



Relationships between plant-parasitic nematode community, fallow duration and soil factors in the Sudano-Sahelian area of Senegal

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Abstract

Before studying the mechanisms by which changes in vegetation influence the nematode community following abandonment of a field, it is necessary to first assess the impact of environmental factors such as soil or climate on these organisms. The study was undertaken on sites of increasing fallow duration located in the same area in the Sudano-Sahelian zone of Senegal: a forest and 10 fallow sites ranging from 1 to 18 years old. Soil samples were collected over 3 years on 17 occasions, along 21 m fixed transects, located in representative vegetation zones. Plant-parasitic nematodes were extracted, identified and enumerated from soil samples. The statistical analysis showed that the sites could be split in three groups according to the plant-parasitic nematode communities. One group, corresponding to young fallows, was characterised by large populations of *Scutellonema cavenessi* and *Tylenchorhynchus gladiolatus*. A second group included most of the older fallows and was characterised by a more diversified nematode community dominated by *Helicotylenchus dihystra*. The forest hosted a particular community partly similar to both of the other groups. Soil physical and chemical analysis split the sites into two groups, the young fallow sites plus the forest, and the older sites.

The study of the annual changes revealed contradictory tendencies, such as a very small increase in *T. gladiolatus* and in the soil clay content, which suggest that the sampling technique had probably slightly influenced the results. If this did occur it did not change the effect of fallow duration on the nematode community. The process of decline of certain nematode populations seemed to be extremely slow and not detectable over three successive years. Nematode species were apparently able to reproduce for a long time on poor host plants, even if one plant cohort disappeared abruptly, as was the case when the field was not replanted. This study demonstrated that the soil had a greater influence on the nematode community structure than the annual climatic variations. Consequently, the soil effect will have to be mathematically

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considered in order to identify the mechanisms by which the plant communities progressively transform the nematode communities.

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1. Introduction

For a parasite to complete its life cycle, the host is essential. For phytoparasitic nematodes the host is a plant upon which they feed, mostly by parasitizing the roots. This dependency is widely exploited to control nematodes, either by using resistant or non-host plants. In temperate or tropical cropping systems replacing an existing plant by another one (cultivated fallow) or by allowing the natural vegetation to re-grow was shown to reduce the plant-parasitic nematode pressure and resulted in much better plant growth (Stirling et al., 2001). In the Sudano-Sahelian area the process is extremely slow, which makes it not compatible with staple food production. For the local farmers to be able to use fallows as a mean of nematode control, it is necessary to accelerate the changes and for this purpose, the mechanisms by which the plant community changes influence the nematode community have to be understood. This includes understanding the impact environmental factors, such as climate and soil, have on these soilborne obligate plant parasites. The simultaneous study in synchronic mode of the plant succession following the abandonment of fields in Senegal demonstrated that the plant-parasitic nematode community evolved in parallel to the plant community. This concerned changes in the number of individuals, changes in the richness and the diversity of plants and nematodes, as well as an increase in plant biomass (Pate et al., 2000; Manlay et al., 2002b). This phenomenon was related to the increasing amount of energy and matter fluxes accompanying the change in vegetation from the herbaceous state to the ligneous state of the theoretical climax forest stage. Through the rather specific host–parasite relationships, these developments of the nematode community were predictable, under the pressure of the change in vegetation (Masse et al., 1997, 2004), which affects all living organisms.

However, the presence of a suitable host plant does not mean that it will necessarily be attacked by the feuded nematode species, even if they are artificially inoculated. Indeed, some faunistic surveys demonstrated that the distribution of certain nematode species strongly correspond to that of soil type (Blair et al., 1999). This was the case with *D. dipsaci* in the Netherlands (Seinhorst, 1956). In contrast, spatial variability of phytoparasitic nematode distribution was recorded at a field scale with the same soil type and the same plant (Cadet et al., 2004). In this study, the content of certain physical and chemical soil factors varied in the topsoil in parallel to the abundance or the relative proportions of certain nematode species. Norton (1989) also observed that the distributions of certain nematode species were found to be dependent on abiotic soil factors, explaining partly their aggregated distribution.

Annual variations in rainfall sequences affect soil moisture content and are likely to influence aquatic organisms like nematodes. Annual changes of soil physical and chemical characteristics are obviously extremely small particularly under natural vegetation. However they can be detected on a rather short time scale (Masse et al., 1998). According to the fact that nematodes are extremely susceptible to minute change in their environment, what is the magnitude of these abiotic factor effects on the nematode community changes compared to those observed between the sites? This question is even more important for a synchronic study as it is unlikely that the soil will be exactly the same for all sites. In this study, it is assumed that the vegetation has changed according to the usual succession with time. Knowing the factors of secondary but not insignificant importance, which affect nematodes, will enable nematode densities to be statistically adjusted before analysing the plant–parasite mechanisms at community level. To tackle this issue, nematode communities and soil characteristics were simultaneously analysed in several fallow land in Senegal at two time scale: annually over 3

years (diachronic mode) and according to fallow age (synchronic mode).

2. Material and methods

2.1. Location and climate

The forest plot and the fallow lands used in this study were located in Senegal near Sonkorong, in the Thyssé-Kaymor region (13°45N to 15°40W), North of Gambia. This region is considered as highly anthropised according to its agronomic potentialities, with more than 70 ha/km² and 650 mm annual rainfall on average. The soil is a lixisol, with about 120 g kg⁻¹ of clay (FAO, 1998).

2.2. Site description

Eleven sites were studied ranging from a 1-year-old fallow field to a never cultivated forest (Table 1).

Table 1
Sampling sites and rainy season characteristics

	Cultivated period before abandonment	Fallow age at the beginning of the study (year)	Fencing	Transect no. and site no.
(A) Age of the fallow ^a				
Plot 1	About 40 years	1	No	1
	About 40 years	1	Yes	2
Plot 2	About 10 years	1	No	3
	About 10 years	1	Yes	4
Plot 3	Unknown	8	No	5 and 6
Plot 4	Unknown	18	No	7 and 8
		18	Yes	9 and 10
Plot 5	Never cultivated	–	No	11
(B) Sampling occurrences per year and rainy season characteristics ^b				
Season	Year 1	Year 2	Year 3	
Dry season	End of May	June	June	
Beginning of the rainy season	July	July	July	
Rainy season	September	End of August	End of August	
End of the rainy season	October	October	October	
Dry season	November	November	November	
Dry season	March	March		
Annual rainfall (mm)	691	545	564	
Rainy season duration (days)	147	105	109	
Daily rainfall (mm)	4.7	5.2	5.2	
Rainy days	47	38	38	
Rainfall intensity	14.7 (14.6)	14.3 (12.9)	14.8 (14.2)	

^a Age of the fallow when the study started, occurrence of a fence and transect number.

^b Sampling occurrences per year and rainy season characteristics at Thyssé-Kaymor (standard deviation is indicated for the rainfall intensity parameter).

The fallow lands were cultivated plots abandoned by the peasants to the natural vegetation, usually because of low production and weed invasion. These sites were not only characterised by different length of fallow but also by the existence of a fence to prevent grazing, fire and wood cutting and by the previous cropping history (Table 1).

The forest and the oldest fallow plots were located at the top of the toposequence. The youngest, more frequently cultivated plots were located on the slope of the catchment, closer to the village. Distance between the plots did not exceed 2 km, except for the forest, which was at least 15 km far. However, it was the same ferrallitic soil type.

2.3. Experimental design and sampling procedure

At each site a 1-ha plot was delimited and within each plot permanent transects were laid out in a zone representative of the surrounding natural vegetation. Along each transect 16 soil samples were collected at

1.5 m intervals, every year around the same spot. About 500 cm³ of soil were collected in the topsoil between 5 and 15 cm deep on 17 occasions over 3 years during the dry and rainy seasons (Table 1). Because plant and animal life only occurred during the rainy season, most of the samples were done during this 4 months period (July–October). Two sampling sets at the beginning and at the end of the 8 month dry season were sufficient to describe this period, when most of the water dependent organisms are under resistant forms (seed or anhydrobiosis for nematodes).

2.4. Sample processing for nematode study

In the laboratory, each soil sample was thoroughly mixed and divided into two parts. One part of 250 cm³ was used for nematode processing (one analysis per date and sampling point). The rest was mixed by year to provide a bulk soil sample, representative of the year, for soil analysis (one analyses per sampling point

and per year, 11 × 16-point transects = 176 per year, 528 in total over 3 years). The nematodes were extracted from the soil by elutriation (Seinhorst, 1962) then identified and numbered under the dissecting microscope. Identity of the species was confirmed by the laboratory of nematology of the Plant Protection Research Institute of Pretoria, South Africa.

2.5. Matrices organisation

A table was built with the eight most numerous species of nematodes in columns (Table 2) and 2992 rows. These 2992 rows correspond to the 11 × 16-point transects, sampled 17 times. Four samples were lost during the first year, in November (date 5), site 3, No. 15 and 16 and site 4, No. 1 and 2 and were replaced by the average for the transect at the corresponding date. These 2992 nematode counts were reduced to 528 (176 per year) after averaging samples collected in the same year, to fit the soil table.

Table 2

Average abundance in 250 cm³ of soil of the nematode taxa in the natural fallow lands and the forest at Thyssé-Kaymor

	Abundance	Relative abundance (%)	Relative abundance in the group (%)
Free-living nematodes	5297	76.5	
Fongivorous nematodes	670	9.7	100
<i>Filenchus</i> group	419	6.0	62.6
<i>Ditylenchus myceliophagus</i>	204	2.9	30.4
<i>Aphelenchus</i> group	47	0.8	7.0
Plant-parasitic nematodes	952	13.8	100
<i>S. cavenessi</i>	218	3.1	22.9
<i>H. dihystra</i>	209	3.0	21.9
<i>Tylenchorhynchus gladiolatus</i>	179	2.6	18.8
<i>P. pseudopratensis</i>	108	1.6	11.4
<i>Tylenchorhynchus mashhoodi</i>	107	1.6	11.3
<i>G. parvula</i>	74	1.1	7.8
<i>Trichotylenchus falciformis</i>	40	0.6	4.2
<i>Tylenchorhynchus avaricus</i>	6	0.08	0.6
<i>Xiphinema parasetariae</i>	4	0.06	0.5
<i>Tylenchorhynchus ventralis</i>	3	0.04	0.3
<i>Aphasmatylenchus variabilis</i>	2	0.03	0.2
<i>Criconemella curvata</i>	1	0.01	0.1
<i>Rotylenchus reniformis</i> & <i>R. borealis</i>	0.12	–	0.01
<i>Longidorus pisi</i> & <i>L. brevis</i>	0.07	–	0.007
<i>Triversus annulatus</i>	0.03	–	0.003
<i>Hemicycliophora belemnii</i>	0.03	–	0.003
<i>Tylenchorhynchus sulcatus</i>	0.003	–	0.0003
Total	6918	100	

Overall average abundance, relative abundance and the average abundance corresponding to the trophic groups. The species selected for the analysis are in italics.

Fifteen soil physical and chemical characteristics were analysed in each sample: clay, fine and coarse silt, fine and coarse sand in g kg^{-1} ; C g kg^{-1} , N g kg^{-1} and total P content; exchangeable bases: Ca, Mg, Na, K and cation exchange capacity (CEC) (cmol kg^{-1}); saturation rate in % (Sat) and the wilting point 4.2 (Wp4) (Page et al., 1982). Finally averaging the results per site reduced the tables to 8 and 15 columns, respectively, for nematode and soil data, and 33 rows (11 sites per year).

2.6. Statistical analysis

Partial triadic analysis (PTA) used in this study was derived from triadic analysis (Tucker, 1966) and introduced in ecology by Thioulouse and Chessel (1987). The name “partial” triadic analysis comes in fact from Kroonenberg (1989). Many examples of application can now be found in ecology. Partial triadic analysis, like all the methods of the STATIS family (Lavit, 1988), comprises three steps: the interstructure, the compromise, and the trajectories (Lavit et al., 1994). The aim is to analyse a three-way table (i.e., a data cube; for example, species \times sites \times soil parameters), seen as a sequence of two-way tables. More precisely, PTA searches for structures that are stable among the sequence of tables.

First step: the interstructure. This step gives the “importance” of each table: a matrix of scalar products between tables is computed, and the components of the first eigenvector of this matrix are used as weights for the tables to compute the compromise.

Second step: the compromise. This is the main step of the analysis: the compromise table is computed as the weighted mean of all the tables of the series, using the components of the first eigenvector of the interstructure as weights. This table is called the compromise, and it has the same dimensions and the same structure and meaning as the tables of the series. It is analysed by a PCA, giving a picture of the structures common to all the tables.

Third step: the trajectories. The rows and columns of all the tables of the sequence are projected on the factor map of the PCA of the compromise as additional elements. This step summarizes the variability of the series of tables around the common structure defined by the compromise.

The differences between years at each site, and the reverse, were studied using the between-group PCA analysis.

The study of the nematode–soil relationships was done with the co-inertia analysis (Dray et al., 2003; Thioulouse et al., 2004). Co-inertia analysis belongs to the family of two-table coupling methods, which include canonical correspondence analysis (CCA, Ter Braak, 1986), redundancy analysis (RDA, Wollenberg, 1977), and canonical analysis (Gittins, 1985). However, co-inertia analysis differs from CCA and RDA, and also from canonical analysis. The principle of co-inertia analysis is very simple: it searches for axes that maximize the covariance between the row coordinates of the two tables. This principle is similar to that of canonical analysis, except that it is the covariance that is maximized in co-inertia analysis, instead of the correlation in canonical analysis.

In CCA and RDA there is an additional regression step, ensuring that sampling scores are linear combinations of environmental variables. If there are many variables, the results of CCA tend toward those of a plain CA (correspondence analysis) and the results of RDA toward those of a PCA (principle component analysis). Moreover, if the variables are correlated, CCA and RDA become unstable. In these cases, co-inertia analysis is a robust alternative.

Calculations and graphs were done using ADE4 software (Thioulouse et al., 1997). Nematode numbers were changed to $\log(x + 1)$ prior to calculations.

3. Results

3.1. Nematode community

Nematodes were placed in three groups (Table 2): (1) the free-living nematodes including, bacterivorous, predatory, omnivorous and fungivorous nematodes, which did not belong to the three types mentioned in the fungivorous group; (2) some fungivorous nematodes; (3) the plant-parasitic nematodes, most of them identified to species level. Among these groups, the fungivorous species *D. myceliophagus* and the most frequent species of plant-parasitic nematodes were taken into consideration: *Scutellonema cavenessi*, *Helicotylenchus dihystrera*, *Tylenchorhynchus gladiolatus*, *Tylenchorhynchus mashhoodi*, *Pratylenchus*

pseudopratensis, *Trichotylenchus falciformis* and *Gracilacus parvula*.

3.2. Effect of fallow duration or fencing on the nematode communities

3.2.1. Effect of fallow duration: nematode characteristics of the sites

The partial triadic analysis built a compromise, which summarised the “time \times site” effect. This avoided representing the 2992 points on the factorial plan or comparing 187 plans if these points were split according to the 17 sampling dates and the 11 transects. On the factorial map of the compromise (Fig. 1A), the variable corresponding to *S. cavenessi* was strongly correlated with the negative part of F1 and the positive part of F2. *G. parvula* was opposed to *S. cavenessi* along the diagonal and like *H. dihystrera*, *T. falciformis* and *P. pseudopratensis*, was correlated with the positive values of F1. Along F2, *T. gladiolatus* was also opposed to *S. cavenessi*.

The factorial plan of the compromise (Fig. 1B) for the samples collected in the different sites summarised the time effect per sampling point and the size of the clouds give an idea of the variability of the nematode communities. The points corresponding to the young 1-year-old fallow sites, whatever the previous cropping history, were located in the negative values of F1.

S. cavenessi and *T. gladiolatus* dominated the nematode communities of these sites; *G. parvula* was not present (Table 3). The points corresponding to the two transects in the 8-year-old site were close to the origin or in the positive values of F1, unlike those in the younger fallow sites. The cloud size showed that the nematode community was variable. The same situation was observed for three of the 18-year-old fallows. However, most of the points had positive F1 values and negative F2 values because of nematode communities dominated by *H. dihystrera* and the presence of *G. parvula*, and lower populations of *S. cavenessi* and *T. gladiolatus* (Table 3). The abundance of *S. cavenessi* explained the location of most of the points corresponding to the forest in the 2nd quadrant of the factorial plan (Fig. 1 and Table 3).

3.2.2. Overall annual change of the nematode community among sites

To study the overall annual change within the nematode communities, the partial triadic analysis was performed on the nematological data with, in columns, the 8 nematode species, and in rows, the 16 sampling points for the successive 17 sampling dates and one table for each of the 11 sites. On the factorial plan of the compromise, which summarised the time effect across sites, the three groups of dates corresponding to the 3 years appeared in chronolo-

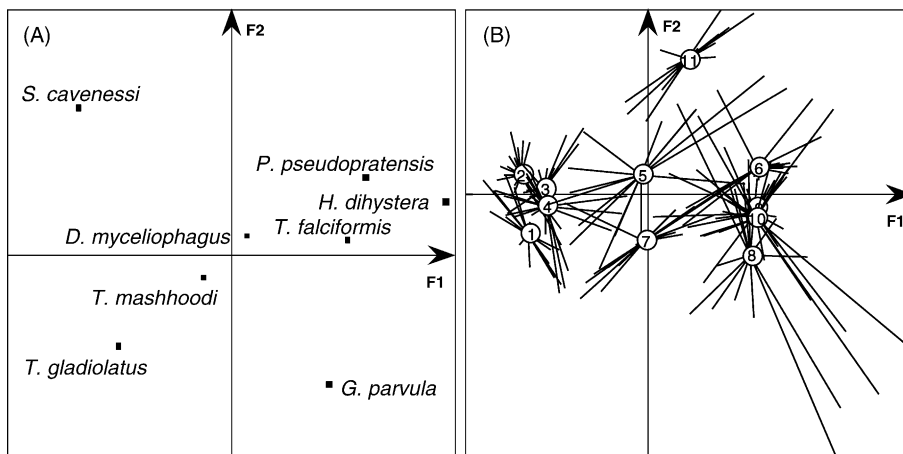


Fig. 1. Between-site study. Results of the partial triadic analysis performed on the nematological data for the 17 dates, the 8 nematode species and the 16 sampling points of the 11 transects, using one table per date (cf. Fig. 1). (A) First factorial plan of the compromise for the nematode species. (B) First factorial plan of the compromise for the transect points (each line joins one point on the transect to the centre of the cloud corresponding to the site) (cf. Table 1 for site situation).

Table 3
Comparison of the most important nematode populations for the triadic analysis between sites and between observation years

Site	<i>D. myceliophagus</i>	<i>G. parvula</i>	<i>H. dihystrera</i>	<i>P. zeae</i>	<i>S. cavenessi</i>	<i>T. gladiolatus</i>	<i>T. mashhoodi</i>	<i>T. falciformis</i>	S.E.							
1	167	24 b	0	33 D	6	80 j	2	22 h	247	60 d	358	10 a	1	6 h	2	6 d
2	279	8 a	4	11 D	30	26 h	1	26 h	749	34 a	256	8 bc	3	3 gh	5	8 d
3	116	14 b	6	109 D	18	41 i	23	18 g	405	22 b	151	20 ef	198	9 c	1	14 d
4	137	12 b	0	71 D	46	43 g	13	22 g	272	32 c	315	23 b	8	13 f	4	8 d
5	186	20 b	0	9 D	219	59 e	198	8 a	215	28 d	230	7 cd	219	19 b	35	4 b
6	160	35 b	1	18 D	386	60 d	70	8 e	38	27 f	67	9 h	5	8 fg	118	3 a
7	236	24 a	70	10 D	111	68 f	143	6 c	37	27 g	166	9 de	226	10 a	1	2 d
8	262	17 a	444	79 A	402	35 c	192	12 b	71	24 e	227	19 cd	59	3 d	94	13 b
9	276	18 a	92	39 C	1257	37 a	29	15 f	10	33 i	90	17 g	4	16 fg	76	15 b
10	232	24 a	303	190 B	1025	107 b	91	22 e	33	42 h	122	23 f	5	33 f	59	22 b
11	301	29 a	1	21 D	326	98 d	131	10 d	509	33 a	52	15 i	32	14 e	31	11 c
Y1	152	7 B	115	27 A	300	24 A	107	9 A	235	17 A	140	7 C	45	5 A	28	4 A
Y2	207	10 A	101	35 A	372	30 A	62	5 B	234	13 A	170	7 B	59	7 B	43	5 A
Y3	272	14 A	40	13 B	364	28 A	79	8 B	236	17 A	237	9 A	99	10 A	43	5 A

The number of nematodes/2.50 cm³ of soil was changed to log(x + 1) prior to performing the ANOVA. Numbers with the same symbol were not statistically different, $P < 0.05$ (S.E.: standard error).

gical order along the second diagonal (Fig. 2A). The five sampling dates of the first year all had positive F1 values. The reverse was true for the 3rd year except for one date. These changes were first explained by the continuous increase of the *T. gladiolatus* populations over the three successive years (Fig. 2B and Table 3).

An annual seasonal cycle was described along F2 (Fig. 2A). Similarities appeared between samples collected at the beginning and at the end of the annual cycles during the dry season: sampling dates 1 and 4 had very close factorial values along F2, as well as sampling dates 6 and 11 or 12 and 17 for the last year. For each year, populations of *S. cavenessi* and *H. dihystrera* were not statistically different between the dates mentioned above (Table 4). Moreover, the similarity between the nematode community observed at the end of a year and the end of the rainy season (October or November) with that observed the following year in March was underlined by the proximity of the two successive sampling date points on the factorial plan. For example, there was no significant difference between the populations of *S. cavenessi* or *H. dihystrera* for the sampling dates 5 and 6 or 11 and 12 (Table 4).

3.2.3. Annual change in the nematode communities per site

The between sites PCA was performed on a table gathering the averages of the annual abundance for the nematode species at each site. On the first axis of the PCA, which expressed 47.4% of the variability, *T. gladiolatus*, *D. myceliophagus* and *T. falciformis* were opposed to *P. pseudopratensis* (Fig. 3A). The F2 axis (18.4% of the variability) was characterised by *T. mashhoodi*, correlated with the positive values, and *S. cavenessi* correlated with the negative values. On the factorial plan (F1 × F2), the three points corresponding to the three observation years were represented for each site separately (Fig. 3B). For all sites, the point corresponding to the last year (c) was located in the positive half of F1, whereas the first year was located in the negative half of F1, except for one of the 1-year-old sites. The overall trend described by the previous analysis, showing a slight increase of *T. gladiolatus* over the 3 years, was observed everywhere and, with one exception, concerned also *D. myceliophagus* (Table 3). How-

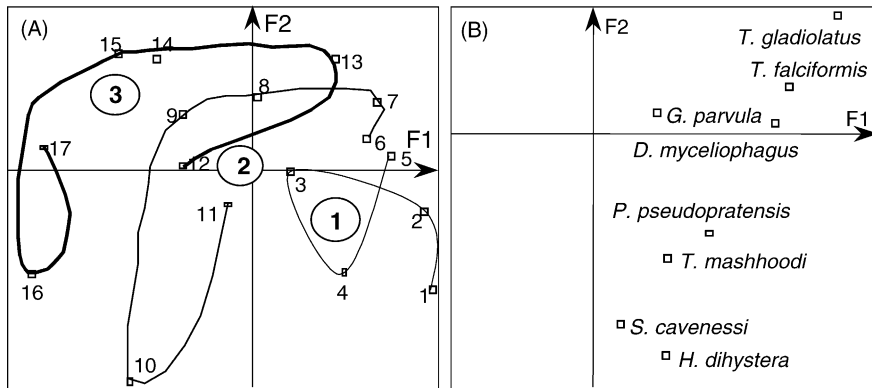


Fig. 2. Between-year study. Results of the partial triadique analysis performed on the nematological data for the 11 transects, the 8 nematode species and the 16 sampling points for the 17 dates, using one table per transect (cf. Fig. 1). (A) First factorial plan of the compromise for the sampling date grouped per year. (B) First factorial plan of the compromise for the nematode species.

ever this tendency did not correspond to a regular process between the first and the third year. The point corresponding to the second year appeared in all four quadrants. The direction of the change between the first and the second year was similar in

Table 4

Comparison of the abundance of *S. cavenessi* and *H. dihystra* during the rainy season, and before and after the dry season during the 3 years of the study, across sites

Season	Sampling date	<i>S. cavenessi</i>	<i>H. dihystra</i>
Rainy	1	a 326	440 a
	2	b 171	150 b
	3	a 219	212 a
	4	a 266	280 a
Dry	5	b 205 a	a 336 a
	6	a 224 a	a 285 a
Rainy	7	a 241	277 a
	8	a 355	121 b
	9	a 252	222 b
	10	b 419	506 a
Dry	11	a 255 a	a 553 a
	12	a 400 a	a 480 a
Rainy	13	b 226	165 b
	14	b 213	212 b
	15	b 153	207 b
	16	a 385	355 a
	17	a 243	459 a

The numbers of nematodes/250 cm³ of soil were changed to log(x + 1) prior to performing the ANOVA (numbers in columns with the same symbol were not statistically different, P < 0.05).

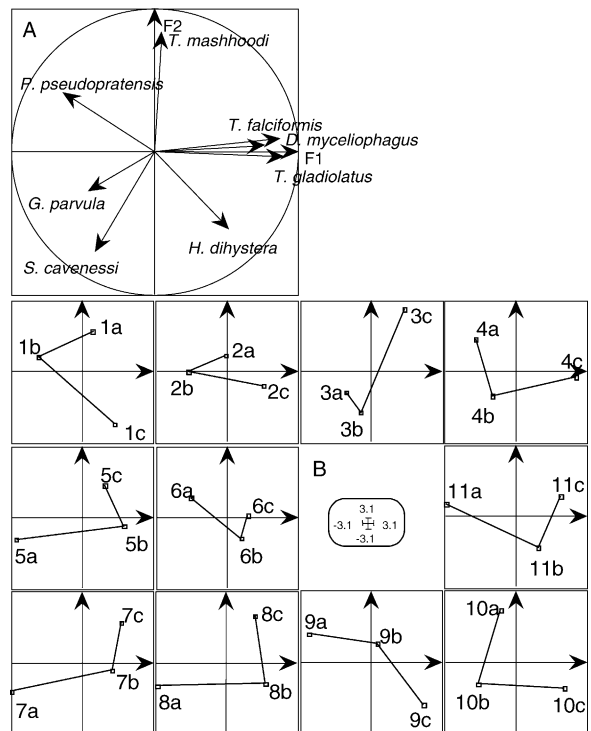


Fig. 3. Between-year analysis per site performed on the nematological data for the average nematode densities per transects and per year (cf. Fig. 1). (A) First factorial plan of the PCA for the nematode species. (B) First factorial plan of the PCA for the sampling dates grouped per site for the three successive years; “a” represents the 1st year and “c” the 3rd year (cf. Table 1 for site situation).

the young fallows according to the previous cultivated period duration, but was independent of the fencing (Fig. 3B). The changes along F1 were also comparable for the 8-year-old fallows, the forest and the 18-year-old not fenced fallows. They were different for the two 18-year-old fenced fallows (transects 9 and 10).

3.3. Comparison of the soil characteristics of the different sites

3.3.1. Soil characteristics of the sites

The factorial map of the compromise issued from the partial triadic analysis performed on the soil data summarised the results per site across the 3 years. The first factor described the particle size gradient with the sand variables located in the negative part, opposed to the clay and related soil parameters such as CEC, wilting point and exchangeable bases (Fig. 4A). Along F2, coarse silt was opposed to the saturation coefficient. However the second factor, which described only 13% of the variability, was of lesser importance compared to the 1st one, 65%.

When the sampling points were projected on the factorial plan $F1 \times F2$, the different sites were distributed along F1 (Fig. 4B). The points corresponding to the young fallows (1–4) and the forest (11) were

located in the negative part of F1, mainly because of a higher proportion of fine sand particles in the soil (Table 5). The within-site variability, indicated by the size of the star, was relatively low, mainly for the forest site. One of the 8-year-old fallow (6) and three of the 18-year-old fallows (7, 9, 10) appeared in the positive part of F1, because of lower level of sand and higher level of clay and related soil factors (Table 5). The remaining 8-year-old fallow (5) and 18-year-old fallow (8) were located in the middle of the factorial plan. The latter site was rather variable, mainly for one of the samples with very high positive F1 and F2 values. For these two sites, the soil characteristics corresponded to the average soil type.

3.3.2. Overall annual changes of the soil characteristics among sites

The triadic analysis of the soil data for the 3 years, the 15 soil variables and the 16 sampling points of the 11 transects was performed using one table per site. On the factorial map of the compromise, the 1st factor described the particle size gradient (Fig. 5A), but not as clearly as for the site comparison. Three variables appeared in the negative part of F1, fine sand, coarse sand and coarse silt (Fig. 5B). The saturation coefficient correlated with the negative part of F2 and was opposed to the CEC, clay and the Na content.

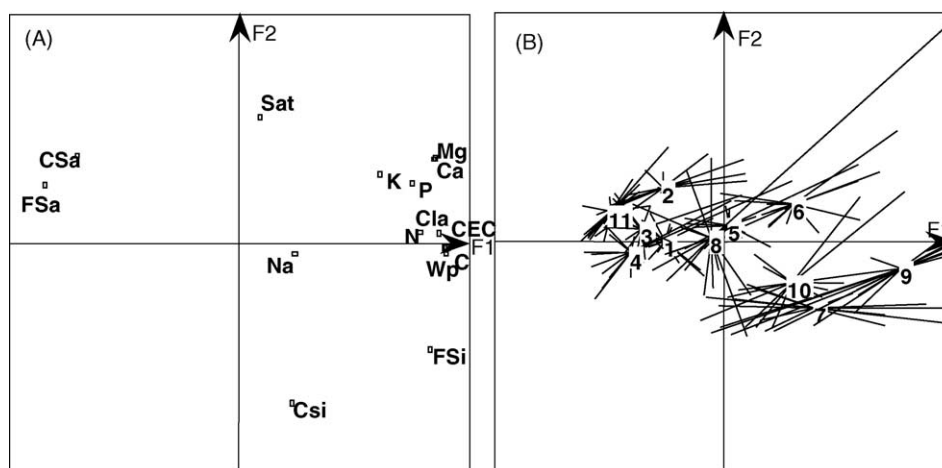


Fig. 4. Between-site study. Results of the partial triadic analysis performed on the soil parameter data for the 3 years, the 15 soil parameters and the 16 sampling points of the 11 transects, using one table per year (cf. Fig. 1). (A) First factorial plan of the compromise for the soil parameters. (B) First factorial plan of the compromise for the transect points represented by a star (each line joins one point on the transect to the centre of the cloud corresponding to the site) (cf. Table 1 for site situation).

Table 5
Comparison of the most soil characteristics for the triadic analysis between sites and between observation years

Site	Ca	S.E.	CEC	S.E.	K	S.E.	Mg	S.E.	P	S.E.	PF4	S.E.	Sat	S.E.	Cla	S.E.	CSa	S.E.	Csi	S.E.	FSa	S.E.	FSi	S.E.	C	S.E.	N	S.E.
1	1.72	0.05 de	3.33	0.09 e	0.05	0.00 f	0.66	0.02 c	66.3	4.0 fg	3.6	0.07 d	0.76	0.02 ab	100	0.0 f	230	3.7 fg	171	3.1 de	398	3.3 a	90	2.1 e	4.88	0.11 ef	0.38	0.01 g
2	1.79	0.10 de	3.38	0.11 de	0.06	0.00 f	0.66	0.03 c	88.0	5.3 bc	3.7	0.16 d	0.75	0.02 ab	105	0.1 ef	286	3.8 c	142	1.7 g	394	3.9 a	64	1.7 f	5.00	0.15 e	0.46	0.02 of
3	1.21	0.04 f	2.86	0.11 f	0.08	0.00 cd	0.49	0.01 d	62.9	1.8 gh	3.2	0.09 de	0.66	0.02 c	94	0.0 f	302	4.5 b	152	2.1 f	363	3.7 b	83	1.5 e	5.26	0.17 e	0.49	0.02 e
4	1.16	0.08 f	2.64	0.15 f	0.07	0.01 df	0.47	0.04 d	56.4	1.8 hi	3.5	0.17 d	0.70	0.04 bc	103	0.1 f	244	4.6 cf	174	2.1 cd	405	4.2 a	68	1.1 f	4.41	0.12 f	0.43	0.01 f
5	1.95	0.07 cd	3.80	0.19 d	0.08	0.00 cd	0.82	0.03 b	73.7	2.0 def	4.5	0.10 c	0.85	0.05 a	131	0.0 d	264	4.1 d	177	2.5 cd	332	3.6 c	91	1.8 de	6.51	0.28 d	0.60	0.02 d
6	2.42	0.09 ab	4.60	0.13 bc	0.09	0.01 cd	1.05	0.04 a	95.5	2.5 b	5.8	0.15 b	0.81	0.03 a	149	0.0 bc	254	4.2 de	172	2.2 d	319	2.9 d	99	2.5 d	7.38	0.25 bc	0.68	0.02 bc
7	2.18	0.08 bc	4.97	0.20 b	0.09	0.00 cd	0.80	0.02 b	75.5	2.3 de	6.0	0.30 b	0.65	0.02 c	138	0.0 cd	219	5.0 g	210	2.4 a	261	5.3 f	168	6.3 b	7.95	0.35 b	0.72	0.04 b
8	1.64	0.14 e	3.39	0.13 de	0.13	0.02 b	0.62	0.04 c	72.9	1.9 ef	4.5	0.20 c	0.71	0.04 bc	116	0.0 e	292	6.9 bc	181	3.5 c	317	4.0 d	88	3.0 e	6.26	0.22 d	0.62	0.02 d
9	2.54	0.19 a	5.61	0.26 a	0.15	0.02 a	1.03	0.07 a	107.0	5.6 a	7.1	0.35 a	0.64	0.03 c	194	0.1 a	170	8.0 I	181	2.9 c	248	7.3 g	199	6.5 a	8.94	0.34 a	0.81	0.03 a
10	1.94	0.11 cd	4.35	0.13 c	0.10	0.00 c	0.81	0.03 b	82.3	2.5 cd	5.9	0.21 b	0.68	0.03 bc	154	0.1 b	196	4.2 h	194	3.1 b	303	4.5 e	147	5.0 c	7.08	0.16 c	0.64	0.01 cd
11	1.26	0.06 f	2.49	0.09 f	0.08	0.01 cd	0.56	0.02 cd	50.9	1.4 I	2.8	0.09 e	0.82	0.05 a	71	0.0 g	347	4.4 a	165	1.9 e	360	3.5 b	52	0.7 g	4.78	0.12 ef	0.48	0.01 e
Y1	1.83	0.46 A	3.71	0.01 B	0.08	0.00 A	0.75	0.39 A	80.1	0.01 A	4.1	0.12 B	0.75	0.02 B	112	0.2 B	268	1.1 A	175	2.0 A	333	1.6 A	103	0.6 A	6.58	0.00 A	0.56	0.44 A
Y2	1.93	0.45 A	3.35	2.29 C	0.09	0.10 A	0.72	0.17 A	72.7	0.00 B	4.7	0.13 B	0.85	0.02 A	119	0.0 B	220	0.0 B	178	4.4 A	341	0.1 A	105	0.2 A	6.39	0.38 A	0.58	0.14 A
Y3	1.64	0.16 B	4.23	0.07 A	0.09	0.00 A	0.71	0.43 A	74.0	0.10 B	5.0	0.16 A	0.59	0.01 C	138	0.1 A	245	3.8 B	171	4.3 A	335	7.1 A	105	0.0 A	5.70	0.19 B	0.58	0.02 A

Percentages were change to arcsin(sqrt(x)) prior to performed the ANOVA. Numbers with the same symbol were not statistically different; $P < 0.05$ (S.E.: standard error).

The first factorial plan of the samples projected per year, across sites, showed that the 3 years could be distinguished along F2 but not along F1, indicating that the changes between the years were minor (Fig. 5A). The 3rd year cloud was set off from the others in the positive part of F2. Years 1 and 2 had lower factorial values and overlapped. Whereas all factorial values of the samples collected in the second year were negative, those of the 1st year were both positive and negative. As a consequence, the 3 years did not appear in chronological sequence along F2. The soil variables correlated with F2 explained the position of the three clouds along this axis. The saturation rate was higher in the second year, than for the 1st one (Table 5). The reverse was true for the CEC. In the 3rd year, Na content was higher as was clay and CEC. The differences between the first and the second year were not significant for clay or for Ca and Na content (Table 5).

3.3.3. Annual change in the soil characteristics per sites

The between-site PCA was performed on a two-dimensional table gathering the annual averages of the soil physico-chemical characteristics at each site for all 16 sampling points. On the first factorial map of the PCA (76.8% of the variability), a particle size gradient was described by F1, 66.8% of the variability (Fig. 6A). F2 was described by fine sand and wilting point, correlated with the positive part of the axis. On the F1 \times F2 factorial map, the point corresponding to the last year had always negative F1 values (Fig. 6B). On the contrary, the points corresponding to the first year had very low or positive F1 values. The overall trends described previously between the observation years across sites corresponding mainly to a slight increase in clay happened at all sites (Table 5). However, as for the nematodes, this change was not progressive over time. The second year, in 10 out of 11 sites, appeared in the second quadrant. The soil characteristics were similar to the first year or similar to the second year.

3.4. Soil–nematode relationship at Thyssé-Kaymor

The co-inertia analysis was performed on the average data for the sampling dates for the 11 transects

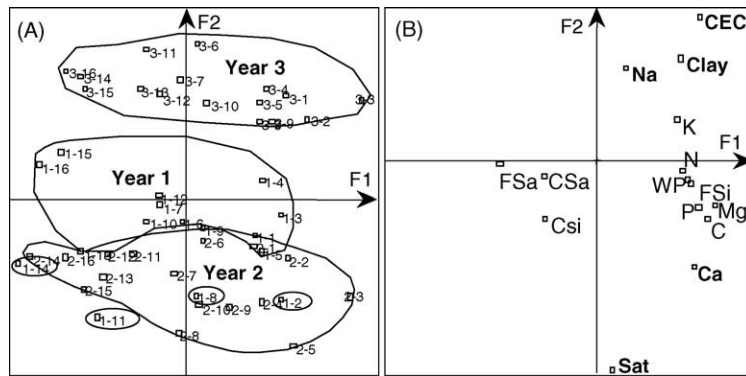


Fig. 5. Between-year study. Results of the partial triadic analysis performed on the soil parameters for the 11 transects, the 15 soil parameters and the 16 sampling points for the 17 dates, using one table per transect (cf. Fig. 1). (A) First factorial plan of the compromise for the sampling date grouped per year. (B) First factorial plan of the compromise for the 15 soil parameters (cf. Table 1 for site situation).

and for the 3 years together for nematodes and soil. On the factorial plan, the three ellipses gathering the annual values of the physico-chemical soil character-

istics and of the nematodes data were slightly offset one from the other (Fig. 7A and B). The variation between the first and the third year, all sites confounded, was of little magnitude and concerned only the second axis of minor importance (4.6% of inertia). The gravity centres of the ellipses issued from the co-inertia analysis moved similarly, slightly to the left for the nematode data and to the right for the soil data. The permutation test was highly significant ($P < 0.0001$). On the co-inertia factorial maps, coarse sand had the lowest negative F2 value, corresponding to *T. mashhoodi*. Conversely, fine sand and clay with the highest positive F2 values corresponded to *T. gladiolatus* (Fig. 7C and D).

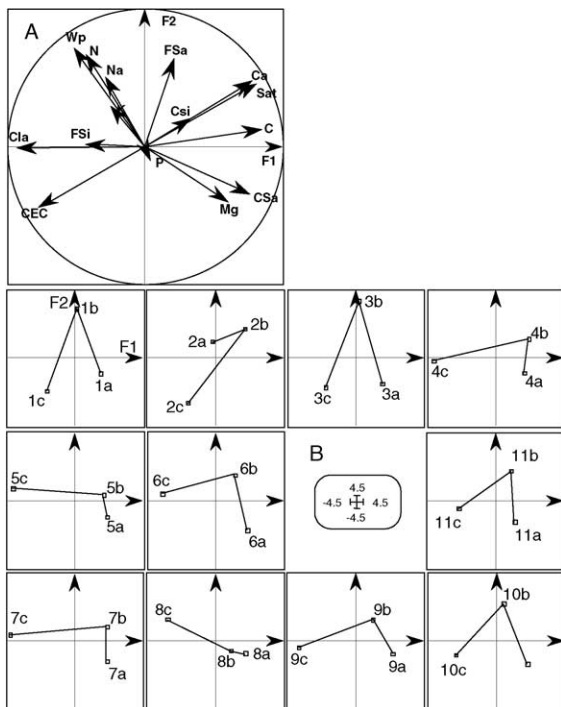


Fig. 6. Between-year analysis per site performed on the soil data (cf. Fig. 1). (A) First factorial plan of the PCA for the soil characteristics. (B) First factorial plan of the PCA for the sampling dates grouped per site for the three successive years; “a” represents the 1st year and “c” the 3rd year (cf. Table 1 for site situation).

These annual relationships between soil abiotic factors and nematode described by the second factor were marginal compared to the main relationships described by the first factor (91.8% of the variability), concerning the sites (Fig. 7E and F). This strong relation between nematodes and soil was mainly driven by the significant positive regression ($P < 0.001$; $R = 0.64$) between one species, *S. cavenessi* and fine sand. *S. cavenessi* with a high negative F1 factorial value was associated with soils with a greater proportion of fine sand particles as occurred in the youngest fallow sites (Fig. 7). Conversely, the finer textured soils of the older fallows had fewer *S. cavenessi* and greater populations of *H. dihystra* and most of the other species. The decrease of *H. dihystra* was proportional to the fine sand content ($P < 0.001$; $R = 0.43$). However, differ-

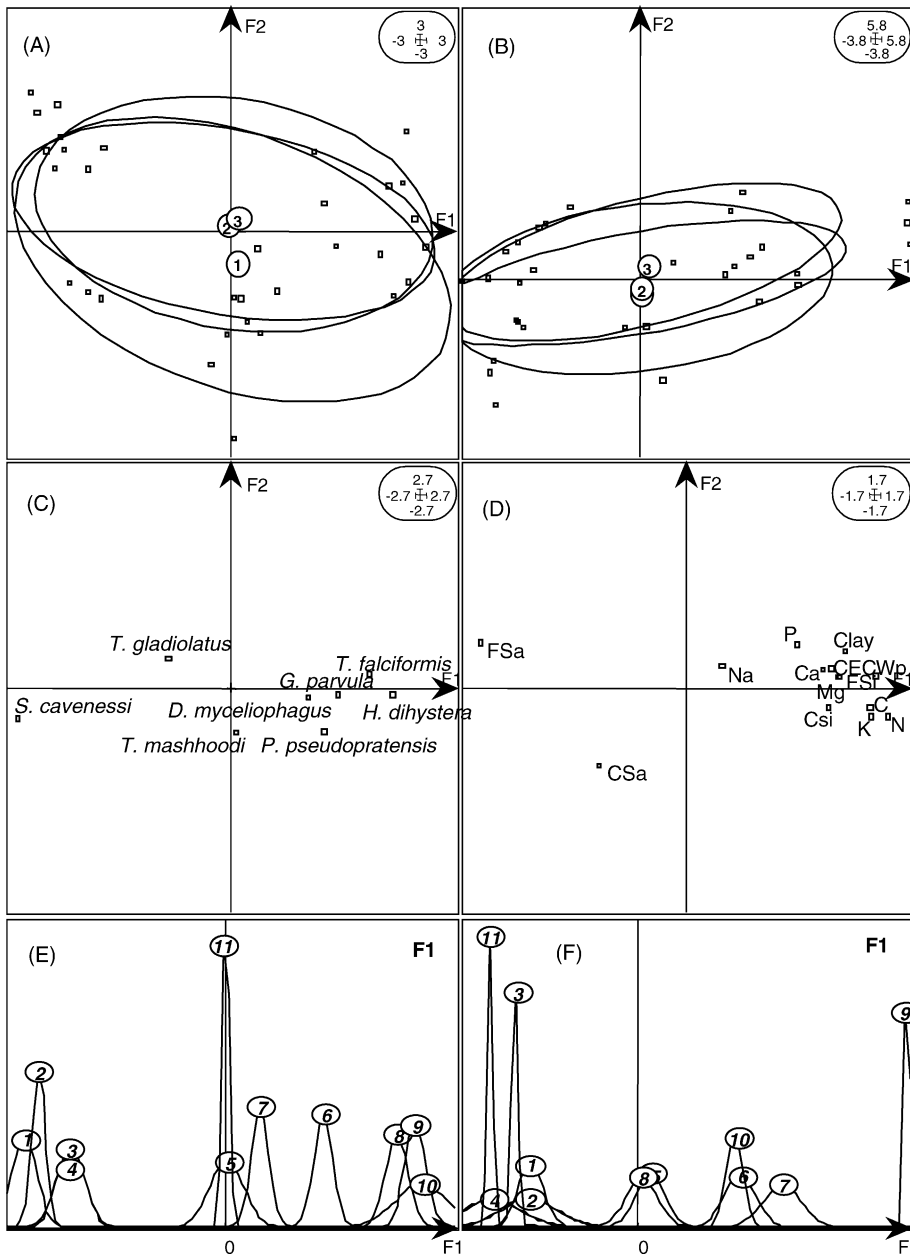


Fig. 7. Study of the similarities between nematodes and soil. (A and B) Relative position of the ellipses gathering 95% of the sampling dates grouped per year, relocated after the nematode and the soil co-inertia analysis. (C and D) First factorial plan of the co-inertia analysis (cf. Fig. 1) for the nematode species and for the soil parameters. (E and F) Relative position of the gauss curves corresponding to the sampling date grouped per site, relocated after the nematode and the soil co-inertia analysis, and projected on the first factor.

ences appeared between the position of certain sites along the F1 axis derived from the nematode co-inertia data and from the soil co-inertia data (Fig. 7E and F). The forest site with the same soil as the young fallows

hosted a different nematode community. Similarly, whereas sites 8 and 10 had similar soil to site 9 (all 18-year-old fallows), they had different nematode communities.

4. Discussion

4.1. Comparison of site sequences

Abandoning cultivated fields result in the re-growth of the natural vegetation. Oversimplified, a fallow period is characterised, in the Sudano-Sahelian, by the development of a shrubby stratus followed by a tree stratus. According to the density of ligneous plants, the herbaceous species, which cover the soil at the beginning of the fallow period, can regress (Donfack et al., 1995). Phytophagous nematodes are obligate parasites and their distribution is necessarily linked with the distribution of the host plants, particularly for species, which do not have a broad host spectrum. As a consequence, the plant-parasitic nematode community structure should be determined by the plant succession, especially over a period of time as long as that running from a field stage to a forest stage. This was not obvious in the present study. With the nematode community analysis, the sites were not ordered chronologically from the youngest to the oldest age. This result indicated a non-negligible mesological effect. However the sites were divided into two groups: one comprising the youngest fallows and one the older fallows. This situation could be expected if the host–parasite relationships were weak, allowing the species to survive for a very long period on a poor plant host or if the host range is wide.

Because this study was pursued on a diachronic mode, all sites were located on the same soil type. But the soil analysis revealed differences in texture going from about 70 g kg⁻¹ clay in the forest to 190 g kg⁻¹ clay in one of the 18-year-old fallows. Excluding these extremes, the clay content ranged from 90 to 150 g kg⁻¹, which corresponds to a sandy loam lixisol according to the soil classification (FAO, 1998). When all parameters were taken into consideration, only site 9 (18-year-old fallow) was clearly outside the cloud gathering the other sites (Fig. 4). Moreover, the sites were not ordered according to the fallow age after the soil analysis. Except for the forest, the youngest and the older fallow sites constituted two groups. They were ordered according to the clay gradient. This situation artificially resulted from the fact that the frequency of cultivation of the land was inversely proportional to the distance from the village (Manlay

et al., 2004) and that the soil characteristics changed according to the position on the toposequence. This situation mostly explained the strong relationship between nematode communities and soil characteristics. Therefore, at this stage, it is not possible to determine if the logical differences observed among the nematode communities in the young and old fallows correspond to plant succession or to the edaphical constraints imposed by slightly different soil characteristics within these two groups. These soil constraints existed from the beginning of the land use history.

4.2. Effect of site location on soil characteristics

Excluding the forest, which after all was not a real fallow, this situation led to a mathematically significant positive log-regression between clay content and fallow duration ($R^2 = 0.219$; $***P < 0.0001$), as well as with the carbon content ($R^2 = 0.84$; $***P < 0.0001$; Fig. 8). Conversely, this regression could also be interpreted as a decline in clay content according to the cultivation frequency, resulting from more intense sheet erosion occurring on the bare soil of the frequently cultivated fields (Roose, 1967). At the beginning of the rainy season, after 8 months of complete drought, heavy rainfalls occurred leading to erosion where vegetation was absent (Lal, 1996; Roose, 1996). However, the model linking level of erosion and land use seemed unrealistic and was more likely to result from the position of the fallow sites. But, the same positive log-regression between carbon content and fallow duration observed on the same sites was considered as reflecting a valid phenomenon of progressive organic matter storage accompanying plant biomasses increase with the plant succession ($R^2 = 0.333$; $***P < 0.0001$) (Greenland and Nye, 1959; Manlay et al., 2002a; Masse et al., 1998). Even if the erosion model was questionable, the phenomenon is a reality and strongly supports the view that soil fertility and soil conservation are of equal importance and not separable. Rehabilitation of the land by fallowing, which both protects the soil and reduces the mining of soil nutrients, appears very important in preventing further desertification in this region.

The position of the forest and of the fallow sites 8 and 10 on the F1 axis, suggested that both factors,

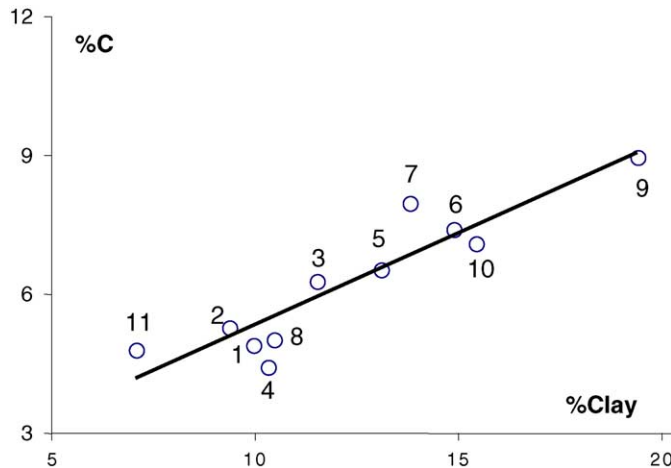


Fig. 8. Relationships between average C and average clay for the different sites (indicated by their number; cf. Table 1 for site situation).

plants and soil, play a role, but that the soil effect was minor. Despite a soil environment similar to that of a young fallow, the nematode community of the forest had features common to both young and old fallows. The sites 8, 9 and 10, corresponding to 18-year-old fallows, had different soil characteristics, but similar nematode communities, suggesting that the length of fallow effect was stronger than the soil environment effect.

However, this study showed that the nematode community was not strongly affected by the fencing. This result is not surprising as fencing had a tendency to reduce the disturbance of vegetation and consequently the plant diversity and thus the potential hosts for the nematode species (Van der Maarel, 1993). In the young fallow, the nematode community appeared to be slightly affected by the cropping history of the field, but not by fencing.

The very tiny and uniform tendency for *T. gladiolatus* to increase between the 1st and the 3rd year at each site appeared very artificial and seemed to result from a technical problem.

This assumption is confirmed by the general increase in clay content. If micro-organism activity is potentially able to promote changes in the chemical characteristics of the soil (Young, 1989; Masse et al., 2004), the 3-year period appeared too short to end up with significant changes in soil texture. The deterioration process of the parent material that produces clay happens over a geological time scale.

Therefore, it is more likely that the repeated sampling around the same spot had created a small depression in the soil, mainly after the second year of sampling (12 occasions), in which runoff water accumulated. The small clay particles transported in the runoff settled in the depression after each rain. Mathematically, this increase in clay was correlated with the annual increase in *T. gladiolatus* over the three years. However, this species was mainly found in the young sandy soil fallows and was not abundant in the site 9 (18-year-old fallow) with the highest clay content. This species was also the most abundant in the surrounding millet fields (Pate et al., 2000). These contradictory results suggested that the reason for this overall slight increase in *T. gladiolatus* the 3rd year was more likely a result of soil disturbance by repeated sampling than by the increase in clay. Actually, it is probably truer to assume that some other species were depressed by the sampling disturbance. This could explain why, even after 20 years of abandonment, the nematode species, except *S. cavenessi* and *T. gladiolatus* disappeared so quickly in the replanted field after one or two crops of millet (Villenave and Cadet, 2000). These results highlight the importance of the sampling technique and the need to collect environmental measurements to enable deductions to be made from statistical analyses.

This annual increase of the *T. gladiolatus* population was contradicting the overall trend accompanying

the aging of the fallowing described by the analysis of the nematode community. However, it was too small to question the validity of the long-term fallowing responsibility on the nematode community changes. The two species, *S. cavenessi* and *T. gladiolatus*, abundant in the young fallows and in the surrounding millet fields, were replaced by numerous other species in the older fallows. The occurrence of *S. cavenessi* in the forest was probably facilitated by the presence of a very sandy soil, similar to that of the young fallow sites, which was probably promoting specific plants. But it is unlikely that the soil particle size will explain entirely the occurrence of this species because the forest seemed to promote the establishment of a particular community, distinct from that found on the other sites. In addition, *H. dihystra*, the dominant species in the older fallows, was as abundant in the forest and in the mid-aged fallows, but was almost absent in the young fallows with similar soil texture. The 18-year-old fallow on site 8, with soil characteristics relatively close to those of the young fallow sites, showed an extremely different nematode community, similar to the community evolving in two of the other older fallow sites with different soil components.

5. Conclusion

This study demonstrated that the changes in the nematode community under successions of natural vegetation were extremely slow, probably because most of the nematode species were able to survive for a certain time on poor plant hosts. It confirmed that plant succession probably had the major impact on the change in the nematode community. The effect of the annual climatic conditions was not significant. Soil physical and chemical characteristics had a much more important influence on the nematodes communities. As a consequence, before investigating the mechanisms by which changes in plant communities affect the nematode communities, the first step will be to “mathematically remove” this soil effect from the observed nematode densities. Knowing these mechanisms will allow to identify the suitable manipulations of the plant communities, which will accelerate the changes in the nematode community to a less pathogenic one.

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