

Successional trends in the characteristics of soil nematode communities in cropped and fallow lands in Senegal (Sonkorong)

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Abstract

Soil nematode communities in the 0–15 cm soil layer are used as indicators for describing the processes of fallow succession in the semi-arid zone of West Africa (Senegal). Abundance of plant feeding nematodes, non-plant feeding nematodes, plant parasite index (PPI), species richness and Shannon evenness of plant parasitic nematodes were measured at five stages of succession: fields, early (1–3 years), intermediate (8–10 years), old (18–20 years) fallows, and forest stage. These nematological indexes were analyzed simultaneously by multivariate analysis to show the indicative properties of nematode communities. Overall, changes in abundance of nematode groups, PPI and diversity, show continuous trends from early fallow to mature stages of the succession; these trends parallel theoretical trends in secondary succession. In addition, soil nematode parameters were meaningful and expressed interactions of various uncontrolled factors with successional processes, such as environmental conditions or cropping history. During the 3 years of the survey, the structure of nematode communities, described by index analysis, showed little temporal change and supported the use of nematodes as stable indicators. ©2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Agriculture in the semi-arid zone of West Africa is mostly based on small-scale farming with low inputs and generally depends on natural ecosystem productivity. In these agro-ecosystems, fallow is the principal means for restoring soil fertility after cultivation and maintaining agricultural yields (Kleinman et al., 1995). In the absence of disturbances such as clearing, tillage, cultivation and harvesting, the regeneration of natural and diverse vegetation during fallow (Corlett, 1995; Donfack et al., 1995) leads to litter pro-

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duction (Szott et al., 1994), organic matter production and accumulation (Masse et al., 1998), development of faunal communities (Auerswald et al., 1996) and microfloral activity (Maggi et al., 1990).

Because of human populations growth, restoration of soil fertility is jeopardized by the increase in cultivated areas at the expense of fallow rotations. This leads to the impoverishment of cultivated soils and the deterioration of soudano-sahelian ecosystems (Pieri, 1989; Szott et al., 1994). Environmental concerns, such as maintaining a balanced environment, are increasing at the same time as concerns about providing for the needs of a rapidly growing human population and requirements to increase agricultural outputs (Swift and Woome, 1993; Izac and Swift, 1994). Reconciliation of these concerns constitutes one of the greatest challenges of agronomic research in the tropics. It requires understanding ecosystem functioning to manage environmental resources and to increase sustainability of agricultural production (Matson et al., 1997).

In this situation, soil fauna can provide useful indicators of ecosystem condition because they have strong relationships with fundamental ecosystem processes such as decomposition and nutrient cycling, and interactions with the microbial community, plant growth and pedogenesis (Parmelee, 1994; Auerswald et al., 1996; Reddy et al., 1996; Andersen and Sparling, 1997). Among soil fauna, nematodes possess attributes potentially making them useful as sensitive indicators for understanding ecosystem functioning (Bernard, 1992). Soil nematodes are abundant in most terrestrial ecosystems, they show species and trophic diversity (Yeates et al., 1993) and their faunas are diverse. Recent developments in soil nematode community ecology have led to recognition that nematodes may respond in predictable ways to ecosystem changes. Nematodes have been found to reflect ecosystem parameters such as soil quality (Neher and Campbell, 1994), ecosystem development (Bongers, 1990), characteristics of terrestrial habitats (Johnson et al., 1974; De Goede and Bongers, 1994), changes in land use (Freckman and Ettema, 1993; Yeates and Bird, 1994) and the bio-availability of pollutants (Korthals et al., 1996).

In this study, nematological data, collected as part of a larger program, were analyzed to demonstrate the utility of soil nematodes as functional indicators of

ecosystems. Abundance of plant feeding nematodes, non-plant feeding nematodes, plant parasite index (PPI), species richness and Shannon evenness of plant parasitic nematodes were measured at five stages of fallow succession: fields, fallows of short, intermediate and long duration, and forest stage. We wished to confirm that these nematological indices changed between fallow stages and to determine whether their trends, in the course of fallow, agree with theories of ecosystem development during secondary succession. Particularly, the abundance of plant feeding and non-plant feeding nematodes should change with changes in their respective trophic resources during the regeneration of natural vegetation and reconstitution of soil that occurs during the fallow period. As in other data sets, and resulting from the establishment of more natural conditions with fallow practice, we predicted PPI (Bongers, 1990) would decrease from agricultural lands to forests. According to theories on ecosystem development, we predicted that nematode communities would become more diverse during the succession and species richness and Shannon evenness would follow this successional trend.

2. Materials and methods

2.1. Plots and sampling method

Sonkorong is a typical site of Senegalese groundnut cultivation (13°45'N, 15°40'W). The tropical ferruginous soils present a sandy texture with sand content about 62%, 28% silt and 10% clay. These soils have a low organic matter content (C: 5.7 mg g⁻¹ soil; N: 0.5 mg g⁻¹ soil) with phosphorus content reported as 68.9 mg g⁻¹ soil and pH 5.8. The soudano-sahelian climate is characterized by rains (600–700 mm per year) spread over 4 months, from July to October. Cultivation occurs during the rainy season when nematodes are active. No rain falls during the dry season. Thus, sampling intensity varied seasonally: sampling was about monthly during the rainy season (three dates per year) and restricted to three dates during the dry season (November, March, June). Sampling was undertaken on 17 occasions from March 1994 to November 1996 to account for climatic variability among years.

Table 1
Characteristics of sampling plots of the fallow succession at Sonkorong: cultivated fields, fallows and forest

Fields						Sample series
Field A	Located near Plots 1 and 2					A
Field B	Located near Plot 3					B
Field C	Located near Plot 4					C
Fallows	Size (ha)	Previous years cropped	Last year of cultivation	Age between 1994–1996	Fallow stage (duration)	Transect
Plot 1	1	20 years	1993	1–3 year old	Short fallow	T1
Plot 2	1	4 years	1993	1–3 year old	Short fallow	T2
Plot 3	1	10 years	1986	8–10 year old	Medium fallow	T3 and T4
Plot 4	1	10 years	1976	18–20 year old	Long fallow	T5 and T6
Forest (Plot 5)						T7

Samples were collected as follows:

- Four fallow plots where the ranges given for ages reflect the duration of our sampling (Table 1): Plot 1 had been cropped for about 20 years before being abandoned in 1993; Plot 2 had been abandoned in 1993 after only 4 years cropping; Plots 1 and 2 corresponded to short fallows; Plots 3 and 4 had been cropped for about 10 years and were abandoned respectively 8 and 18 years ago, in 1994. Plots 3 and 4 represented intermediate and long fallow durations, respectively. Two permanent transects were established in each of these three fallow stages (Table 1) and 16 soil samples (250 cm³ soil from 0–15 cm soil depth) were collected at 1.5 m intervals along each transect and on each sampling date; the dominant vegetation in the plots was a bush and degraded savanna with *Guiera senegalensis*, *Combretum glutinosum* and *C. nigricans*. The herbaceous vegetation was dominated by *Pennisetum pedicellatum* and *Tephrosia pedicellata*.
- Plot 5 was a forest site, representing the mature stage of the succession. Sixteen samples were collected along one permanent transect on each sampling date. The woody vegetation was more developed than in fallow plots with *G. senegalensis*, *C. glutinosum* and *Feretia apodanthera*. Dominant herbaceous species were *P. pedicellatum*, *Spermacoce stachydea* and *Tephrosia pedicellata*.
- Three cultivated fields (A, B, C) in each of which, 10 random soil samples were collected. A was located between Plots 1 and 2, Fields B and C

were respectively located near Plots 3 and 4. Typical crops were rotations of groundnuts, millet and sorghum.

2.2. Nematological data

Nematodes were extracted using the elutriation technique (Seinhorst, 1956, 1962) and nematode identification was carried out at 400× magnification. Nematodes were allocated to two trophic categories whose abundances were determined: plant feeders (all species feeding on roots of higher plants) and non-plant feeders, accounting for more than 75% of soil nematodes. Species identification was focused on confirmed parasites of plants, following Freckman and Virginia (1989), which were likely to induce agricultural yield losses (Table 2). The biodiversity of these plant parasitic nematodes was measured for each soil sample by two indexes: species richness S and Shannon evenness E . Index E was preferred to the Shannon index H' because E is independent of the number of species S encountered in the Eq. (1) (Barbault, 1992):

$$E = \frac{H'}{H_{\max}} \quad (1)$$

with $H' = -\sum_{i=1}^S p_i \log_e p_i$ and $H_{\max} = \log_e S$ where p_i is the relative abundance of species i to abundance of confirmed plant parasitic nematodes.

PPI (Bongers, 1990) is an ecosystem parameter based on life history characteristics of plant feeding nematodes coded as c-p values (Table 2).

Table 2

Plant feeding nematodes encountered in fallows and forest plots, relative abundance in relation to this trophic group (%), and the c-p values allocated to them

Plant feeding nematodes	Relative abundance	c-p value
<i>Confirmed plant parasitic nematodes</i>	69.4	
<i>Aphasmatylenchus variabilis</i>	0.13	3
<i>Criconemella curvata</i>	0.7	3
<i>Gracilacus parvula</i>	5.4	2
<i>Helicotylenchus dihystrera</i>	15.2	3
<i>Hemicycliophora belemnis</i>	0.002	3
<i>Longidorus</i> spp.	0.005	5
<i>Pratylenchus pseudopratensis</i>	7.9	3
<i>Rotylenchus</i> spp.	0.009	3
<i>Scutellonema cavenessi</i>	15.9	3
<i>Trichotylenchus falciformis</i>	2.9	3
<i>Triversus annulatus</i>	0.002	3
<i>Tylenchorhynchus avaricus</i>	0.4	3
<i>Tylenchorhynchus gladiolatus</i>	13.0	3
<i>Tylenchorhynchus mashhoodi</i>	7.8	3
<i>Tylenchorhynchus sulcatus</i>	0.0002	3
<i>Tylenchorhynchus ventralis</i>	0.2	3
<i>Xiphinema</i> spp.	0.3	5
<i>Others</i>		
Tylenchidae	30.6	2

Five index values (plant feeder abundance; non-plant feeder abundance; species richness; Shannon evenness of plant parasitic nematodes; PPI) for each of the 1904 soil samples (7 transects \times 16 samples \times 17 sampling dates) constituted the study data.

2.3. Statistics and computing

At first, we analyzed simultaneously by multivariate analysis these nematological parameters as a set of variables characterizing nematode communities. Subsequently, indices were individually tested between successional fallow stages using analysis of variance to determine the significance of multivariate results.

Triadic analysis, a multivariate technique, was used for analyzing this data set because it is well adapted to the statistical study of surveys when the same variables (indices) are measured on the same individuals (sampling spots) at different times (sampling dates) (Escoufier, 1980; Thioulouse and Chessel, 1987). Data were considered as a chronological series corresponding to sampling dates. Analysis focused on the study of nematode community characteristics in fallow

stages, while taking into consideration the temporal changes.

The triadic analysis presents the classic scheme of multi-table analysis, with interstructure, compromise and intrastructure that define three essential stages. The first stage, 'interstructure', corresponds to a global representation and presents an ordination of the sampling dates. This analysis stage permits the calculation of the 'compromise' table that exhibits the best summary properties of the initial tables (sampling dates). Principal Components Analysis (PCA) of this compromise table represents the second stage of the triadic analysis and provides a simultaneous representation of individuals (sampling spots) and variables (indices). The last stage of the triadic analysis, the 'intrastructure', expresses the deviations at each sampling date from the common model of the compromise (Escoufier, 1980; Thioulouse and Chessel, 1987).

The software employed for triadic analysis was ADE-4 (<http://pbil.univ-lyon1.fr/ADE-4/ADE-4F.html>) and the analytical module used was STATIS (option: table averaging). Before triadic analysis, the abundances were transformed to $\ln(x + 1)$ to reduce the aggregative effect of spatial nematode distribution. The triadic analysis was carried out after normalizing the five nematological variables for each sampling date.

The triadic analysis was completed by a between-transect analysis (Dolédec and Chessel, 1989) of the compromise table. This multivariate analysis is based on the linear model of variance analysis and consists of decomposing variability according to variation between treatments of studied factors. Here, the one-way layout model (with seven categories corresponding to transects and 16 observations or sampling spots per transect) allows focussing on the variations in nematode community parameters between successional stages and expression of the fallow age effect on nematodes. Between-transect analysis was computed with the module Projectors of ADE-4 (options: One Categ Var to Orthonormal basis; PCA on instrumental variable).

Analysis of variance was carried out on each index to compare them between transects (StatView 4.02: ANOVA). These multiple comparisons of average values were done on a compromise table calculated according to triadic analysis but from untransformed data to give actual values of the indices. Data from

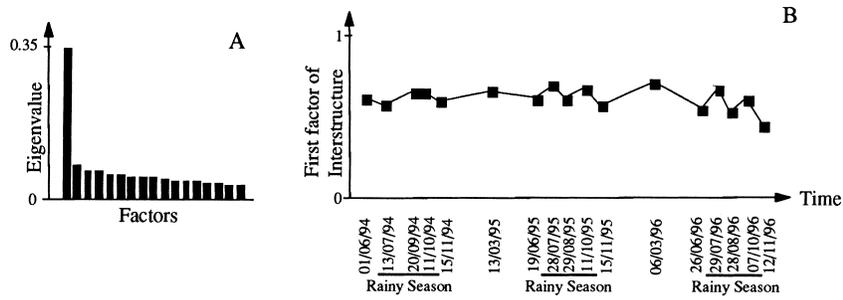


Fig. 1. Results of the interstructure stage of triadic analysis on the 17 tables corresponding to nematode community characteristics (plant feeder abundance, non-plant feeder abundance, species richness, Shannon evenness, and PPI) measured on transects of fallow and forest plots on 17 sampling dates (7 transects × 16 sampling spots × 17 sampling dates=1904 soil samples). Interstructure stage corresponded to an ordination of the data tables corresponding to the 17 sampling dates of the initial multi-table. (A) Graph of relative eigenvalues; (B) First coordinates (F1) of the 17 sampling dates in the interstructure analysis, as a function of time.

cultivated fields were excluded from the triadic analysis and ANOVA because they were not collected at the same sampling points (random sampling) on each sampling date.

3. Results

The interstructure of the triadic analysis showed that temporal variations in nematode communities are mainly projected on the first factor (F1) (Fig. 1A) and that the F1 values of the 17 sampling dates were relatively constant (Fig. 1B). This analysis shows that the structure of the nematode community, described by indices, did not show great change during the 3 years of the survey. Therefore, detailed description of temporal deviations from the common model of the compromise (intrastructure analysis) was not necessary and was omitted from further analyses.

Changes in community characteristics between transects accounted for 48% of the total compromise variability and within-transect variations corresponded to the remaining 52% (Table 3).

Table 3

Inertia decomposition in relation to transects of the compromise table describing nematode communities on the basis of five indices: plant feeder abundance, non-plant feeder abundance, species richness, Shannon evenness, and PPI

Analysis	Total inertia	Relative inertia (%)
Between-transect analysis	2.81	48
Within-transect analysis	3.06	52
Compromise analysis	5.87	100

Between-transect analysis was equivalent to decomposing between-transect variability to factorial axes. This analysis showed 78% of between-transect variability to be projected on the first factor (Fig. 2A). The axis described the trends in characteristics of nematode community during fallow succession, from short fallow with 20 years prior cultivation (Transect 1) to the long fallow (Transect 6) and the forest (Transect 7) (Fig. 2B). The short fallow with only 4 years prior cropping (Transect 2), the fallow of medium duration (Transects 3 and 4) and Transect 5 of the long fallow, all occupied intermediate positions on the axis (Fig. 2B). This ordination of transects, from Transect 1 to Transects 6 and 7 (Fig. 2B), corresponded to variations in index values with overall global increase in the abundance of plant feeding nematodes, non-plant feeding nematodes, species number and evenness (Fig. 2C). However, it corresponded to a decrease of the PPI (Fig. 2C). Soils of recent fallows exhibited low nematode abundance and diversity, but high values for the PPI. In contrast, communities of old fallow and forest soils were characterized by higher abundances and diversity, and lower PPI values.

Results of analysis of variance (Fig. 3) allow specification of significant variation in indices associated with the observed multivariate ordination of transects. With regard to the short fallow with 20 years prior cultivation (Transect 1), the nematode communities were distinguished by low abundance of plant feeding nematodes, specific richness and evenness (Fig. 3). In soils of cultivated fields, recent fallows (Transects 1

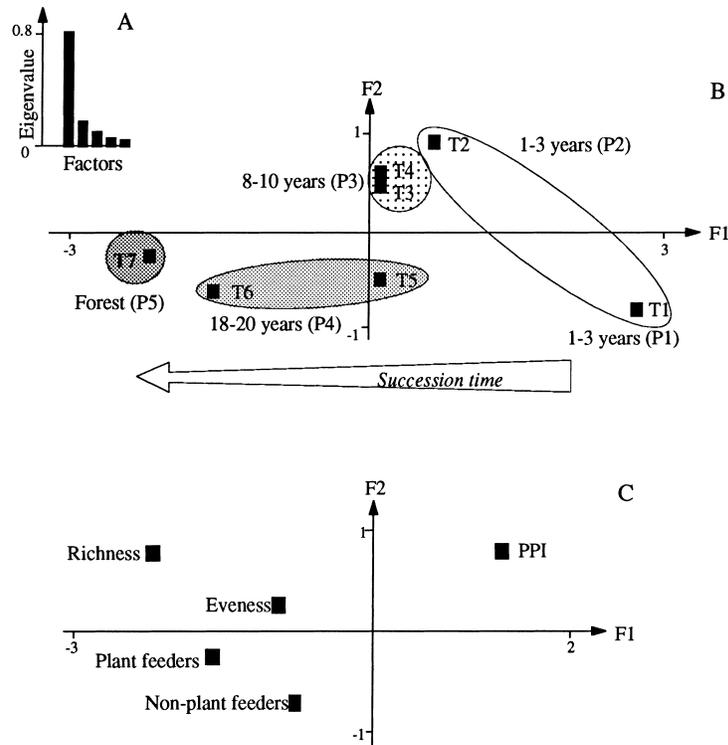


Fig. 2. Results of between-transect analysis on the compromise table of triadic analysis. The compromise table was computed from interstructure stage (Fig. 1) and presented the best summary of nematode characteristics in fallow and forest plots (7 transects \times 16 sampling spots=112 sampling spots) with deletion of temporal dimension. Analysis of compromise table by means of the between-transect analysis focused on the changes in nematode community characteristics between transects. (A) Graph of relative eigenvalues in the between-transect analysis of compromise table; (B) Coordinates of transects (T1–T7) on the first factorial plane F1 \times F2 of the between-transect analysis; (C) Coordinates of the nematological indices on the same plane.

and 2) and fallow of medium age (Transects 3 and 4), abundance of non-plant feeders was low to intermediate and nematode communities of these fallow stages (Transects 1–4) showed high values of PPI, except in Transect 4 where the PPI value was intermediate.

Among the nematode community indices, abundance of plant feeders, specific richness and evenness were larger in short fallow with brief cropping (Transect 2) and in the intermediate fallow stage (Transects 3 and 4) than in the recent fallow with long cropping (Transect 1) (Fig. 3). In relation to the abundance of plant feeding nematodes, non-plant feeding nematodes and specific richness the community of Transect 5 of the old fallow had nematode indices close to those of shorter fallows.

In Transect 6 of the old fallow, and in the forest, nematode communities were distinguished by high abun-

dance of nematodes, whether plant feeding or not, and low PPI values (similar to those in Transect 5 and in cultivated field). Specific richness increased progressively with fallow stage resulting in highest number of species in forest communities. Evenness had intermediate values in the plot of long fallow duration (Transects 5 and 6), but the highest value of evenness was observed in forest soils.

4. Discussion

4.1. Successional progress

Simultaneous analysis of nematological indices has shown that fallow age was the principal factor associated with changes in the nematode community of the

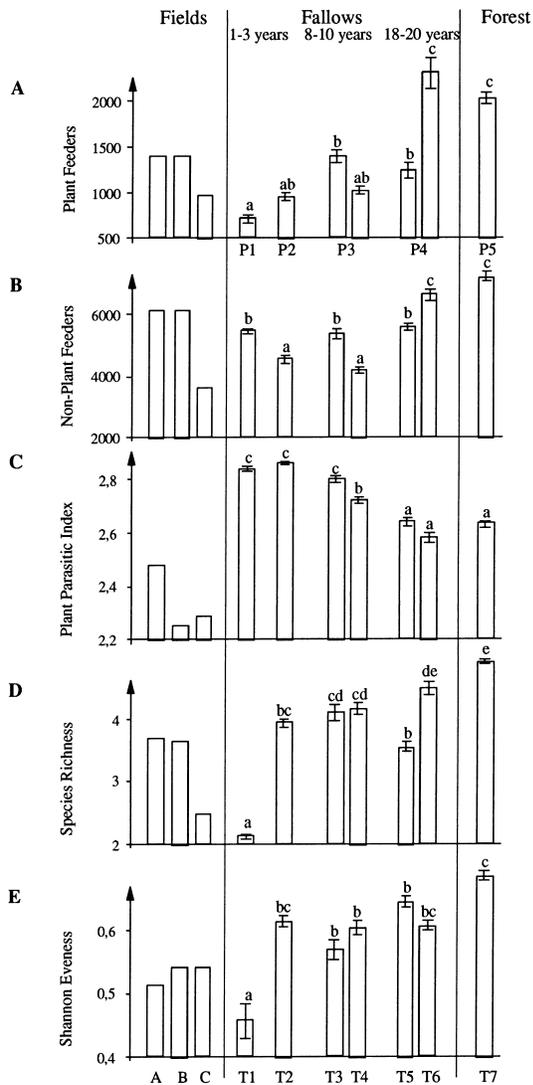


Fig. 3. Characteristics of nematode communities in fields, fallows and forest. Each histogram corresponded to one nematological index: (A) abundance of plant feeding nematodes in 250 cm³ soil; (B) abundance of non-plant feeding nematodes in 250 cm³ soil; (C) plant parasite index; (D) specific richness and (E) Shannon evenness of plant parasitic nematodes. Within a histogram, the bars illustrate for each field and each transect (16 sampling spots) the average of compromise data as computed by triadic analysis (without initial transformations such as logarithmic or normalizing) and the error bars correspond to standard errors. Results of analysis of variance of these compromise data (16 observations — sampling spots; 7 treatments — transects; significance level < 0.05) appear in letter form for each nematological index; within a histogram, bars with the same letter indicate non-significantly different means (Fisher's protected LSD; 16 observations — sampling spots; significance level < 0.05).

sandy ferruginous soils of the studied area. This agrees with the fundamental changes expected to occur as an ecosystem develops (Odum, 1969).

Changes in trophic structure may be related to variations in food supplies and ecosystem processes such as productivity, flow of materials, and decomposition pathways (Freckman and Caswell, 1985; Neher and Campbell, 1994; Wardle et al., 1995). Although increase in number of nematodes during succession has not been demonstrated in most studies, our results confirmed, like those of Háněl (1995) and Chalupsky (1994), increase in abundance of nematodes with increased fallow age.

The greater abundance of plant feeding nematodes in older fallow and forest reflect the regeneration of natural vegetation (Szott et al., 1994; Donfack et al., 1995) and especially the root development during fallow succession (Torquebiau and Kwesiga, 1996). As has been found in other recent work (Hodda et al., 1997; Neher et al., 1998), fallow, especially of long duration, did not appear to be an efficient method of nematode control because abundance of root feeders increased during succession. However, greater emphasis would have to be put on the species composition of the plant parasitic nematode community before making firm conclusions.

In this study, values of PPI decrease with increased fallow age. Fallow is characterized by reduced tillage, low but increasing soil fertility, and an increasingly diverse vegetation. In intensively managed agroecosystems, the PPI decreases with decreasing nutritional level and increasing diversity of the vegetation (Bongers et al., 1997). Under the present conditions, the increase in soil fertility is probably overshadowed by the effects of secondary succession leading to a decrease in PPI. Most of the plant feeders in our samples belonged to the c-p 3 group, and the decrease in PPI mostly resulted in an increase in the (relative) number of nematodes belonging to Tylenchidae family (c-p value of 2). Both *Tylenchorhynchus gladiolatus* and *Helicotylenchus dihystrera* are given in a c-p value of 3. However, Villenave et al. (1997) showed experimentally strong differences in the reproductive strategies of these two species. *H. dihystrera* is characteristic of more natural conditions; *T. gladiolatus* reproduces much faster. Also, van Bezooijen (1979) showed that *Helicotylenchus* disappears from Dutch grasslands if the nitrogen application is increased

from 200 to 400 kg ha⁻¹. It is apparent that c-p values for plant feeding nematodes will need to be reviewed when more evidence has become available.

The observed high abundance of non-plant feeding nematodes in old fallow and forest stages agrees also with theories of succession and the ecological significance of individual trophic groups included in this group. For example, increase in abundance of bacterial and fungal feeding nematodes, that probably dominated numerically the group of non-plant feeding nematodes, indicates growth in numbers of microorganisms (Freckman and Caswell, 1985; Wardle et al., 1995), and increase in soil organic matter (Griffiths et al., 1994) with fallow age (Szott et al., 1994).

Between cultivated soils and fallows of short and medium duration (1–3 and 8–10 years old), there was no great difference in the abundance of plant feeding and non-plant feeding nematodes. In the earlier successional stages, vegetation regeneration was probably slow and occurred at the expense of organic matter stocks in the soil, while little litter was produced. This may explain why nematodes indicated a limited effect of fallow practice on vegetation and organic matter reconstitution in the early successional stages. At Sonkorong, it took at least 18–20 years of fallow time to reveal significant changes in nematode abundance, compared to cultivated soils.

Increase in plant parasitic nematode diversity (i.e. specific richness and evenness) from cropped fields to forest, probably resulted from increasing diversity of vegetation with the regeneration which occurs during fallow succession. This leads to an increase in the number of potential hosts for parasitic nematode populations and increases potential species diversity of plant parasitic nematodes. Nevertheless, because they were sampled from soil rather than roots, the nematode species found in this study were mostly migratory ectoparasites (Yeates et al., 1993). Species with this feeding habit generally show lower specific relationships to vegetation than other plant parasitic nematodes do (e.g. endoparasites).

Quantitative and qualitative development of ecosystem resources during succession controls the establishment of biotic interactions and defines species arrangement and diversity (Barbault and Hochberg, 1992). Better understanding of changes in the diversity of nematode communities could lead to a closer understanding of the biological aspects of ecosystem func-

tioning (Lawton et al., 1996). For example, the observed increase in evenness from the short fallow with a long duration of previous cultivation to forest indicates the establishment of more balanced communities with fallow age. Trends such as this suggest the development of a network of internal biotic interactions which usually fashion plant parasitic nematode assemblages (Quénéhervé, 1990) so as to favor more efficient resource use (Chapin et al., 1997). This should be reflected in the successional replacement of communities initially determined by external and physical factors, with dominance of few species, in biologically accommodated and balanced communities, leading to the development of a biological control of ecosystem resources (Margalef, 1968; Odum, 1969). Our results show a progressive increase in species richness with fallow age. According to the 'rivet hypothesis', the growth of species number is positive for ecosystem properties and enhances its functioning and productivity. At the present time, this hypothesis is questioned (Wardle et al., 1997), and if the 'redundant species hypothesis' (Walker, 1992) is correct, species richness (or diversity) has no effect on ecosystem functioning. Nevertheless the number of species is critical for maintaining ecosystem processes in the face of disturbance (Bloemers et al., 1997) and the enhancement of nematode species number, which we observed, should logically improve the resilience of ecosystem functioning as fallow duration increases.

4.2. *Underlying factors and previous land management*

Nematode community indices showed great (52%) but residual variability between sampling points on a given transect and plot. Field studies are affected by multiple underlying factors which occur at varying scales. The resulting spatial heterogeneity may interact on successional trends and it may modify, according to changes in nematode habitat (Freckman and Caswell, 1985; Noe and Barker, 1985; Yeates and Bird, 1994), parameters of the communities at each successional stage (Neher et al., 1995; Thioulouse et al., 1998).

The sensitivity of nematode communities to natural heterogeneity (Robertson and Freckman, 1995) probably also explains, but at different scale, the differences in indices of the nematode community

between the two transects of the old fallow, and between the two plots corresponding to recent fallows. In the latter case, nematode community characteristics indicated that one recent fallow plot corresponded more closely to an earlier successional stage than to the second short fallow plot (although they are of the same age); low values of evenness and species number in the first plot should reflect less balanced communities and a limited functional resistance as observed in cultivated fields. This plot had about 20 years of continuous cultivation before fallow and corresponded before abandonment to a more disturbed and degraded soil than did the second short fallow which underwent only 4 years of cultivation. These differences between two plots of recent fallows illustrate the consequences of previous land management on the initial state of ecosystem and restoration processes: repeated, or prolonged, disturbances lead to less mature communities with low levels of internal interactions, poorer feedback mechanisms (Odum, 1985; Hendrix et al., 1986; Freckman and Ettema, 1993) and thus a lower ability to recover when the stress is removed.

In this study, in addition to successional changes, nematode communities were sensitive to numerous factors, acting at both plot and sampling point scales. The selection of a spatial study scale is critical for determining the indicative powers of the soil nematode communities analysed. At the temporal scale, however, the fluctuations of the nematode community indices were slight and had little impact on the structure of the nematode communities. This relative stability of community characteristics supports the use of nematodes as indicators of fallow succession in Senegalese soils.

5. Conclusions

Trends in nematode community parameters agreed with theories of fallow succession, linking community parameters with ecosystem functioning. The simultaneous analysis of nematological indices showed that characteristics of nematode communities tended to develop with fallow age as the principal factor. Long fallows are not a good means to reduce populations of plant parasitic nematodes, but greater emphasis would have to be put on the species composition before draw-

ing conclusions on pathogenetic changes in the nematode community. Our results support the use of soil nematodes for indication of ecosystem state in secondary succession. Moreover, multivariate analysis of tables of indices provides a basis for the build up of a synthetic index, as a linear combination of simple indices. This synthetic index theoretically optimizes the differences between studied situations and presents, on principle, the best indicator properties.

However, investigations are required in further sites with differing climates, soils and land management. Nematological information may be balanced with crop yields before developing applied strategies of fertility management based on indicator properties of soil nematodes for monitoring the sustainability of developing agroecosystems.

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