Fig. 3A).

On Fig. 3B, the convex hulls for the six fallow periods are partly superimposed, particularly for the last three ages (13, 18 and 26 years), but the hull centers were broadly ordered along F1 from left to right. Middle aged fallow plots (4 and 7 years) have negative

values on the F2 axis because the amounts of litter and carbon were higher in these fallows (Fig. 4).

Fig. 4 shows the variation of several variables according to the length of fallow. Coarse root biomass increased while herbaceous biomass decreased. The youngest fallow had a small amount of dead wood.

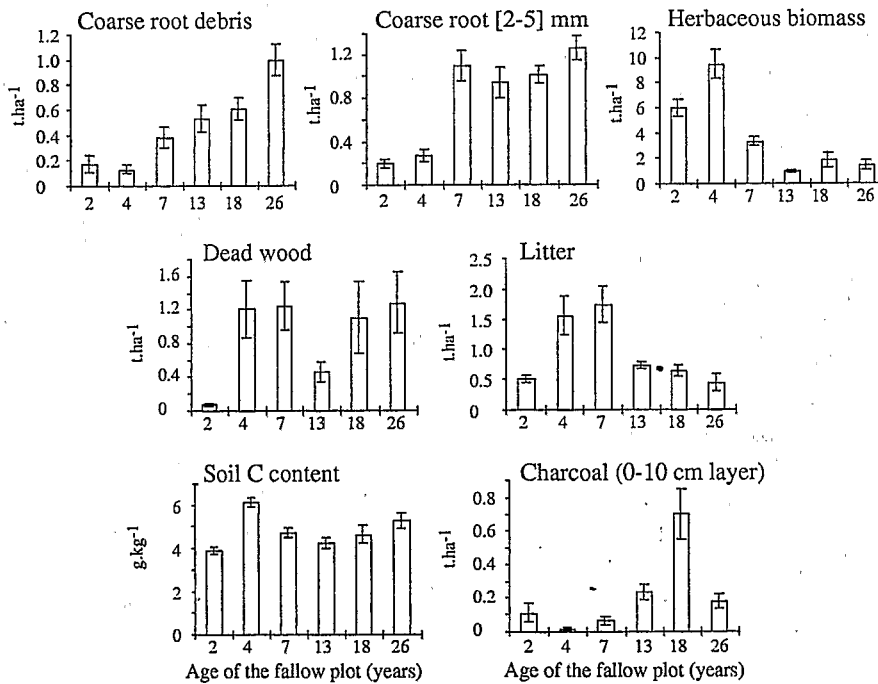


Fig. 4. Plot means and standard errors for selected variables related to organic matter status of plots (see Tables 1 and 2 for codes and units).



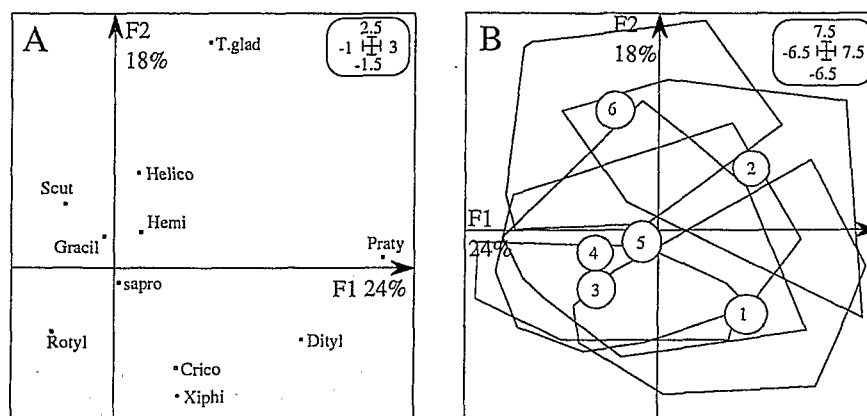


Fig. 5. PCA of the nematological characteristics according to fallow age. (A) factorial plan of the variables; (B) factorial map of the samples grouped per fallow age (see Section 2.4.5 for names of species).

### 3.3. Analysis of nematode populations according to length of fallow

Fig. 5A shows the PCA on covariance matrix of the nematode table. *Pratylenchus* and *Ditylenchus* have positive co-ordinates on the F1 axis in contrast to *Scutellonema* and *Rotylenchus*, which have negative co-ordinates. On the F2 axis, *Tylenchorhynchus* has positive co-ordinate and *Xiphinema* and *Criconebella* negative ones. The convex hulls corresponding to the six fallow ages are superimposed (Fig. 5B). The youngest fallows had positive co-ordinates on F1, due to the presence of high populations of *Pratylenchus* and *Ditylenchus*, and low populations of *Scutellonema* and *Rotylenchulus*. The converse is true for older fallows. The younger and older fallows were opposed on the F2 axis, the younger had higher populations of *Ditylenchus* and *Xiphinema* and the older had higher populations of *Tylenchorhynchus* (Fig. 6).

### 3.4. Nematode — organic matter relationships

The factor maps of the co-inertia analysis between nematodes and the organic matter table (Fig. 7A) were very similar to those of the PCA (Fig. 5A). The first axis, F1, was defined by the biomass of roots with a diameter in the 2–5 mm range and the biomass of coarse root debris, as opposed to herbaceous biomass. On the second axis, soil carbon content was opposed to soil bulk density and to fine elements ((0–50)  $\mu\text{m}$

fraction, *Frac1*). Litter was of less importance than in Fig. 3A.

In contrast, co-inertia analysis inverted axes 1 and 2 (Fig. 7B) as compared to those defined by the PCA performed on 'organic matter' data (Fig. 3A). This stresses several relationships: *Scutellonema* and *Helicotylenchus* were associated with fine and coarse roots, but *Helicotylenchus* was more associated with large diameter roots (found in old fallows) than *Scutellonema*, which had a strong negative correlation with the biomass of the herbaceous vegetation (Fig. 7A–B). *Helicotylenchus* also had a negative correlation with soil bulk density and fine elements. These correlations were weaker for *Scutellonema*.

In contrast, the presence of *Ditylenchus*, *Pratylenchus*, and *Tylenchorhynchus* was associated with large herbaceous biomass found in young fallows (Fig. 7). The abundance of *Xiphinema* was related to high values of soil bulk density, mainly observed in the youngest fallow. No relationship could be established between microbial biomass and nematode populations.

## 4. Discussion

### 4.1. Physical-chemical characteristics in the topsoil layer (0–5 cm)

Despite statistically significant differences in the proportion of sand recorded in the 2–4 years-old and

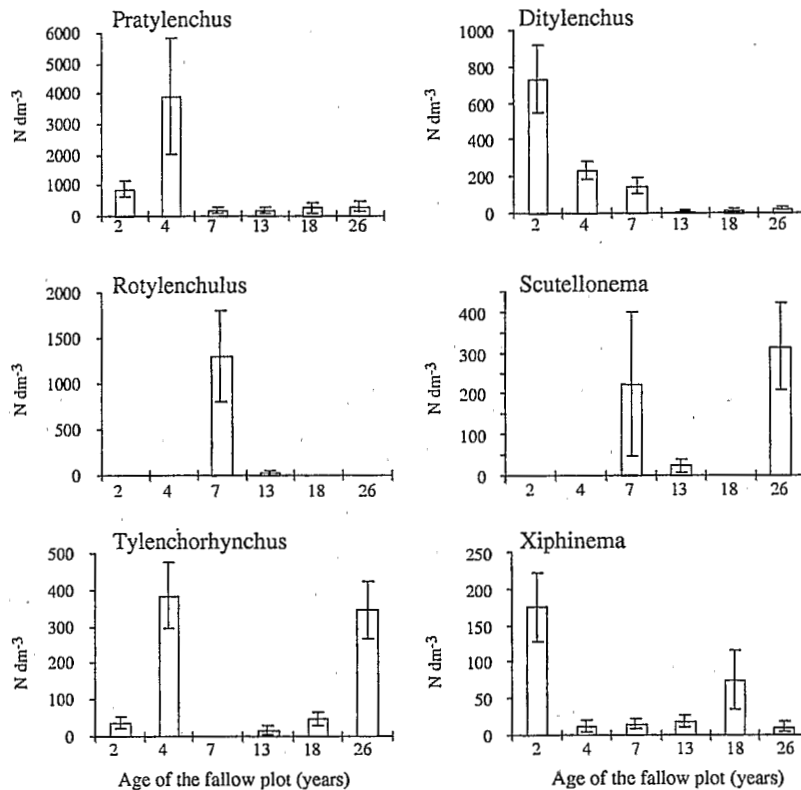


Fig. 6. Plot means and standard errors for some of the nematode genera (units: nematode  $\text{dm}^{-3}$  of soil).

the 7 years-old fallows, all soils had a similar clay content (<10%, Fig. 1A). The absence of any textural heterogeneity between plots thus validates the synchronic sampling approach. This is especially important, because, except for climate, clay+fine silt content of soil is the best predictor for organic matter content of tropical soils with low-activity clay (Feller and Beare, 1997). Thus, the higher organic carbon content, CEC and exchangeable bases recorded here in the upper (0–5 cm) soil layer of oldest fallows, as compared to those of the young fallows can be related to an increase in tree root biomass and larger litter inputs (Nye and Greenland, 1960; Floret et al., 1993). The control of soil organic matter over CEC and some cations such as calcium and magnesium (Fig. 1) has already been widely reported for this class of soil (Asadu et al., 1997). More unexpected was the small variation in the concentration of phosphorus and potassium through the chronosequence (Fig. 1A).

#### 4.2. Below-ground organic status in the 0–10 and 0–40 cm layers

The strong negative relationship between herbaceous biomass and the duration of the fallow period (Fig. 4) apparently reflects the competition for light between trees and herbaceous plants. The settlement of stumps and coarse roots provides below-ground evidence for the shift occurring towards woody formation in plots left to fallow, even a few years after crop abandonment. As a matter of fact, the closure of canopy after 10 years of fallow has been reported by Donfack et al. (1995) too in a study in north Cameroon. On our study site, the increase of fine root biomass was variable, depending on the sampling layer. The lowest progression was found in the upper soil layer (0–10 cm), as a result of the progressive shift occurring in its origin (from grass to tree layer) during the fallow period. More qualitative investiga-

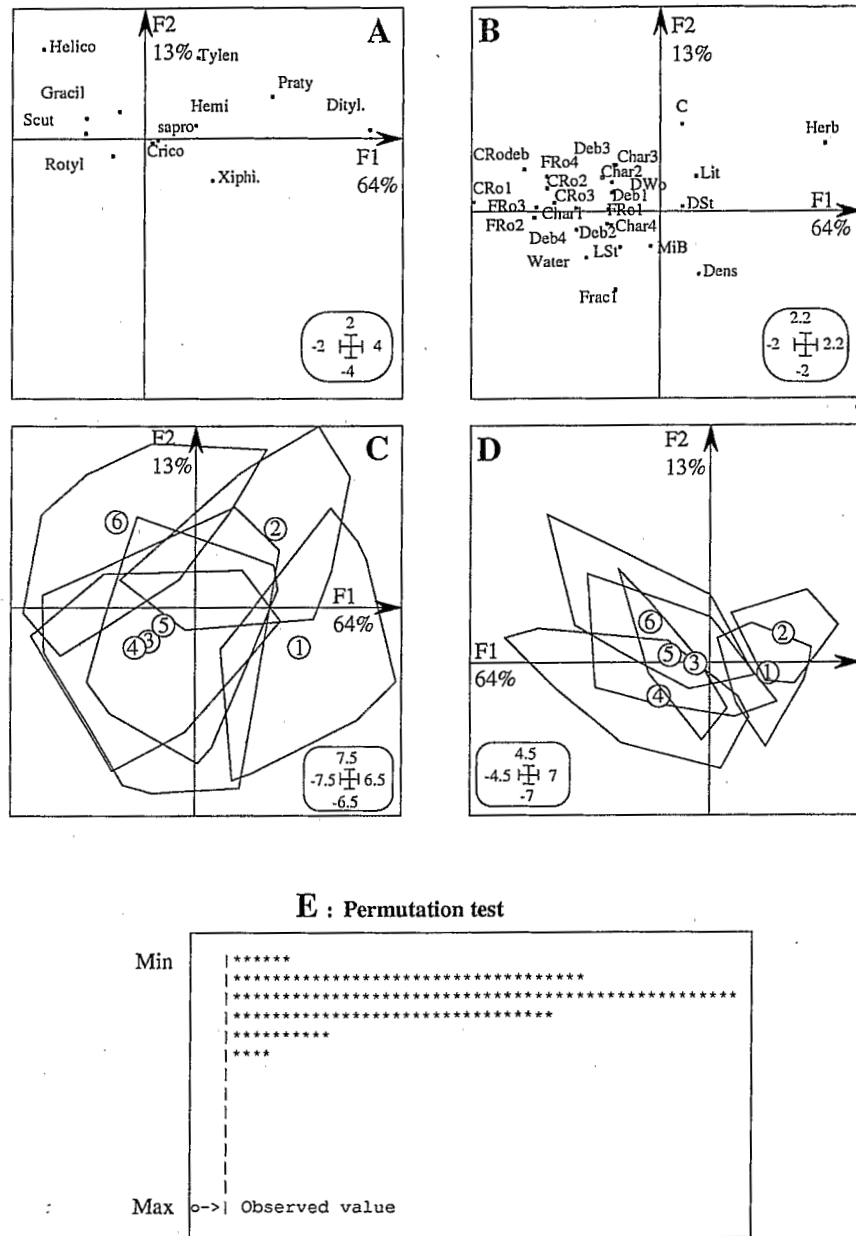


Fig. 7. Relationships between nematodes and organic matter status variables with the co-inertia analysis. (A) and (B): factorial maps of the nematode and environmental variables, respectively. (C) and (D): factorial plans of the sampling spots grouped according to fallow age; (E): permutation test (number of permutations: 1000; observed value: 36.68; Histogram: minimum=8.371, maximum=36.68. Number of simulations  $X < \text{observed value}$ : 1000 (frequency: 1.000E+00). Number of simulations  $X \geq \text{observed value}$ : 0 (frequency: 0.000E+00).

tions with the help of such tools as carbon natural isotopic abundance measurement would be needed to confirm this hypothesis based on the findings of Mordelet et al. (1997) in a more humid savanna.

The abundance of charcoal particles in the 0–10 cm soil layer of older fallows testifies to the higher frequency of fires occurring in these plots (located closer to the forest, where fires occur most often) together

with higher wood biomass available for burning, thus indicating potentially significant withdraw of carbon from the ecosystem due to abiotic events. This may thus seriously restrict inputs of organic material to soil organic pools. However, the role played by fires in controlling organic matter content of soils of the WAS may not be so critical. In Mali for instance, Masse et al. (1997) recorded similar soil organic contents (SOC) in soil of young fallows whether or not protected from fires.

This study indicates that soil microbial biomass is dependent upon transient carbon pools such as litter, dead wood and soil organic matter, but this dependence is limited, or even non-existent with roots. Furthermore, our results do not provide much evidence for a significant contribution of fine roots to soil organic carbon content. Both observations concerning the absence of a close association between microbial biomass and roots with SOC are rather unexpected. Roots are indeed often reported to be the main providers of carbon to the subsoil of savannas experiencing regular fire (Nye and Greenland, 1960; Floret et al., 1993).

However, sampling was performed at the end of the rainy season, during which massive 'grazing' of soil carbon and microfloral biomass occurs as a result of favourable below-ground water conditions (Singh et al., 1989). Macrofaunal activity may also be put forward to explain high SOC turnover during the fallow period in the area. On our study site there was a three-fold increase in the density of macrofaunal populations within the first 10 years of fallow (Fall, 1998). Termites and ants are known to be the most efficient organisms in reallocating SOM and increasing its availability for mineralization. For instance, termites may channel up to 90% of the plant biomass net productivity towards their mounds for the satisfaction of their own energy needs (Jones, 1990). As a result, even decaying roots are quickly decomposed and only a small proportion of the carbon they contain may be stabilised in the soil. This was confirmed by an on-going mesh-bag experiment conducted in the study site indicating that at least 70% of woody roots may disappear within the first year of on-field incubation (Manlay, unpublished data). In so doing, soil macrofauna disrupts the functional continuity expected between both root and soil carbon pools.

Clearly, further sampling is needed to re-estimate the links between the main below-ground carbon pools

(SOC, root and microbial biomass) at the beginning of the rainy season and to investigate the impact of seasonality on our data. In addition, measurements on termite mounds need to be made in order to assess the real gain or loss of SOC experienced by the ecosystem after crop abandonment.

#### 4.3. Relationships between nematodes and forms of soil organic matter

Soil microbial biomass did not affect the abundance of phytoparasitic and free living nematodes (Fig. 7), although the latter feed upon soil micro-organisms. This group includes also a small proportion of predatory, omnivorous and fungal feeding nematodes. The abundance of *Helicotylenchus* in the old fallow may have been driven by the presence of large roots favouring its development. In contrast, fine roots seemed to support larger populations of *Scutellonema*, this species being observed in middle aged and oldest fallows. As the relation appeared only in the deeper layers, such roots might have originated from young trees but not from herbaceous plants. In contrast, the abundance of *Ditylenchus* and *Pratylenchus*, which were associated with the herbaceous biomass, decreased when trees developed in more mature fallows.

Much published work indicates that the population structure of phytoparasitic nematodes could be manipulated, and thus controlled, by managing the vegetation (grass versus woody layers), nematodes abundance being closely related to root size. The pathogenicity of the nematode community as a whole depends on its specific composition (Cadet and Spaul, 1985). For instance, increasing the presence of the weak pathogen *H. dihystra*, is associated with a reduction of the pathogenic impact of the whole nematode community because it seems to stimulate root development (Villeneuve and Cadet, 1997). Therefore, the composition of the nematode community at each period of fallow should be defined to predict the sustainability of this practice. However, the persistence of each species once the fallow land is recultivated should also be addressed. Field studies on the dynamics of phytoparasitic nematodes have shown that *H. dihystra* disappears within the first crop in WAS, probably due to the decomposition of coarse tree roots. Therefore, where fallow practice can no longer be promoted, agroforestry could be a suitable way to

increase the numbers of *H. dihystra* and to reduce the impact of phytoparasitic nematodes, enabling both crops and trees to coexist (Buresh and Tian, 1997). Host-parasite relationships, commonly very specific, should not impede the establishment of *H. dihystra* since it could multiply on various hosts including the food crops commonly grown in this area (Siddiqi, 1992).

In this study, the presence of other nematode species was not related to food quality only. Unlike *H. dihystra*, *Xiphinema* seemed to be closely related to high top soil bulk density. This may explain the observations of Harris (1975), who reports that this species is usually more abundant in deeper soils layers, where bulk density is higher than in the upper soil.

## 5. Conclusion

This study suggests that caution should be taken when describing fallow as a means for recovering soil chemical fertility. Its beneficial effect on chemical characteristics of the topsoil (0–5 cm) undoubtedly rely on the biologically induced increase in the soil organic carbon content. But the steady level of this property through the chronosequence as measured in the 0–10 cm layer indicates that the improvement of soil fertility in the entire layer exploited by plants relies on the displacement of biological rather than chemical equilibria.

This work introduces a new concept concerning the control of phytoparasitic nematodes. It is based on the relationships between the quality of below-ground organic matter (soil, fine or coarse roots, and heterotrophic biota), and the abundance of phytoparasitic nematodes. Controlling the development of these plant parasites through the management of woody species is a feasible strategy, since coarse roots of trees clearly play a key role in maintaining nematode diversity. The clearing of fallow enhances the development of herbaceous vegetation, and favours the multiplication of phytoparasitic nematodes species, that are frequently observed in cropped fields of this zone.

Although the mechanisms of this relationship are not well known yet, any strategy aimed at preventing the development of phytoparasitic nematodes should take into account the impact of trees on the soil biota, in order to select the most appropriate species.

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