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Changes in nematode communities following cultivation of soils after fallow periods of different length

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Abstract

The composition of the nematofauna was studied in four soils that differed in the length of fallow restoration period since previous cultivation. The longest fallow period was 21 years. Plots were sampled for 2 years after starting cultivation of the fallow soils. The treatments were ranked following a restoration–exploitation gradient depending on fallow duration and the number of years of millet cultivation after fallow clearing; components of the nematofauna were analysed for correlation with this ranking.

The nematode community structures at the first date of sampling during cultivation clearly reflected the length of the fallow period. Nematode community structures in the fallow soils rapidly approached those in the continuously cultivated soil; they were hardly distinguishable during the second year of cultivation.

One-third of the recorded nematode taxa exhibited pronounced responses to the cultivation. Mononchidae, Anatonchidae, Tylencholaimoidea, *Acrobeles*, *Pseudacrobeles*, Tylenchidae and *Helicotylenchus* preferred sites of more mature successional status, while Dorylaimoidea, *Tylenchorhynchus* and Rhabdolaimidae dominated the cultivated sites. The maturity index (MI) did not distinguish the management regimes. The plant parasite index (PPI) tended to decrease with higher restoration status linked to greater abundance of the Tylenchidae in these situations. The decrease of fungal to bacterial feeders reflected a decreasing importance of the fungal decomposition pathway after resuming cultivation.

Keywords: Nematodes; Fallow; Low input cropping system; Senegal; Community structure

1. Introduction

Setting aside agricultural fields is a common practice to restore the soil properties in tropical, low input cropping systems. Fallowing of exhausted soil aims at improving soil structure, increasing nutrient content, and fostering antagonistic potential against crop pests (Masse et al., 1998; Cadet and Floret, 1995). In the Sahelian-Soudanese zone of Senegal, the extent of land placed in fallow, and the duration of the fallow periods, have been reduced due to intensification of agricultural practices and the need to increase food production. Only minimal soil restoration is practised currently and there is a need to understand and optimise the length of time required for restoration. Moreover, there is recent interest in

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monitoring biological factors as indicators of soil restoration.

Nematodes offer promising perspectives as bioindicators. Freckman and Ettema (1993) compared nematode communities in agroecosystems varying in the level of human intervention and Yeates and Bird (1994) compared agroecosystems with shrubs in Australia, both demonstrating the potential of nematode communities as bioindicators for monitoring the state of agricultural soils (see also Bongers et al., 1997; Wasilewska, 1997; Bongers and Ferris, 1999; Lenz and Eisenbeis, 2000).

Concerning restoration of tropical soils, it has been shown recently that the number of plant-feeding and free-living nematodes increases with the extention of the fallow period (Pate et al., 2000). Moreover, the structure of the plant-feeding nematode community changes and the density of the genera that are most pathogenic to rainfed crops decreases with duration of fallow periods (Villenave et al., 1997; Masse et al., 1998; Villenave and Cadet, 1999). In contrast, the density of root-hair feeders, mainly Tylenchidae, increases with duration of fallow. However, it is not known how long this suppression of the most pathogenic fauna, and of changes in the whole nematofauna does persist after cultivation.

The aims of this study are (1) to identify changes in nematode communities after cultivation of soils maintained undisturbed through fallow periods of different lengths and intensities of protection, and (2) to explore the potential for analysis of soil nematode communities as bioindicators of the biological status of soils in low input shifting cultivation in Senegal.

2. Material and methods

2.1. Study sites and experimental design

The study was carried out at one of the experimental field stations of the Institut Sénégalais de Recherche Agronomique (ISRA) and the Institut de Recherche pour le Développement (IRD) in Thysse Kaymor (13.45′N, 15.40′W) in the Sahelian-Soudanese zone of Senegal. The climate is characterised by 600–700 mm mean annual precipitation, confined to the period between July and October, and by a complete lack of rain during the dry season. The soil is a typical oxisol. During the fallow period, a shrub vegetation dominated by *Combretum glutinosum* and *Guira senegalensis* developed in the investigated plots.

Four plots of ca. 20 m × 30 m were compared, each representing a different period of fallow restoration, or of continuous cultivation:

F21f: cultivation of millet after 21 years of fallow during which the plot was fenced and protected against grazing, fire and public access.
F21g: cultivation of millet after 21 years of grazed fallow.
F11g: cultivation of millet after 11 years of grazed fallow.
CU: continuous cultivation of a biennal rotation of peanut and millet for more than 20 years.

Millet (*Pennicetum glaucum* cv. Suma III) was sown in all plots in July and harvested in October. No fertiliser was applied. The fallow plots were sampled during the first 2 years after fallow clearing, i.e. in 1997 and 1998, but the continuously cultivated site was sampled only in 1998, when millet was grown according to the rotation scheme.

Seven treatments were available, which were ranked along a restoration–exploitation gradient, depending on fallow duration and the number of years of millet cultivation after fallow clearing. The fenced site was considered to have a higher restoration status than unfenced sites; the second year of cultivation was considered to have greater exploitation than the first:

F21f-97 (rank 6), F21g-97 (rank 5), F11g-97 (rank 4), F21f-98 (rank 3), F21g-98 (rank 2), F11g-98 (rank 1) and CU-98 (rank 0).

2.2. Sampling design

Three 16 m^2 subplots were selected in each plot. Samples were taken during the wet season at the beginning of August and October, in the first and the second year of the study. Five subsamples were taken from each subplot and pooled. Soil subsamples were dug from the upper 10 cm of soil of each subplot with a shovel and pooled to form bulk samples of about 1 kg. Thus, 42 bulk samples were obtained in total, based on 210 subsamples. Bulk samples were carefully hand mixed and aliquots of about 500 g were taken for further processing. The aliquots were analysed for soil

microbial biomass as well as for taxonomic composition and functional structure of the nematode community.

In June 1997, before the clearing of the fallows, additional bulk samples (six replicates) were taken from the 0–10 cm soil layer in the four investigated plots. The replicates were pooled and a range of physico-chemical soil parameters were determinated on a subsample.

2.3. Soil analysis

Mineral particles of the clay, silt, and sand size fractions were determined by mechanical analysis, following the destruction of organic matter with hydrogen peroxide and the total dispersion of the particles in a NH_4Cl solution (1 M final concentration). The cation exchange capacity (CEC) was measured with ammonium acetate at pH 7 (Page et al., 1989). The main exchangeable cations, calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K) were estimated with a flame spectrometer after exchange with ammonium acetate. Plant-available phosphorus (P) was determined after Olsen modified by Dabin (1967). Microbial biomass 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 $\mu g\,C\ 100\,g^{-1}$ soil on an oven-dry basis (105°C).

2.4. Nematode analysis

Nematodes were extracted from 250 cm^3 of soil using the Seinhorst elutriation method (Seinhorst, 1950, 1962), counted, fixed with formalin, transferred to glycerin and subsequently mounted in bulk on glass slides. From each sample, about 160 nematodes were identified under a microscope at 400×, to family or genus level.

Nematode taxa were assigned to trophic groups following Yeates et al. (1993) then allocated to cp-classes following Bongers (1990). Several taxa, particularly the dorylaimids, were difficult to classify in trophic groups. Nematodes which could not be assigned to a trophic group with certainty were classified in the group of the taxon having the most similar morphological feeding structure.

2.5. Data analysis and statistics

In order to eliminate mass effects, relative abundance of nematode groups rather than absolute abundance was chosen for statistical analysis. Total numbers of nematodes were analysed separately. For a descriptive comparison of nematode community structure across sites and dates, principal component analysis was performed on nematode taxa. Factor scores were calculated and used to specify the loadings of nematode taxa on the principal components. Correlations between soil parameters, nematode parameters and restoration–exploitation rank of treatments were tested by means of Spearman's rank order correlation. Means of the two sampling dates per year for each plot were used for these analyses. The Statistica for Windows package (StatSoft, Tulsa, USA) was used for all statistical analyses.

3. Results

3.1. Soil properties

On average, the fallow soils had greater clay (+51%) and greater silt (+35%) content than the soil of the continuously cultivated field (Table 1). Carbon content and nutrient status of the fallow soils

Table 1
Soil physico-chemical characteristics of the different plots and percentage differences between the average values of soil properties of the fallows and the continuously cultivated field(F-CU)[a]

Parameter	CU	F11g	F21g	F21f	F-CU (%)
Clay, 0–2 μm (%)	8.8	13.2	12.5	14.1	+51
Silt, 2–50 μm (%)	28.5	38.8	40.3	36.6	+35
Sand, 50–2000 μm (%)	61.8	47.8	47.6	50.7	−21
C (mg/g DM soil)	6.0	9.6	11.0	8.2	+60
N (mg/g DM soil)	0.5	0.7	0.8	0.6	+35
C/N	11.5	13.7	13.9	13.5	+19
P (μg/g DM soil)	10.2	12.0	16.2	13.0	+34
pH/H_20	4.8	5.5	5.6	5.2	+13
Ca (meq.%)	2.32	2.1	2.5	1.4	−14
Mg (meq.%)	0.85	1.0	1.0	0.6	+2
K (meq.%)	0.08	0.1	0.2	0.1	+67
Na (meq.%)	0.06	0.1	0.1	0.1	+67
CEC (meq.%)	2.87	3.8	4.1	2.4	+20

[a] CU: continuously cultivated; F11g: 11-year old fallow, grazed; F21g: 21-year old fallow, grazed; F21f: 21-year old fallow, fenced; DM: dry mass.

were considerably greater than those of the continuously cultivated soil (C: +60%, N: + 35%, P: +34%, K: +67%). In the three fallow sites, soil microbial biomass decreased in the second year on average by a factor of 2.5, and was then, not significantly different significantly from the microbial biomass of the cultivated soil (Table 3).

3.2. Nematode communities

3.2.1. Nematode taxa

Except for the Tylenchidae, plant-feeding nematodes were identified to genus level. Four taxa (*Tylenchorhynchus gladiolatus*, Tylenchidae, *Helicotylenchus*, and *Scutellonema*) represented 84% of the plant feeders (averaged across all treatments) (Table 2). The nematode group 'Aphelenchina' were mainly represented mainly by *Aphelenchus* and *Aphelenchoides* spp. The group 'Anguinidae' included several fungal-feeding *Ditylenchus* species. The group 'Tylencholaimoidea' comprised the Leptonchidae and Tylencholaimidae with *Tylencholaimus* being the most frequently encountered genus. 'Belondiridae' referred mostly to *Dorylaimellus*. These four nematode groups were considered to be fungal feeders. The relative abundance of each of these four groups ranged from 3 to 7% (averaged across all treatments).

The bacterial feeders were categorised to family level except for the Cephalobidae. The Cephalobidae were identified to genus level because of their high abundance and their high dominance among the bacterial-feeding nematodes (87%; averaged across all treatments). However, the differentiation between *Cephalobus* and *Acrobeloides* caused severe problems in routine identification (De Ley, 1997), and these two genera were therefore combined into the group '*Cephalobus*'.

Predators were represented by five taxa: Ironidae, Mononchidae, Anatonchidae, Discolaiminae and Nygolaimidae.

The group 'Dorylaimoidea' (sensu Jairajpuri and Ahmad, 1992) was used to specify a heterogeneous group of dorylaims comprising Dorylaimidae, Qudsianematidae, Thornenematidae and Aporcelaimidae. These Dorylaimoidea, which comprised subgroups of cp4 and cp5, were allocated to cp4 as a whole and considered as omnivorous.

3.2.2. Analysis of the nematode communities

The first two components of principal component analysis explained 82% of variance in nematode taxa. Fallow restoration plots during the first year of cultivation were located in the upper sector of the graph, while cultivated soil and fallow plots during the second year of cultivation were grouped in the lower right side (Fig. 1). Immediately after cultivation, nematode community structures in the fallow plots approached those in the cultivated soil and were hardly distinguishable from the latter in the second year of cultivation (indicated by a circle in Fig. 1).

During the first year of cultivation, the plot F21f was located in the left sector of the graphs, while the plots F21g and F11g were located to the right. Succession of the nematode community during the fallow period was amplified by the protection of the fallow against fire and grazing (F21f-1).The nematode taxa with the highest scores on the PCA factors were Tylenchidae, *Helicotylenchus*, Belondiridae, Tylencholaimoidea, *Acrobeles*, *Pseudacrobeles*, Dorylaimoidea, *Tylenchorhynchus gladiolatus* and Rhabdolaimidae.

About one-third of the taxa discriminated appeared to be barely affected by the different fallowing practices and were well represented in all plots. These taxa are classified as 'ubiquitous taxa' in Table 2. Five nematode taxa with high relative abundance (>3% on average) were ubiquitous: *Scutellonema*, Anguinidae, Aphelenchina, Belondiridae, and *Cephalobus*.

A further group of the taxa was too rare to allow judgement of treatment effects ('rare taxa'). In contrast, the last set of taxa ('differential taxa') exhibited pronounced preferences for particular groups of plots and formed a succession series. Mononchidae, Tylenchidae, Tylencholaimoidea, *Acrobeles*, *Pseudacrobeles*, *Macrolaimellus*, Anatonchidae, *Helicotylenchus* and *Pratylenchus* preferred sites with higher restoration status,. while Dorylaimoidea, *Tylenchorhynchus gladiolatus*, Rhabdolaimidae and *Stegelleta* were dominant in the cultivated sites. *Tylenchorhynchus mashoodi* occurred in the intermediate stages of cultivation, while *Chiloplacus* featured a reduced dominance in the soil with the highest protection (F21f-97).

Taking into account only the most dominant nematodes (>3% on average of all sites), the nematode com-

Table 2
Relative abundances of nematode taxa in the different plots and correlations with recovery–exploitation rank[a]

Parameter	Type of distribution	cp-classes	1997			1998			1998	Rank correlation	
			F21f[b] 6[c]	F21g 5[c]	F11g 4[c]	F21f 3[c]	F21g 2[c]	F11g 1[c]	CU 0[c]	*r*	*P*-level
Plant feeders											
Tylenchorhynchus gladiolatus	Differential	3	4.97	4.63	2.55	**13.5**	**10.9**	**7.37**	**13.0**	−0.61	0.1482
Tylenchidae	Differential	2	**14.2**	**10.9**	**7.75**	2.90	4.74	1.05	1.93	0.93	**0.0025**
Helicotylenchus	Differential	3	**12.6**	**3.04**	**6.21**	**4.86**	1.42	0.36	0.04	0.89	**0.0068**
Scutellonema	Ubiquitous	3	**3.45**	0.69	0.54	**9.66**	**3.97**	**1.47**	**5.40**	−0.43	0.3374
Pratylenchus	Differential	3	**2.18**	**4.00**	**1.90**	**4.82**	1.51	1.05	0.00	0.75	**0.0522**
Trichotylenchus	Ubiquitous	4	**1.65**	0.28	**2.47**	**1.08**	0.00	**1.08**	0.48	0.32	0.4821
Tylenchorhynchus mashoodi	Differential	3	0.00	**0.17**	**0.12**	**0.05**	**2.21**	0.00	0.00	0.22	0.6317
Criconemella	Rare	3	**0.10**	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.1438
Xiphinema	Rare	5	0.07	0.00	**0.79**	**0.16**	**0.20**	0.00	0.08	−0.07	0.8780
Longidorus	Rare	5	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	1.0000
Ecphyadophora	Rare	2	0.00	0.00	**0.24**	**0.19**	**0.28**	**0.21**	0.00	−0.26	0.5742
Fungal feeders											
Anguinidae (*Ditylenchus*)	Ubiquitous	2	**6.77**	**4.72**	**5.83**	**5.30**	2.25	**8.69**	**4.70**	0.29	0.5345
Aphelenchina	Ubiquitous	2	1.68	**9.28**	**8.07**	1.98	**7.04**	**9.71**	**5.89**	−0.25	0.5887
Tylencholaimoidea	Differential	4	**7.70**	**4.19**	**5.01**	2.44	2.10	2.96	0.73	0.86	**0.0137**
Belondiridae	Ubiquitous	5	**12.0**	**7.47**	**9.24**	**8.16**	2.86	4.01	**7.58**	0.57	0.1802
Bacterial feeders											
Cephalobidae (*Chiloplacus*)	Differential	2	4.59	**18.6**	**13.7**	**18.1**	**21.3**	**28.8**	**21.3**	−0.79	**0.0362**
Cephalobidae (*Cephalobus+Acrobeloides*)	Ubiquitous	2	3.35	**4.03**	**7.24**	**3.49**	**6.04**	**7.16**	**11.0**	−0.71	0.0713
Cephalobidae (*Acrobeles*)	Differential	2	**6.44**	**4.95**	**6.29**	2.59	2.00	2.47	1.70	0.93	**0.0025**
Cephalobidae (*Pseudacrobeles*)	Differential	2	**5.66**	**6.16**	**4.57**	0.61	1.38	1.56	2.51	0.61	0.1482
Rhabdolaimidae	Differential	3	0.39	0.61	0.49	**3.76**	**12.1**	**1.03**	**3.55**	−0.68	0.0938
Prismatolaimidae	Ubiquitous	3	**1.08**	0.19	**2.27**	0.00	**3.02**	**1.25**	**1.57**	−0.39	0.3833
Cephalobidae (*Zeldia*)	Ubiquitous	2	0.45	**1.69**	0.09	**1.67**	**1.71**	**1.00**	**1.68**	−0.32	0.4821
Cephalobidae (*Cervidellus*)	Ubiquitous	2	**0.45**	**0.82**	**1.76**	0.00	**0.74**	**3.37**	0.15	0.04	0.9394
Cephalobidae (*Macrolaimellus*)	Differential	2	**0.77**	**0.82**	**1.03**	0.00	0.23	0.00	0.15	0.65	0.1150
Rhabditidae	Ubiquitous	1	0.14	0.17	**0.52**	**0.35**	0.00	**0.76**	**0.55**	−0.57	0.1802
Cephalobidae (*Stegelleta*)	Differential	2	0.00	0.06	0.07	**0.28**	**1.00**	**0.41**	**0.47**	−0.89	**0.0068**
Alaimidae	Ubiquitous	4	**0.53**	**0.19**	**0.13**	0.00	**0.14**	**0.36**	**0.22**	0.04	0.9394
Cephalobidae (unidentifiable)	Rare	2	0.00	**0.44**	0.00	0.05	0.00	**0.46**	**0.57**	−0.63	0.1294
Plectidae (*Plectus & Wilsonema*)	Rare	2	0.00	0.00	**0.15**	0.00	**0.14**	**0.65**	**0.15**	−0.78	**0.0393**
Monhysteridae	Rare	2	**0.19**	**0.19**	**0.47**	0.00	**0.14**	0.00	0.00	0.78	**0.0393**
Desmodoridae (*Prodesmodora*)	Rare	3	0.00	**0.09**	**0.11**	0.00	0.00	0.00	0.00	0.45	0.3165
Drilocephalobus	Rare	2	0.00	0.00	0.00	0.00	**0.11**	0.00	**0.06**	−0.58	0.1731
Panagrolaimidae	Rare	1	0.00	0.00	0.00	0.00	0.00	0.00	**0.12**	−0.61	0.1438
Predators											
Anatonchidae	Differential	4	**0.70**	**0.81**	**1.87**	0.27	0.14	0.00	0.00	0.85	**0.0162**
Discolaiminae (*Discolaimus*)	Ubiquitous	5	**0.70**	**0.45**	**0.39**	**0.44**	**0.76**	**0.36**	**0.45**	0.32	0.4821
Ironidae (*Ironus*)	Ubiquitous	5	**0.57**	**0.19**	**0.24**	0.00	0.00	**0.67**	**0.31**	−0.09	0.8477
Discolaiminae (*Discolaimoides*)	Rare	5	**0.40**	**0.50**	0.00	**0.26**	0.00	**0.51**	0.00	0.26	0.5742
Mononchidae	Differential	4	**0.10**	**0.16**	0.00	0.06	0.00	0.00	0.00	0.77	**0.0436**
Nygolaimidae (*Nygolaimus*)	Rare	5	0.00	**0.13**	0.00	0.00	0.00	0.00	**0.16**	−0.27	0.5623
Omnivorous											
Dorylaimoidea	Differential	4	6.22	9.36	7.88	**12.8**	**9.55**	**11.2**	**13.6**	−0.86	**0.0137**

[a] Taxa are classified into ubiquitous taxa (relative abundance not significantly different between treatments), differential ubiquitous taxa (relative abundance significantly different between treatments) and rare taxa (absent in several treatments and relative abundance less than 1%); Taxa are sorted according to their relative abundance in each trophic group. High dominances (% relative abundance) within each taxon are emphasised in bold. Assessed preference ranges of differential taxa are marked in bold and underlined characters. *r*: Spearman rank correlation coefficient, *P*: error probability. Significant correlations are emphasised in bold ($P \leq 0.05$).

[b] F21f: cultivation of millet after 21 years of fenced fallow; F21g: cultivation of millet after 21 years of grazed fallow; F11g: cultivation of millet after 11 years of grazed fallow; CU: continuously cultivated.

[c] The seven treatments are ranked along a restoration–exploitation gradient, depending on fallow duration and the number of years of millet cultivation after fallow clearing: F21f-97 (rank 6), F21g-97 (rank 5), F11g-97 (rank 4), F21f-98 (rank 3), F21g-98 (rank 2), F11g-98 (rank 1) and CU-98 (rank 0).

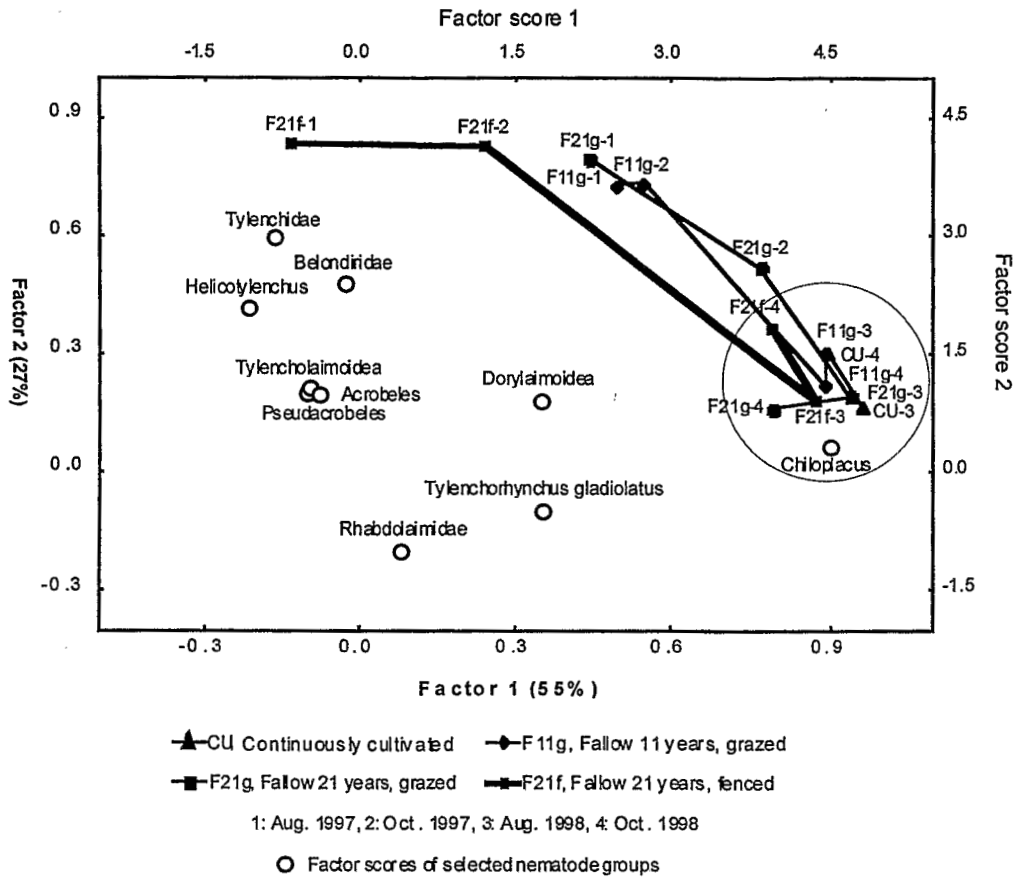

Fig. 1. Comparison of nematode community structures based on principal component analysis. The fallow plots during the second year of cultivation and the continuously cultivated field are located in the circle.

munities of agricultural fields in the first year of cultivation after a long period of fallow (rank 6–4) were characterised by high relative abundance of *Helicotylenchus dihystera*, Tylenchidae, Tylencholaimoidea, *Acrobeles* and *Pseudacrobeles* as compared to the second year of cultivation and to continuous cultivation (rank 3–0). In contrast, agricultural fields in the second year of cultivation after a long fallow period, as well as the continuously cultivated field (rank 3–0) were characterised by a higher relative abundance of *Tylenchorhynchus gladiolatus*, and Dorylaimoidea as compared to the plots of rank 4–6.

The fallow plots during the first year of cultivation (F21f, F21g and F11g in 1997; rank 6, 5 and 4) differed from the same plots during the second year of cultivation by higher relative abundance of *Helicotylenchus* and Tylenchidae, as well as a lower relative abundance of *Chiloplacus* in F21f (rank 6) as compared to the two other fallow plots.

A higher restoration–exploitation rank of the plots was correlated with higher nematode abundance (Table 3). Dominance of fungivores with high cp-values (Fu4-Fu5, Bongers, 1990) and root hair feeders (Pp2) decreased from the plot with the highest restoration status (F21f-97) to the plot with the highest exploitation status (CU 98), while dominance of omnivores increased with exploitation status. Predators showed a nearly significant tendency to decrease as the exploitation increased ($P = 0.07$). The abundance of predatory nematodes was highly significantly correlated with total nematode abundance (Spearman, $r = 0.79$, $P = 0.007$).

Table 3
Soil parameters and nematode groups, and their correlation with recovery–exploitation rank. High parameter values are emphasised in bold[a]

Parameter	1997			1998			1998	Rank correlation	
	F21f[b]	F21g	F11g	F21f	F21g	F11g	CU	*r*	*P*-level
	6[c]	5[c]	4[c]	3[c]	2[c]	1[c]	0[c]		
Soil parameters									
Soil water content (% DM soil)	**16.0**	**15.4**	**13.0**	10.4	9.7	11.5	11.8	0.68	0.0938
Soil microbial biomass (μg C/g DM soil)	**379**	**386**	**541**	118	176	201	108	0.71	0.0713
Nematode abundance (Ind./100 g FM soil)	**2391**	**2385**	1670	951	1134	736	1555	0.75	**0.0522**
cp-feeding leagues (% dominance)									
Bacterial feeders cp1	0.14	0.17	0.52	0.35	0.00	0.76	0.67	−0.57	0.1802
Bacterial feeders cp2	21.9	37.7	35.4	26.8	34.8	45.9	39.7	−0.64	0.1194
Bacterial feeders cp3	1.46	0.89	2.87	3.76	15.1	2.28	5.12	−0.68	0.0938
Bacterial feeders cp4	0.53	0.19	0.13	0.00	0.14	0.36	0.22	0.04	0.9394
Fungal feeders cp2	8.44	14.0	13.9	7.28	9.29	18.4	10.6	−0.21	0.6445
Fungal feeders cp4	**7.70**	**4.19**	**5.01**	2.44	2.10	2.96	0.73	0.86	**0.0137**
Fungal feeders cp5	**12.0**	**7.47**	**9.24**	**8.16**	2.86	4.01	7.58	0.57	0.1802
Fungal feeders cp4–5	**19.7**	**11.7**	**14.2**	10.6	4.96	6.97	8.31	0.82	**0.0234**
Plant feeders cp2	**14.2**	**10.9**	**7.99**	3.09	5.02	1.26	1.93	0.93	**0.0025**
Plant feeders cp3	23.3	12.5	11.3	32.9	20.0	10.2	18.4	0.25	0.5887
Plant feeders cp4	1.65	0.28	2.47	1.08	0.00	1.08	0.48	0.32	0.4821
Plant feeders cp5	0.07	0.00	0.79	0.21	0.20	0.00	0.08	−0.04	0.9389
Plant feeders cp3–5	25.0	12.8	14.6	34.2	20.2	11.3	19.0	0.21	0.6445
Omnivores cp4	6.22	9.36	7.88	**12.8**	**9.55**	**11.2**	**13.6**	−0.86	**0.0137**
Predators cp4	**0.79**	**0.97**	**2.02**	0.33	0.28	0.65	0.15	0.75	**0.0522**
Predators cp5	1.67	1.27	0.63	0.70	0.76	1.54	0.92	0.18	0.7017
Predators cp4–5	**2.46**	**2.24**	**2.50**	1.03	0.90	1.54	0.92	0.71	0.0713
Nematode indices									
Nematode richness (*number of taxa*)	30	33	32	28	29	28	30	0.51	0.2431
Fungivores/bacterivores	**1.17**	**0.66**	**0.72**	0.58	0.28	0.51	0.41	0.86	**0.0137**
Maturity index (MI)	3.19	2.74	2.80	2.98	2.67	2.54	2.75	0.57	0.1802
Plant parasite index (PPI)	2.68	2.55	2.82	**2.96**	**2.82**	**2.99**	**2.94**	−0.71	0.0713
Bacterivore index (BaMI)	2.10	2.03	2.07	2.11	2.31	2.05	2.11	−0.32	0.4821
Fungivore index (FuMI)	3.82	3.20	3.34	3.64	2.90	2.71	3.28	0.57	0.1802

[a] *r*: Spearman rank correlation coefficient, *P*: error probability. Significant correlations ($P \leq 0.05$) are emphasised in bold.
[b] F21f: cultivation of millet after 21 years of fenced fallow; F21g: cultivation of millet after 21 years of grazed fallow; F11g: cultivation of millet after 11 years of grazed fallow; CU: continuously cultivated; DM: dry matter.
[c] The seven treatments are ranked along a restoration–exploitation gradient, depending on fallow duration and the number of years of millet cultivation after fallow clearing: F21f-97 (rank 6), F21g-97 (rank 5), F11g-97 (rank 4), F21f-98 (rank 3), F21g-98 (rank 2), F11g-98 (rank 1) and CU-98 (rank 0).

Nematode taxonomic richness, as well as the dominance of bacterial feeders, lower scaled fungivores (Fu2), and higher scaled plant feeders (Pp3–5), did not correlate with restoration status. As a consequence of the diverging responses of bacterial feeders and fungal feeders, the fungivore/bacterivore ratio increased with restoration status (Table 3).

Among the indices of maturity that were analysed, viz. the general maturity index, the plant parasite index, and similar indices for bacterivores and fungivores, only the plant parasite index showed a nearly significant tendency to decrease with higher restoration status ($P = 0.07$) (Table 3).

4. Discussion

Total nematode abundance was about 15,000 specimens per dm^3 of soil, i.e. around 1.5 million specimens per m^2. These numbers are comparable to those reported by Hodda et al. (1997) for a Cameroon forest, but higher than those given by Coleman et al. (1991) for an East African savanna. These differences are likely to reflect the strong seasonal fluctuations in nematode abundance that occur under subtropical conditions. Nematode abundance increases with increasing fallow duration (Pate et al., 2000), and we found a strong decrease during the first 2 years of cultivation. Soil microbial biomass exhibited the same trend.

Differences in clay content and other soil properties between fallow plots and the cultivated site did not have a strong influence on the soil nematode community, as indicated by the high similarity of all communities in the second year of the investigation, i.e. after 2 years of cultivation.

The nematode maturity index (MI) was relatively low in our study with an average of 2.81, compared to the value of 3.58 calculated in the Mbalmayo Forest Reserve in Cameroon (Bloemers et al., 1997); this result could be expected as our experiment was conducted in a seasonal rainfall area whereas Mbalmayo Forest, as a tropical rainforest, is a more stable environment. However, as in the latter study, the MI did not discriminate our disturbed sites from the undisturbed sites, nor did the indices based on bacterivores (BaMI) and fungal feeders (FuMI). Only the plant parasite index declined with increasing restoration–exploitation rank of the soils ($P = 0.07$).

Plant feeders were the most dominant group (39%) in the site with the highest restoration status (F21f), bacterial-feeders were relatively fewer (24%). During the first year of cultivation, the lower scaled plant feeders (cp2) were relatively dominant. In the second year, their numbers decreased, while the relative abundance of higher scaled plant feeders remained stable. Consequently, the PPI was higher in 1998 than in 1997. The abundance of lower-scaled plant feeders in recovered soils is possibly linked to a higher plant diversity during the fallow, and the decline of the subclinical pathogens (sensu Yeates et al., 1985) after cultivation might reflect an increasing pathogenic pressure.

Of the plant feeders, abundance of *Helicotylenchus* decreased rapidly within the first year of cultivation after fallow clearing, whereas abundance of *Tylenchorhynchus gladiolatus* increased during the second year of cultivation. These two nematodes are known to multiply on millet (Villenave and Cadet, 2000), so the decrease of *Helicotylenchus* may be linked to changes in soil conditions rather than to the absence of a 'favorable' host plant. Moreover, *Helicotylenchus* counteracts negative *Tylenchorhynchus* effects on millet growth under experimental conditions (Villenave and Cadet, 1998). Therefore, the decrease of *Helicotylenchus* may lead to an increasing pathogenic pressure.

Provided that the allocation of the Leptonchidae, Tylencholaimidae and *Dorylaimellus* to the fungal-feeding group is correct, the ratio between fungal feeders and bacterial feeders decreased strongly, from 1.17 to 0.41, with increasing anthropogenic influence. Decomposition channels became more bacteria dominated as vegetation was cleared and organic residues were incorporated into the soil during cultivation, which stimulated soil microbial biomass. The increase of dorylaimid fungivore nematodes (cp4–cp5) indicated the development of a stable fungal biomass during the restoration fallow, which rapidly declined again following cultivation. The abundance of predatory nematodes was tightly linked to the availability of their main prey, i.e. of the other nematodes, and decreased with disturbance (soil exploitation). The increase in the relative abundance of omnivores within the nematode community with increasing exploitation status was linked to the decline in the majority of other nematodes; in fact, omnivore abundance was indifferent towards restoration status.

The fact that the lower-scaled species of the plant feeders, reacted in the same way as the higher-scaled species of the fungal feeders confirms the inverse relationship between the plant parasite index and the maturity index (Bongers et al., 1997).

Improvements of bioindication could arise from a consideration of particular nematode taxa. *Rhabdolaimus*, under Senegalese conditions, appears to be particularly frequent in impoverished soils. For example, *Rhabdolaimus* was more abundant in unfertilised sites than in those treated with manure (publication in preparation). In contrast, *Pseudacrobeles* and *Acrobeles* significantly decreased during the second year of cultivation in the present study. *Acrobeles* is known to be sensitive to perturbations (Korthals et al., 1996). The whole Cephalobidae family may warrant

particular attention because of the high abundance and diversity of these nematodes in the Senegalese agroecosystems. Moreover, among the seven Cephalobidae taxa, five exhibited pronounced associations with particular groups of plots; three predominated in sites with high restoration rank whereas two were more abundant in plots with lower restoration rank.

Cultivation induced very rapid responses of the nematode fauna in this investigation, leading to near identity of all communities within 2 years. In contrast, the changes of in the nematode community structure during fallow, are known to occur slowly (Pate et al., 2000). In fact, the principal components analysis clearly indicated that after 21 years of fallow, the nematode community is different from that after 11 years of fallow, and that protection against fire and grazing results in further successional development even in old fallows of 21 years.

The nematode community mirrors some of the important soil biological processes during the cycle of fallow and cultivation in low input cropping systems of the Senegalese peanut area. In the present investigation, nematodes indicated shifts in the decomposition pathway and changes in the risk of plant pathogenic infestations. In particular, the nematode data suggested that full restoration of the soil was not achieved within 10 years of fallow, and could even be improved by additional protection against grazing and fire after periods as long as 20 years while soil quality was strongly degraded soon after the second year of cropping.

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