Journal of Tropical Ecology (2003) **19**:279–290. Copyright © 2003 Cambridge University Press
DOI:10.1017/S0266467403003316 Printed in the United Kingdom

Relationship of nematode communities to human demographics and environment in agricultural fields and fallow lands in Senegal

Patrice Cadet[1], Emmanuelle Pate and Jean Thioulouse

Institut de Recherche pour de Développement, Biopedology, BP 1386 Dakar, Sénégal

(*Accepted 5 June 2002*)

Abstract: One hundred and nine soil samples were collected in 69 different localities along two transects, one North–South, about 900 km in length, and the other East–West (750 km in length), across Senegal and Gambia. The first transect followed a rainfall gradient and the second a human density gradient. The relationship between carbon content, C/N ratio and soil type on the abundance and species distribution of the nematodes along the transects was studied. Results showed that short-term fallows did not influence the specific structure of the communities, when compared with the nematode communities of fields located in the immediate vicinity, where *Scutellonema cavenessi* and *Tylenchorhynchus gladiolatus* were the dominant species. The expected negative influence of human disturbance on nematode occurrence seemed to be compensated by greater crop diversity, mainly near the towns. Less-disturbed areas also maintained a high diversity, but were characterized by the presence of particular species such as *Xiphinema* spp. Soil type was the most important factor affecting the species composition of the nematode community. As a result, nematode communities followed a distribution in areas, corresponding to the successive soil types, but did not change in relation to the human or climatic gradients. At a large scale, the study of plant-parasitic nematodes can give both different and complementary information on the ecological trends of an area to that of free-living nematodes.

Key Words: climatic gradient, environmental factors, fallow lands, fields, human density gradient, soil type

INTRODUCTION

Among the soil metazoa, nematodes are the most abundant (Bachelier 1978, Freckman & Mankau 1977, Sohlenius 1980). They have the necessary biological qualities with which habitats can be described, namely ubiquity, specific and functional diversity and low mobility (Freckman 1988, Wright & Coleman 1993, Yeates *et al.* 1993). Several studies have shown the potential of nematodes as bio-indicators of the state of the environment as well as for understanding the bio-functioning of the soil or ecosystem (Bongers 1990, de Goede & Bongers 1994, Freckman & Ettema 1993, Neher & Campbell 1994). Most of these studies dealt with free-living nematodes, which represent, in most situations, up to 90% of the soil nematode community. However, species are difficult to identify and a large number of them are not yet described, therefore complicating the quantification of the composition of the free-living nematode community in the samples.

Conversely, plant-parasitic nematodes are less diverse and less numerous than free-living nematodes. Their presence requires a host plant on which they will feed, limiting the field study to vegetated areas. Moreover, observations have demonstrated that the number of plant-parasitic species increases where cultivated land is left undisturbed (fallowed) for several years. The pathogenic species observed on crops were progressively replaced by many other, less-pathogenic species (Cadet & Floret 1995, Pate *et al.* 2000, Thioulouse *et al.* 1998). Host specificity of many plant-feeding nematodes links their existence to the simultaneous presence of suitable host plants. They might not be expected to be suitable for characterizing ecosystems. However, strong relationships between plant-parasitic nematodes and abiotic environmental factors have been demonstrated. *Meloidogyne* is mainly observed in sandy soil (Netscher & Sikora 1990) and *Helicotylenchus retusus* in vertisol (Cadet & Van Den Berg 1992). This latter species was not found in other soil types, even when the principal host plant was present. These examples demonstrate that plant-parasitic nematodes are also sensitive to their environment. Moreover, they are easier to identify than free-living nematodes.

In this study, the species of plant-parasitic nematodes and the free-living nematodes as a group were studied in millet and recently abandoned fields, where the natural vegetation was re-growing, at the very large scale of Senegal. The same plants were selected for sampling to minimize host–parasite effects. The species abundance and ecological indices were analysed to determine how they were

---

[1] Corresponding author. Email: cadet@sugar.org.za

associated with ecological parameters, such as location (latitude, longitude), rainfall, soil type, vegetation, organic matter status (C/N ratio), and even human pressure (measured through population densities) was analysed in relation to plant-parasitic nematodes. Free-living nematodes are known to respond to these factors and can be used to monitor and predict related changes in the ecosystem (Villenave *et al*. 2001, Yeates & Bongers 1999). This study aims to determine if plant-parasitic nematodes could be used as ecological indicators as accurately as free-living nematodes when the host-plant influence is reduced.

METHODS

Sampling

The study was made by means of two transects across Senegal, one, *c*. 900 km North–South and the other 750 km, West–East. Sampling was designed to exploit the existing natural gradients on the Senegalese territory. The North–South gradient was characterized primarily by increasing rainfall, from 150 mm y^{-1} in the North to more than 1000 mm y^{-1} in the South. The human population was usually quite dense along the Senegalese coast. As a consequence, the fallow lands were always young and the natural vegetation never reached, in cultivated regions, the status of forest. The *Combretum* or *Guiera* shrubs ranged from 1 m high in the North to 2 m in the South. The West–East gradient was characterized by decreasing demographic pressure (most of the important towns are located on the West part of the country) and an increasing rainfall gradient, ranging from 400 mm y^{-1} in Dakar to more than 1000 mm y^{-1} near Kedougou. As a consequence, the average height of the plants in the fallow land increased from 0.5–1 m near Dakar, to 4–5 m around Kedougou, where forests are common.

In total, 109 soil samples were collected in 69 different localities. These samples were distributed at about 20-km intervals along two main roads crossing the country, North–South from Richard Toll to Kolda, including Gambia, and West–East, from Dakar to Kedougou (Figure 1a). For each locality, the geographical (latitude in degrees) and the rectangular co-ordinates were determined. With this information, the distribution of the 69 localities was projected on a map (Figure 1a).

A handful of soil was collected at a depth of 5–15 cm, at three places 10–20 m apart, to constitute the 0.5–l soil sample corresponding to one situation at a site. The same plant was targeted, usually *Combretum* spp. or *Guiera* spp. and the soil was collected adjacent to the sprouts. This procedure was followed for the sampling of an adjacent millet field when it was possible to find one. Between one and five samples were collected at each site during the rainy season (July–September), when nematode populations were abundant (Pate 1997).

Nematodes

Nematodes were extracted from soil within 3 d after sampling with Seinhorst's (1962) method and counted alive under the microscope. Bacterivorous and predatory nematodes were enumerated together and the fungivorous nematodes were divided into two groups: the Aphelenchidae and the genus *Ditylenchus*, easily distinguishable under the microscope. Nematode species collected in different samples were identified by the Plant Protection Research Institute of Pretoria (South Africa). The taxonomic classification of Maggenti *et al*. (1988) has been used throughout.

Soil type and organic matter

The carbon and nitrogen content as well as the derived C/N ratio were calculated for 88 of the 109 samples. The Senegal soil map was used to identify the soil type for the 69 localities (Orstom-IRD, 1965, scale 1/1 000 000) (Figure 1b).

Rainfall

The average annual rainfall for the past 5 y (1994–1999) came from the 38 rainfall stations of the national meteorology organization, selected along the two sampling transects (Figure 1c).

Demographic pressure

The demographic data (number of inhabitants per km^2) were collected from the Statistics Department at Dakar and based on a 1988 population census. The average density of the populations was used for localities situated at the border of two adjacent districts (Figure 1d).

Statistical analysis

Prior to analysis, numbers of the 23 taxa, total number of plant parasites and number of non-parasitic nematodes were transformed as log (x+1) to reduce variability. Sample number 48 on the West–East transect was eliminated because of an extremely large number of *Scutellonema cavenessi* that influenced the abundance of the plant-parasitic group. The factors that influenced the nematode communities were studied by principal components analysis (PCA) performed on a table with, in columns, the nematode abundance and, in rows, the samples collected along the transects (ADE-4 Software, Thioulouse *et al*. 1997). A complementary study of the nematode community was conducted using five ecological indices; the total

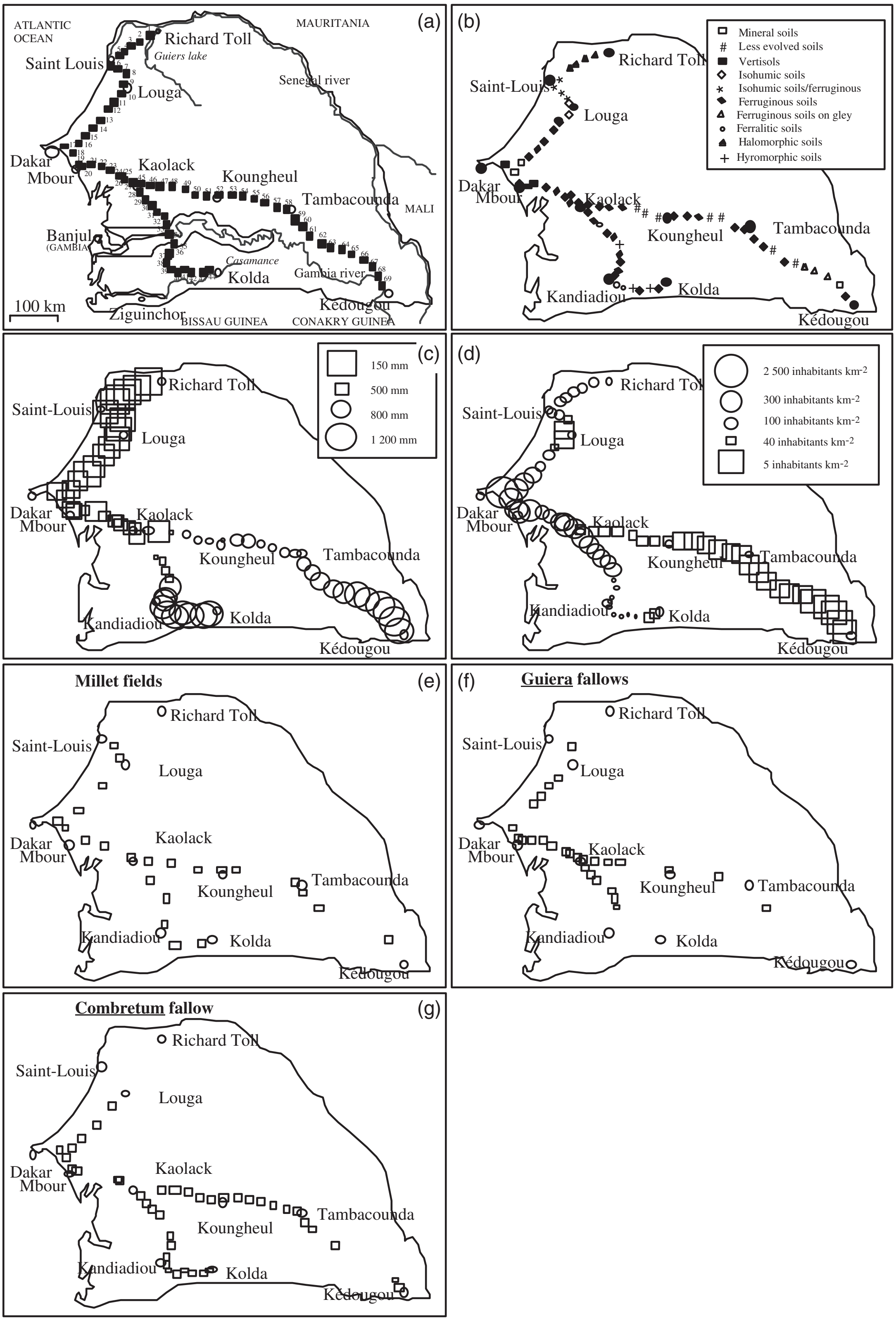

Figure 1. Map of (a) sampling sites; (b) soil types; (c) rainfall distribution and (d) demographic distribution around sampling sites on gradients crossing the Senegalese territory. (c): Data corresponding to the annual rainfall average of the previous 5 y were centred. Squares represent negative values (below average), whereas circles represent values above average. Symbol size is proportional to the distance from the average. (d): Actual human population density per department; number of inhabitants per km^2 transformed to log (x+1) then centred. (c) and (d): Squares represent values below average, whereas circles represent values above average. Symbol size is proportional to the distance from the average. (e), (f) and (g): Distribution of sample sites according to plant groups.

abundance of free-living and plant-parasitic nematodes (numbers changed to log (x+1)), the richness (average number of species encountered per site) and the Shannon indices of diversity and evenness (Shannon & Weaver 1949). A PCA was performed on the table gathering these five indices in columns.

Spatial structure of nematode communities

A Mantel test was used to estimate whether the similarities between the nematode communities were dependent on the geographical distance that separated the samples (Manly 1994, Mantel 1967). With this test, it was possible to determine if the correlation between the two distance matrices was significant. The 'nematological' distances between the samples corresponded to canonical or factorial distances (PCA) and were compared with the geographical distances. Spatial structures were extracted with Moran analysis (Thioulouse *et al*. 1995). This resulted in a coupling between the initial PCA of the nematological data and a neighbouring matrix of proximity. This latter matrix considered that two samples were neighbours if the distance between them was less than 30 km. The Moran analysis broke down the initial inertia of the data set into two parts; one part explained by the neighbouring relationships and the other part that is independent from it. It pointed out the overall spatial structure in the nematode communities by underlining the similarities between adjacent samples. Nematological characteristics of the determined zones were compared by ANOVA and Fisher's LSD.

Plant groups

Influence of the plants on the nematode communities was analysed with a particular PCA, the between-class PCA, performed on the nematological data. This method points out the differences observed between the modalities of a categorical variable, in this case the plant groups (Dolédec & Chessel 1989). For the variables (taxa) contributing to the axes of the PCA, the differences were compared by ANOVA ($P < 0.05$). Only data corresponding to samples collected in the millet fields (Figure 1e) or in the *Combretum* or *Guiera* fallows (Figure 1f and g) were used for this analysis. Other less-represented plant groups, mainly localized in the North, were not taken into account.

Soil type and environmental variables

Soil types were coded into 10 classes. Between-class PCA was used to study the influence of the soil type on nematodes.

Population densities, annual rainfall and organic matter content are quantitative variables. Impact on nematode communities of these environmental variables was studied by PCAIV (PCA on instrumental variables) that belongs to the same family as the canonical correspondence analysis (ter Braak 1986) or the analysis in explaining components (Obadia 1978). Twenty-one samples for which organic matter content was missing, as well as those of the Dakar region (Pikine district) where population density was 10 times higher than that of the other districts, were not taken in account. The correlation coefficient calculated for the nematological variables that determine the axes and the environmental variables were tested with the r-in-z test of Fisher ($P < 0.05$).

RESULTS

Plant groups

Soil carbon and nitrogen contents varied according to plant groups. They were significantly higher in the *Combretum* fallow soils than in millet fields or *Guiera* fallows (Table 1). The variability explained by the vegetation differences only represented 2.1% of the total variability of the 23 plant-parasitic nematode data set. The Monte Carlo test (1000 permutations) confirmed that this percentage was not significant ($P = 0.51$) and that the species composition of the plant-parasitic nematode communities were not different in a millet field, a *Combretum* or a *Guiera* fallow.

Spatial structures of nematode communities

Among the samples, 32 plant-parasitic species were encountered, eight of which were not identified to specific level (Table 2). These species were always very rare and for this reason could not be included in the analysis. Because one species of each plant-parasitic nematode genus was dominant in abundance in the samples and the others always rare, certain species were grouped together under the generic name (Table 2). This gave a total of 23 taxa of plant-parasitic nematodes.

The Mantel test was significant for the species composition of the nematode communities ($r = 0.25$, $P < 0.001$). Differences between nematode communities and geographical distance were positively correlated. Overall spatial structure of nematode communities were significant.

Table 1. Comparison of carbon content, nitrogen and C/N ratio according to plant associations. (In a column, numbers followed by the same letter are not statistically different, ANOVA, $P < 0.05$.)

Vegetation	Carbon content (mg g^{-1})	Nitrogen content (mg g^{-1})
Millet fields	4.88a	0.43a
Guiera fallows	5.43a	0.51a
Combretum fallows	7.72b	0.67b

Table 2. Trophic classification, identification level of the nematodes encountered in the samples and phytoparasitic nematode grouping done before analysis (Maggenti *et al.* 1988).

Trophic groups	Level of identification[1]
Phytoparasites	*Aorolaimus* sp.
	Aorolaimus macbethi
	Aphasmatylenchus variabilis
	Criconemella curvata
	Gracilacus parvula
	Helicotylenchus dihystera
	Hemicycliophora belemnis
	Hemicycliophora typica
	Heterodera sp.
	Hoplolaimus pararobustus
	Longidorus sp.
	Longidorus pisi
	Mesocriconema xenoplax
	Paralongidorus bullatus
	Paratrichodorus sp.
	Paratylenchus spp.
	Pratylenchus pseudopratensis
	Scutellonema cavenessi
	Senegalonema sorghi
	Trichotylenchus spp.
	Triversus annulatus
	Tylenchorhynchus avaricus
	Tylenchorhynchus germani
	Tylenchorhynchus gladiolatus
	Tylenchorhynchus sulcatus
	Tylenchorhynchus ventralis
	Tylenchorhynchus mashhoodi
	Tylenchorhynchus phaseoli
	Tylenchorhynchus sp.
	Xiphinema elongatum
	Xiphinema attodorum
	Xiphinema sp.
Non-phytoparasites	
Fungivorous	Aphelenchidae
	Ditylenchus spp.
Bacterivorous	All types
Predators	All types

[1] Taxa taken into account in the PCA: *Aorolaimus* spp., *Aphasmatylenchus variabilis*, *Criconemella* spp., *Gracilacus parvula*, *Helicotylenchus dihystera*, *Hemicycliophora* spp., *Heterodera* sp., *Hoplolaimus pararobustus*, *Longidorus* spp., *Paratrichodorus* sp., *Paratylenchus* spp., *Pratylenchus pseudopratensis*, *Scutellonema cavenessi*, *Senegalonema sorghi*, *Trichotylenchus* spp., *Triversus annulatus*, *Tylenchorhynchus avaricus*, *Tylenchorhynchus germani*, *Tylenchorhynchus gladiolatus*, *Tylenchorhynchus sulcatus*, *Tylenchorhynchus ventralis*, *Tylenchorhynchus* spp., *Xiphinema* spp., Aphelenchidae, *Ditylenchus* spp.

The specific composition of the nematode communities presented strong overall structures shown by the first factor of the Moran analysis (Figure 2a). Three geographic areas were identified. One region located in the North (localities 1 to 25) showed a species composition close to that observed in the South-East region (localities 58 to 69). The third was situated in the centre of the country (localities 26 to 57) (Figure 2b). The nematode community from the North included numerous *Tylenchorhynchus ventralis*, *T. sulcatus* and *T. germanii* and no *T. avaricus* compared with the two other areas (Figure 2c). *Tylenchorhynchus gladiolatus*, *S. cavenessi*, *Helicotylenchus dihystera* and *T. avaricus* were relatively abundant in the communities of the central region. *Pratylenchus pseudopratensis* populations were extremely low in the South-East region (Table 3).

The Mantel test was significant for the nematological indices ($r = 0.12$; $P = 0.007$). The first factor of the Moran analysis of this table (trace = 1.44) described strong structures (Figure 2d). When projected on the sampling map, the first factorial values described three areas. The central region, with mostly positive factorial values, is opposed by the north and the eastern regions with negative factorial values (Figure 2e). The richness and the abundance of nematodes were lower in the North (Figure 2f). The two other areas had similar species richness (Table 4). In the central region, all ecological indices were higher.

Soil type

The species composition of the major plant-parasitic nematodes differed from one soil to another. The inertia of the between-soil analysis (21.2% of the species composition data inertia; permutation test: $P < 0.001$) was mainly expressed on the first factor (54.5%) (Figure 3a). This factor distinguished two groups, one group comprising the halomorphic, mineral and isohumic soils, including isohumic with ferruginous tendencies and a second group gathering the less-evolved, ferruginous, ferralitic and hydromorphic soils (Figure 3b). The nematode communities of the first group of soils were characterized by large populations of *T. ventralis* (except in the isohumic and mineral soils), low populations of *S. cavenessi* (especially in the halomorphic soils) and of *H. dihystera* (except for the mineral soils) and by the absence of *T. gladiolatus* and *T. avaricus* (Figure 3c, Table 4). The communities of the second soil group showed inverse characteristics: large populations of *S. cavenessi*, *T. gladiolatus* and *H. dihystera* and low populations of *T. ventralis*.

Large populations of *T. sulcatus* in the isohumic soils, including those with a ferruginous tendency determined the second factor (16.5% of the variability). *Xiphinema* spp. and *P. pseudopratensis* were absent from these latter soils (Table 4, Figure 3). These two taxa were abundant in the mineral soils and vertisols.

Environmental variables

The variability explained in the specific composition of the plant-parasitic nematode communities by the environmental variables was 14.5% of the total (Figure 4). Variable effect on the nematode communities was significant (permutation test: $P < 0.001$). The first two factors of the PCAIV represented 42.1 and 38.7% of the inertia explained by the environmental variables (Figure 4a). The first canonical factor was negatively correlated with the human population density (Figure 4c). The second factor was negatively correlated with the three other

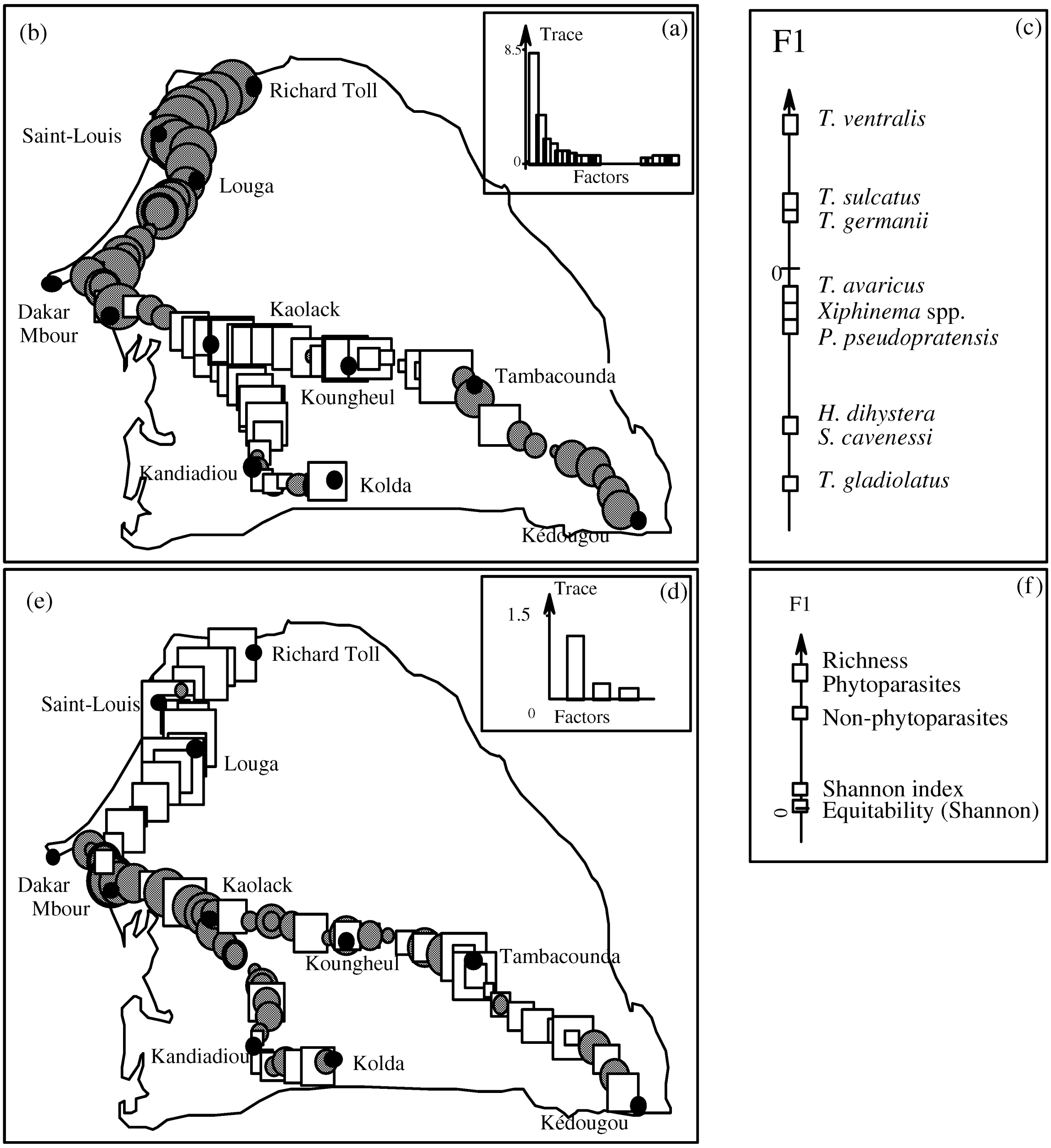

Figure 2. Moran analysis of the composition of the major plant-parasitic nematode communities and of the ecological indices (Phytoparasites, Non-phytoparasites: log of number of plant-parasitic or non-plant-parasitic nematodes). (a) and (d) Eigenvalues; (b) and (e) first factorial co-ordinates of the samples in the Moran analysis (squares represent values below average, whereas circles represent values above average. Symbol size increases as the distance from the average increases). (c) and (f) Distribution of the taxa on the first factor.

environmental variables, carbon content, C/N ratio and rainfall (Figure 4f). On the first axis, this analysis pointed out a parallel increase of the abundance of *P. pseudopratensis*, *S. cavenessi*, *T. ventralis*, *T. germanii* and the human population density (Figure 4d, Table 5). The second factor described a positive relation between *T. gladiolatus* or *S. cavenessi* and the human population density. Conversely, the relationship of these two species with the carbon content was negative (Table 5). This relationship appeared in the wetter, southern part of the country.

The environmental variables (carbon content, C/N ratio, rainfall and human population density) have a significant effect (Monte Carlo test: P = 0.025) on the indices describing the nematode communities. They explained 10.4% of the variability of the table gathering the nematological indices. Most of this variability (79%) was described by the first canonical factor of the PCAIV (Figure 5a). This factor highlighted a West–East gradient (Figure 5c). From East to West, the richness, the abundance of the two groups of nematodes increased in relation

Table 3. Comparison of the abundance (number in 250 cm^3 of soil) of the most abundant phytoparasitic species and the group of free-living nematodes contributing to the axes of the Moran analysis performed on the species composition of the nematode communities, according to the geographic areas identified by the analysis. (Within a column, numbers followed by the same letter are not statistically different, ANOVA performed on numbers transformed to log(x+1), $P < 0.05$.)

Species	North area	Central area	South-East area
H. dihystera	108a	244c	140b
P. pseudopratensis	90ab	65b	7a
S. cavenessi	235b	503c	46a
T. avaricus	0a	17b	15b
T. germani	21b	0.5a	0a
T. gladiolatus	11a	257b	177a
T. sulcatus	8b	3a	0.3a
T. ventralis	130b	2a	16a
Free-living nematodes	1749a	5088b	2521b

Table 4. Comparison of the nematological index averages with positive first factorial values after Moran analysis. (Within a column, numbers followed by the same letter are not statistically different, ANOVA, $P < 0.05$.)

Geographical zones	Richness	Shannon index	Total number of phytoparasites per 250 cm^3 of soil	Total number of non-phytoparasites per 250 cm^3 of soil
North	3.5a	1.17a	315a	1749a
Centre	5.6b	1.56b	1227b	5088b
South-East	4.8b	1.45ab	695ab	2521ab
Overall	5.0	1.45	923	3837

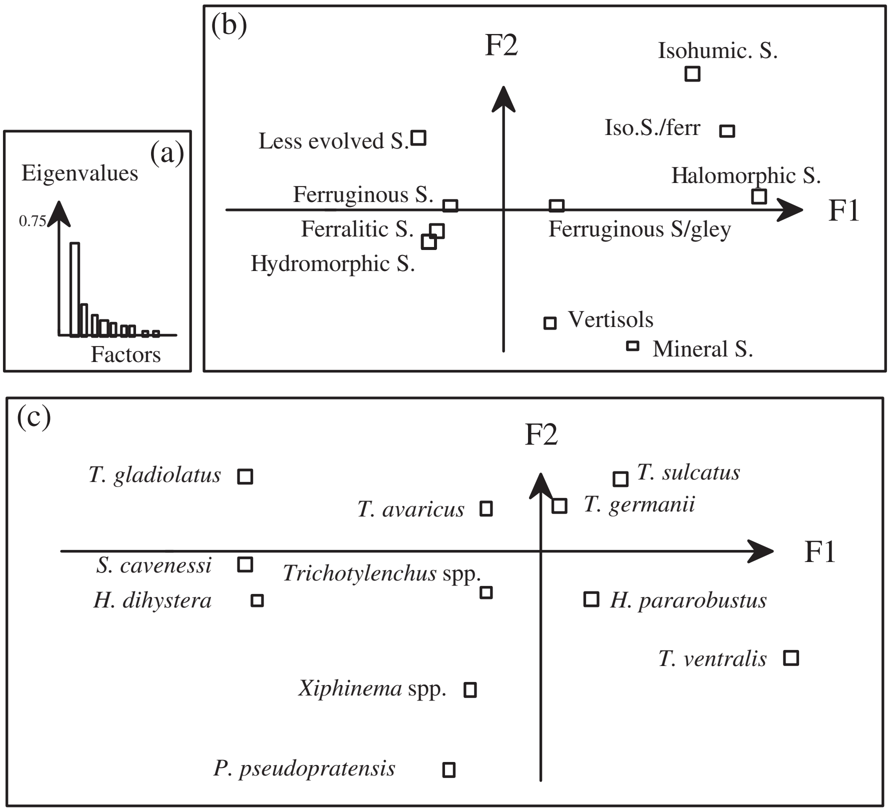

Figure 3. Between-soil type PCA of the composition of nematode communities. (a) Eigenvalues, (b) distribution of the different soil types in the first factorial map, (c) distribution of the taxa on the first factorial map.

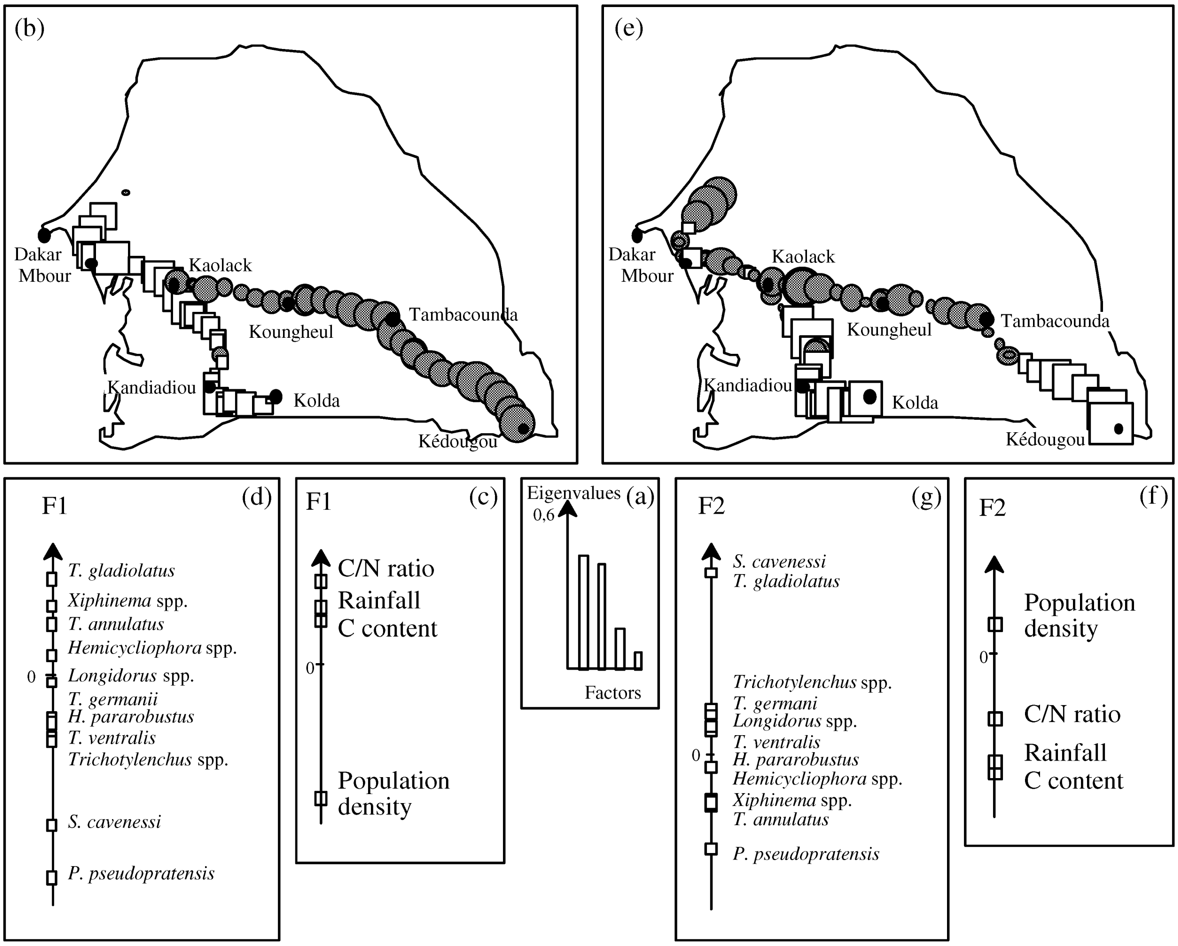

Figure 4. PCA of the composition of the phytoparasitic nematode communities made under the constraint of the four environmental variables, carbon content, C/N ratio; rainfall and demographic level. (a) Eigenvalues; (b) first factor canonical coordinates of the soil samples projected on the map of Senegal; (c) distribution of the canonical correlation coefficient on the first factor; (d) distribution of the nematode taxa contributing to the first canonical axes; (e) canonical coordinates of the soil samples on the second canonical factor; (f) distribution of the canonical correlation coefficient of the environmental variables on the second factor; (g) distribution of the nematode taxa contributing to the second canonical axes. (No soil analysis in the first 21 samples.) Symbols on maps as in Figure 2.

Table 5. Comparison of the abundance (number in 250 cm^3 of soil) of the most important phytoparasitic nematode species contributing to the axes of the inter-soil analysis, in the different soil types. (Within a row, numbers followed by the same letter are not statistically different, ANOVA performed on numbers transformed to log(x+1), $P < 0.05$.) Soil classes: 1 = mineral soils, 2 = less-evolved soils, 3 = vertisols, 4 = isohumic soils, 5 = isohumic soils with ferruginous tendency, 6 = ferruginous soils, 7 = ferralitic soils with pseudo-gley, 8 = ferralitic soils, 9 = halomorphic soils, 10 = hydromorphic soils.

	Soil type									
	1	2	3	4	5	6	7	8	9	10
H. dihystera	90 abc	284 c	156 bc	2 a	4 a	212 c	60 c	194 c	15 ab	109 c
P. pseudopratensis	392 bc	9 a	89 c	0 a	0 a	53 ab	0 a	81 ab	27 ab	85 c
S. cavenessi	193 abc	205 cd	212 bcd	12 ab	57 abc	462 d	59 a-d	466 d	2 a	406 bcd
T. avaricus	0 a	26 b	0 a	0 a	0 a	4 a	9 ab	93 b	0 a	0 a
T. gladiolatus	0 a	418 b	19 a	0 a	0 a	202 b	0 a	50 a	0 a	88 b
T. sulcatus	0 a	13 a	6 a	13 b	16 b	3 a	0 a	0 a	0 a	0 a
T. ventralis	342 c	3 a	26 ab	0 a	73 bc	17 a	16 a	0 a	40 c	0 a
Xiphinema spp.	37 c	42 bc	22 c	0 a	0 a	18 bc	64 c	19 bc	1 ab	17 bc
Phytoparasites (All genera)	1132 c	1069 c	752 c	57 a	179 ab	1079 c	281 bc	1012 c	626 bc	987 c

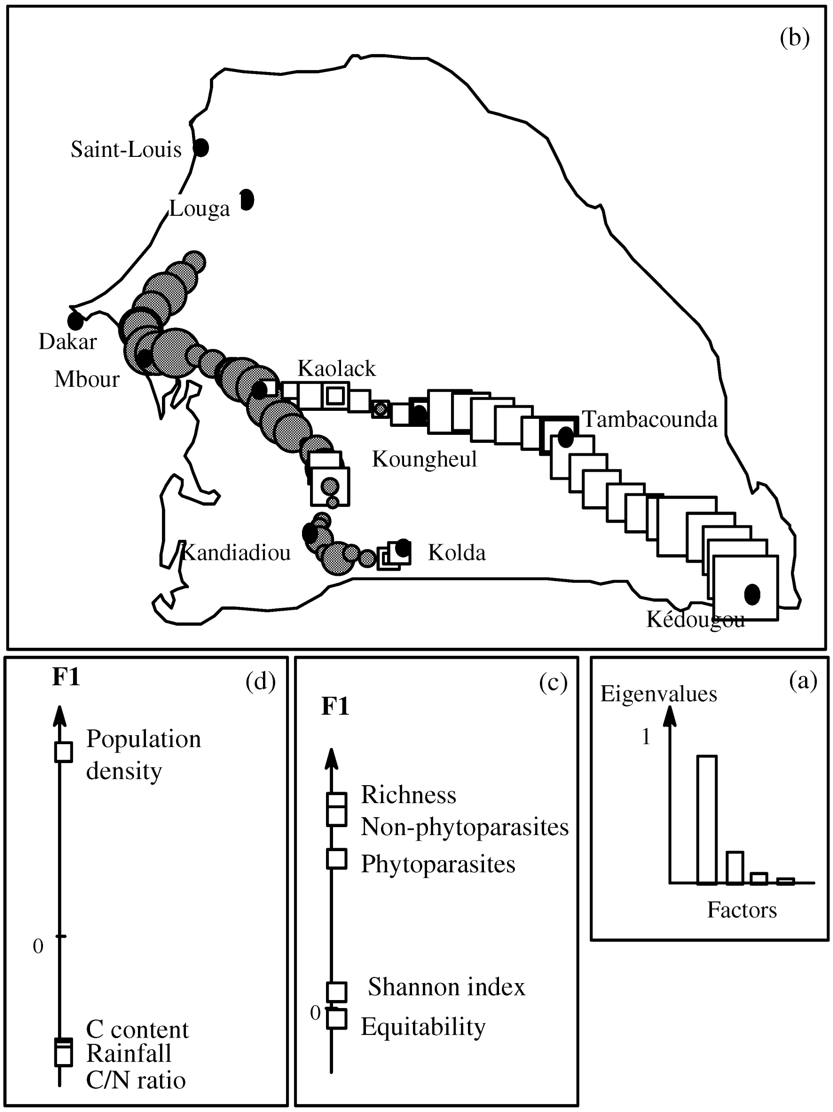

Figure 5. PCA of the nematological indices made under the constraint of the four environmental variables, carbon content, C/N ratio, rainfall and demographic level. (a) Eigenvalues; (b) first factor canonical coordinates of the soil samples projected on the map of Senegal; (c) distribution of the canonical correlation coefficient on the first factor; (d) distribution of the nematological indexes contributing to the first canonical axes. (No soil analysis in the first 21 samples.) Symbols on map as in Figure 2.

with demographic pressure (Figure 5 b, c and d). The nematode abundance decreased with the increase of rainfall and organic matter in the soil. This decrease is significant for the plant-parasitic nematodes (Table 6).

DISCUSSION

Because of their feeding strategy, phytoparasitic nematodes are directly dependent on the vegetation (Sohlenius *et al.* 1986). Paradoxically, in this study, nematode communities were not significantly different between millet fields and *Guiera* or *Combretum* fallow at both local and national scales. Two hypotheses might explain this situation. First, most of the species recorded were polyphagous ectoparasitic species with less specific host–parasite relationships than endoparasites (Baujard *et al.* 1995, de Goede 1993, Freckman & Caswell 1985, Yeates *et al.* 1993). Secondly, and more likely, *Guiera* and *Combretum* fallows were too young and too frequently cultivated (located near the fields) for significant differences to develop between the cultivated areas. A previous study made in the central region (Thysse Kaymor) showed that 8–10 y of fallow were necessary to induce a change in the species composition of the nematode community (Pate *et al.* 2000, Thioulouse *et al.* 1998). Moreover, the organic matter status, estimated by the C/N ratio, did not show any variation between the fields and the fallow lands. At the national scale, abundance, diversity and spe-

Table 6. Correlation coefficients calculated between the environmental variables and the abundance of nematological taxa or ecological indices contributing to the canonical axes of the PCAIV, together with the results of the Fisher r-in-z tests (* Significant test, $P < 0.05$).

	Environmental variables					
	C content	C/N ratio	Rainfall	Demography	Longitude (West–East)	Latitude (South–North)
Hemicycliophora spp.	+ 0.33 *	+ 0.33 *	+ 0.40 *	– 0.27 *	+ 0.27 *	– 0.35 *
Longidorus spp.	– 0.25 *	– 0.28 *	– 0.31 *	+ 0.13	– 0.21	+ 0.37 *
P. pseudopratensis	– 0.02	– 0.14	+ 0.05	+ 0.35 *	– 0.30 *	– 0.06
S. cavenessi	– 0.43 *	– 0.44 *	– 0.44 *	+ 0.39 *	– 0.43 *	+ 0.34 *
T. avaricus	+ 0.35 *	+ 0.34 *	+ 0.37 *	– 0.36 *	+ 0.45 *	– 0.30 *
T. germanii	– 0.16	– 0.19	– 0.33 *	+ 0.36 *	– 0.36 *	+ 0.38 *
T. gladiolatus	– 0.26 *	+ 0.01	– 0.11	– 0.13	+ 0.08	+ 0.05
T. ventralis	– 0.005	– 0.13	– 0.28 *	+ 0.27 *	– 0.29 *	+ 0.43 *
Phytoparasites	– 0.422 *	– 0.286 *	– 0.287 *	+ 0.261 *	– 0.290 *	+ 0.244 *
Free-living nematodes	– 0.161	– 0.226 *	– 0.201	+ 0.483 *	– 0.443 *	+ 0.049
Richness	– 0.080	– 0.114	– 0.134	+ 0.232 *	– 0.180	+ 0.190

cies composition of the nematode communities in Senegal appeared less sensitive to the vegetation than to the type of soil where the biological cycle of the ectoparasitic nematode species takes place.

Soil organic matter had a negative impact on the plant-parasitic nematodes. This could be explained if organic matter favours the development of a network of biotic interactions that, in some way, limits the abundance of the phytophagous nematodes (Freckman & Caswell 1985). Conversely, bacterivorous nematodes are usually indirectly related to the soil organic matter status as they feed on the microorganisms, which are the main agents decomposing organic matter (Bachelier 1978, Freckman 1988, Freckman & Caswell 1985). The abundance of bacterivores is known to be correlated with organic matter decomposition and indirectly to the amount of soil nitrogen resource (de Goede 1993, Niblack 1989, Sohlenius *et al.* 1986). However, in this study, the number of non-plant-parasitic nematodes did not show any relationship with the level of soil organic matter as estimated through the carbon content. But the relationship between low abundance of free-living nematodes and high C/N ratios suggests that high carbon levels, represented by undecomposed organic matter (root fragments), may indicate a low level of activity of microbial mineralization (Yeates *et al.* 1993). A low level of bacterial prey would explain smaller populations of bacterivorous nematodes found.

In this study, abundance of free-living nematodes varied with the vegetation. These nematodes were lower in the cultivated soil than in the *Combretum* fallows. These differences were in agreement with the lowest carbon or nitrogen levels being observed in the fields compared with the fallows. The low level of organic matter in the *Guiera* fallows could result from intensive human use of this fallow, which favoured the development of this plant (Fournier *et al.* 2001).

These paradoxical relationships between plant-parasitic or free-living nematode abundance and food resources could indicate the occurrence of strong interactions and more complex mechanisms than the simple trophic relationships in the establishment of the nematode communities (Francl 1993, Wallace *et al.* 1993).

At a national scale, soil type, organic-matter status, demographic pressure and climate influenced the species composition of the nematode communities. As a result, the communities did not follow a continuous gradient, but showed an aggregated distribution. The nematode communities located in the North were clearly different from those in the centre, but showed similarity with the communities located in the South despite tremendous differences in rainfall. The nematode communities of the North area had fewer individuals and were less diverse. They were characterized by three species, *T. ventralis*, *T. sulcatus* and *T. germanii*, which are presumably well adapted to tolerate the limited food resources (poor plant development) of this scarce and erratic rainfall area (100–200 mm y^{-1}). Moreover, the isohumic and halomorphic soils provide a poor medium for the plant-parasitic nematodes. The former soil hosted low populations of plant-parasitic nematodes except *T. sulcatus* and the latter hosted low-diversity communities dominated by *T. ventralis*.

In the central region but also in the vertisols, diversity as well as size of the nematode communities were higher than in the North. The rainfall conditions were more suitable for plant growth. More resource availability could explain the presence of more numerous populations and plant-parasitic species such as *P. pseudopratensis*, *S. cavenessi*, *T. gladiolatus*, *H. dihystera* or *T. avaricus*. Two species, *P. pseudopratensis* and *S. cavernessi*, have a tendency to occupy the northern part of this area, whereas *H. dihystera* and *T. avaricus* characterized the southern part.

The nematode communities of the less-developed ferruginous, ferralitic and hydromorphic soils of this central region were dominated by abundant populations of *S. cavenessi*, *T. gladiolatus* and *H. dihystera*, but by low populations of *T. ventralis*. The highest human population density also occurred in this region, leading to a paradoxical relationship between demographic pressure on the environment and number of plant-parasitic nematode species. In this study, increasing rainfall and decreasing human pressure from West to East was surprisingly not associated with an increase in nematode diversity, but the reverse. Two hypotheses can be drawn to explain this. The sampling limited to field and recently abandoned fields did not reflect the diversity and the state of the ecosystems of the areas. The natural vegetation is much more developed in the sparsely populated eastern regions compared with the densely inhabited region around the capital. However, the millet fields hosted many species in common, such as the most pathogenic species, *S. cavenessi* and *T. gladiolatus*, which were mostly found in this region of intensive small-scale agricultural activity (Fortuner 1975, Fortuner & Merny 1973). However, human activity around towns could contribute to an increase in the heterogeneity of the environment through crop rotation, crop diversity and field history. Fields around towns are usually occupied by many different crops, mainly vegetables or ornamental plants, which are rotated or intercropped with food crops, each of which leaves its own nematological signature, leading to an increase in species richness.

In the South, despite high rainfall and well-developed vegetation, nematode communities were of average size as regards number of individuals. Human pressure, as measured by population size, was low and ecosystems were less disturbed. This stability could lead to a low availability of the resources because of their immobilization (C/N ratio, wood, humification). In turn, this could explain the overall relatively low nematode abundance and the occurrence of particular species like *T. annulatus*, *Hemicycliophora* spp. and *Xiphinema* spp., which usually occur in low numbers but which were relatively abundant. They may be indicators of environment stability. Conversely, nematode communities of the gleyed ferruginous soils showed a reduced number of species. This situation did not correspond to the nematological characteristics of the area. This result highlighted the impact of hydromorphic soils on the nematode communities independent of their geographical location.

CONCLUSION

This study revealed that if a limited range of plants is considered, as in this study, the main factor, which determined the nematode community structure, was the soil type. From an ecological point of view, a reduction in the length of fallow will lead to a uniform plant-parasitic nematode community in rural areas, in relation to a decrease in inter-cropping plant diversity. A reduced diversity of plant-parasitic nematode communities has been shown to be associated with increasing pathogenicity towards crops (Cadet *et al.* 2000). Plant-parasitic nematode community studies can reveal that highly human disturbed areas can keep a high nematode diversity potential, in terms of species richness, comparable with that observed in undisturbed areas, but concerning different species of nematodes.

ACKNOWLEDGEMENTS

Authors thank the Department of Animal Biology of the University of Dakar (Senegal), as well as the Plant Protection Research Institute of Pretoria (South Africa) for nematode identifications, and Dr V.W. Spaull for his advice. This work was supported by the Economic Union project: ‘Fallow land decrease, biodiversity and sustainable development in Central (Cameroon) and in West Africa (Senegal, Mali)’ (nº TS3-CT93-0220, DG12HSMU) and the ‘Action Incitative Interinstitutionnelle’: Tropical soil biofunctioning and sustainable management of land.

REFERENCES

BACHELIER, G. 1978. *La faune des sols. Son écologie et son action.* ORSTOM. Paris. 391 pp.

BAUJARD, P., BOUR, E. & MARTINY, B. 1995. Incidence des nématodes phytoparasites sur la culture du sorgho dans la zone sahélienne du Sénégal, Afrique de l’Ouest. *Afro-Asian Journal of Nematology* 5:1–10.

BONGERS, T. 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83:14–19.

CADET, P. & FLORET, C. 1995. An initial study of fallow periods on the nematode community in the Soudanese-Sahelian zone of Senegal. *Acta Oecologica* 16:77–88.

CADET, P. & VAN DEN BERG, E. 1992. Les nématodes phytoparasites de la montagne Pelée à la Martinique. *Compte-Rendus de la Société Française de Biogéographie* 68: 89–104.

CADET, P., BOIS, J. F., PATE, E., N’DIAYE-FAYE, N. & FLORET, C. 2000. Diversité des nématodes parasites et durabilité du système culture-jachère au Sénégal. Pp. 268–276 in Floret, C. & Pontanier, R. (eds). *La jachère en Afrique tropicale. Rôles, aménagements, alternatives*. John Libbey Eurotext, Paris.

DE GOEDE, R. 1993. *Terrestrial nematodes in a changing environment*. Department of Nematology, Agricultural University, Wageningen. 137 pp.

DE GOEDE, R. G. M. & BONGERS, T. 1994. Nematode community structure in relation to soil and vegetation characteristics. *Applied Soil Ecology* 1:29–44.

DOLÉDEC, S. & CHESSEL, D. 1989. Rythmes saisonniers et composantes stationnelles en milieu aquatique. II. Prise en compte et élimination d’effets dans un tableau faunistique. *Acta Œcologica, Œcologia Generalis* 10:207–232.

FORTUNER, R. 1975. Les nématodes parasites des racines associés au riz au Sénégal (Haute-Casamance et régions Centre et Nord) et en Mauritanie. *Cahier ORSTOM, Série Biologie* 10:147–159.

FORTUNER, R. & MERNY, G. 1973. Les nématodes phytoparasites des racines associés au riz en Basse–Casamance (Sénégal) et en Gambie. *Cahier ORSTOM, série Biologie* 21:3–20.

FOURNIER, A., FLORET, C. & GNAHOUA, G. 2001. Végétation des jachères et succession post-culturale en Afrique tropicale. Pp. 123–168 in Floret, C. & Pontanier, R. (eds). *La jachère en Afrique tropicale* (Volume 2). John Libbey Eurotext, Paris.

FRANCL, L. J. 1993. Multivariate analysis of selected edaphic factors and their relationship to *Heterodera glycines* population density. *Journal of Nematology* 25:270–276.

FRECKMAN, D. W. 1988. Bacterivorous nematodes and organic-matter decomposition. *Agriculture, Ecosystems and Environment* 24:195–217.

FRECKMAN, D. W. & CASWELL, E. P. 1985. The ecology of nematodes in agroecosystems. *Annual Review of Phytopathology* 23:275–296.

FRECKMAN, D. W. & ETTEMA, H. C. 1993. Assessing nematode communities in agroecosystems of varying human intervention. *Agriculture, Ecosystems and Environment* 45:239–261.

FRECKMAN, D. W. & MANKAU, R. 1977. Distribution and trophic structure of nematodes in desert soils. *Ecological Bulletin* 25:511–514.

MAGGENTI, A. R., LUC, M., RASKI, D. J., FORTUNER, R. & GERAERT, E. 1988. A reappraisal of *Tylenchina* (Nemata). 11. List of generic and suprageneric taxa, with their junior synonyms. *Revue de Nématologie* 11:177–188.

MANLY, B. F. 1994. *Multivariate statistical methods. A primer*. Chapman & Hall, London. 215 pp.

MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209–220.

NEHER, D. A. & CAMPBELL, C. L. 1994. Nematode communities and microbial biomass in soils with annual and perennial crops. *Applied Soil Ecology* 1:17–28.

NETSCHER, C. & SIKORA, R. A. 1990. Nematodes parasites of vegetables. Pp. 237–283 in Luc, M., Sikora, R. A. & Bridge, J. (eds). *Plant parasitic nematodes in subtropical and tropical agriculture*. CAB International, Wallingford.

NIBLACK, T. L. 1989. Applications of nematode community structure research to agricultural production and habitat disturbance. *Journal of Nematology* 21:437–443.

OBADIA, J. 1978. L'analyse en composantes explicatives. *Revue de Statistique Appliquée* 24:5–28.

PATE, E. 1997. *Analyse spatio-temporelle des peuplements de nématodes du sol dans les systèmes de culture à jachères, au Sénégal*. Thèse de doctorat, Université de Lyon I. 210 pp.

PATE, E., NDIAYE-FAYE, N., THIOULOUSE, J., VILLENAVE, C., BONGERS, T., CADET, P. & DEBOUZIE, D. 2000. Successional trend in characteristics of soil nematode communities in cropped and fallow lands in Senegal (Sonkorong). *Applied Soil Ecology* 14:5–15.

SEINHORST, J. W. 1962. Modifications of the elutriation method for extracting nematodes from soil. *Nematologica* 8:117–128.

SHANNON, C. E. & WEAVER, W. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbana. 117 pp.

SOHLENIUS, B. 1980. Abundance, biomass and contribution to energy flow by soil nematodes in terrestrial ecosystems. *Oikos* 34:186–194.

SOHLENIUS, B., BOSTRÖM, S. & SANDOR, A. 1986. Long-term dynamics of nematode communities in arable soil under four cropping systems. *Journal of Applied Ecology* 25:131–144.

TER BRAAK, C. J. F. 1986. Canonical correspondance analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 69:69–77.

THIOULOUSE, J., CHESSEL, D. & CHAMPELY, S. 1995. Multivariate analysis of spatial patterns: a unified approach to local and global structures. *Environmental and Ecological Statistics* 2:1–14.

THIOULOUSE, J., CHESSEL, D., DOLÉDEC, S. & OLIVIER, J. M. 1997. ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing* 7:75–83.

THIOULOUSE, J., PATE, E., N'DIAYE, N. & CADET, P. 1998. Influence de la jachère sur les peuplements de nématodes phyto-parasites au Sénégal: protocoles de collecte et d'analyses des données et premiers résultats. Pp. 129–139 in Laloe, F. & Perrier, X. (eds). *De l'observation à l'analyse, implication de la biométrie dans les pays en développement*. Société Française de Biométrie, France.

VILLENAVE, C., BONGERS, T., EKSCHMITT, K., DJIGAL, D. & CHOTTE, J-L. 2001. Cultivation of soils after different lengths of fallow period: changes in nematodes communities. *Applied Soil Ecology* 495:1–10.

WALLACE, M. K., RUST, R. H., HAWKINS, D. M. & MACDONALD, D. H. 1993. Correlation of edaphic factors with plant-parasitic nematode population densities in a forage field. *Journal of Nematology* 25:642–653.

WRIGHT, D. H. & COLEMAN, D. C. 1993. Patterns of survival and extinction of nematodes in isolated soils. *Oikos* 67:563–572.

YEATES, G. W. & BONGERS, T. 1999. Nematode diversity in agroecosystems. *Agriculture, Ecosystems and Environment* 74:113–135.

YEATES, G. W., BONGERS, T., DE GOEDE, R. G. M., FRECKMAN, D. W. & GEORGIEVA, S. S. 1993. Feeding habits in soil nematode families and genera. An outline for soil ecologists. *Journal of Nematology* 25:315–331.