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Relationships between ferrisol properties and the structure of plant parasitic nematode communities on sugarcane in Martinique (French West Indies)

Patrice Cadet (*°), Jean Thioulouse (**) and Alain Albrecht (*)

(*) *ORSTOM, Nématologie & Pédologie, BP 8006, Fort-de-France, Martinique.*
(°) *Present address: ORSTOM, Nématologie, BP 1386, Dakar, Sénégal.*
(**) *CNRS URA 243, Biométrie, Génétique et Biologie des Populations, Université Claude-Bernard, Lyon-I, 69622 Villeurbanne Cedex, France.*

Abstract

The relationships between the structural variations of a ferrisol and the plant parasitic nematode communities of sugarcane were studied along three transects. These transects, about 20 m long, started in horizon A and ended in a levelled area where horizon C began. Results were analysed with the co-inertia analysis method, which allowed us to study simultaneously the soil and nematode data. Progressive variations of the content of some physico-chemical soil elements (organic matter, phosphorus, pH) appear linked to those of the abundance of some nematode species (*Hemicriconemoides* and *Pratylenchus*). This analysis also shows relations that do not vary according to a gradient along the transects. For instance, the abundance of *Helicotylenchus* can be correlated with the existence of high calcium grades.

Keywords: West Indies, ferrisol, communities, plant parasitic nematodes, soil properties, co-inertia analysis.

Résumé

Les relations entre les variations de la structure d'un ferrisol et celles des peuplements de nématodes phytoparasites de la canne à sucre ont été étudiées le long de trois transects. Ces transects, d'une vingtaine de m de long commencent dans un horizon A et se terminent dans une zone remodelée où affleure l'horizon C. Les résultats ont été analysés à l'aide d'une analyse de co-inertie qui permet d'étudier simultanément un tableau pédologique et un tableau nématologique. La variation progressive des teneurs de certains éléments physiques et chimiques du sol (matière organique, phosphore, pH) s'accompagne de variations progressives de l'abondance de certaines espèces de nématodes (*Hemicriconemoides* et *Pratylenchus*). Cette analyse révèle également des relations qui n'évoluent pas selon un gradient le long du transect: l'abondance d'*Helicotylenchus* peut, par exemple, être mise en parallèle avec l'existence de fortes teneurs en calcium.

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INTRODUCTION

Over many years, several authors have observed the strong relationships existing between soil type and the distribution of parasitic nematode species associated with local crops (SEINHORST, 1956 ; CADET & DEBOUZIE, 1989). In Martinique, for perennial sugarcane crops, agricultural engineering has resulted in local changes (extending about ten meters wide) in the initial soil characteristics (CHEVIGNARD *et al.*, 1987). These fields have been continuously cropped with sugarcane, so they are climatically and agronomically homogenous.

On soil areas sharply differentiated by hillock levelling, previous research has shown that consistent differences are also observed in the nematode communities. For instance, the abundance of *Hemicriconemoides cocophilus* is inversely proportional to the carbon content of the soil (CADET & ALBRECHT, 1992).

However, in these studies it is possible that the observed biological structures were the result of particular local conditions, because the reference soil areas used in the study were not contiguous. To avoid this difficulty, observations have been repeated, but along transects including transition zones between soil horizons. This method should allow a more straightforward identification of the soil components that influence the development of some nematode species in the community.

MATERIAL AND METHODS

Localisation of the plots and definition of the hillock levelling

The sugarcane field under study (Abricot) is located in the Galion farm, North-East of Martinique. The sugarcane (variety B5993) was in the seventh ratoon. The soil is an oxysoil, overlying volcanic rock. Hillock levelling, executed in the 1970s, consisted of mechanical land levelling to flatten the slopes and facilitate the mechanization of the sugarcane harvest. This levelling of the mesorelief has brought soil layers B or C to the surface. These layers were initially located deep in the soil profile (CHEVIGNARD *et al.*, 1987).

In the field, levelled and non-levelled areas are differentiated by the colour of the outcropping layer: dark brown for layer A, red for layer B, and yellow to violet for layer C (BARRET *et al.*, 1991). The three transects (fig. 1) start in an area where the soil is not disturbed and end in a more or less levelled area. Their main characteristics are:

– transect 1: rapid transition from a non-levelled area (outcropping layer A) to an extensively levelled area (outcropping layer C),

– transect 2: gradual transition from a non-levelled area (outcropping layer A) to an extensively levelled area (outcropping layer C),

– transect 3: transition from a non-levelled area (outcropping layer A) to a slightly levelled area (outcropping layer B).

Sampling and analysis

The transects cross twelve sugarcane rows, with about 1.60 m between each row. Close to each row, two soil samples were taken at the same place, one of 300 cm^3 for nematode counts and the other of 500 cm^3 for soil analysis. Soil samples were collected the same day in June, 3 months after harvest, between 5 and 15 cm deep, where 80% of the nematodes are located (SPAULL & CADET, 1990). Based on the results of a previous study (CADET & ALBRECHT, 1992), only one replicate was made per sampling point. Nematodes were isolated from soil using SEINHORST's (1962) method;

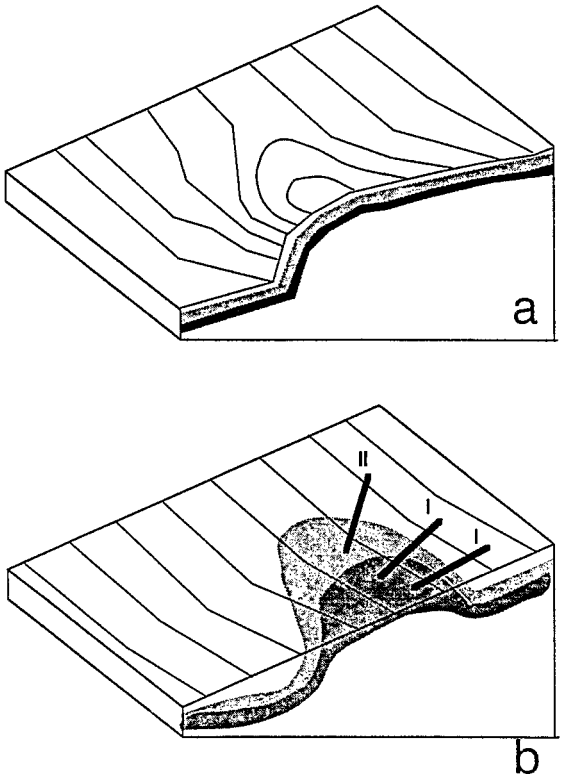

FIG. 1. – Schematic representation of the land hillock levelling. a: initial situation (concave-convex slope); b: situation after levelling (straight slope) with the position of the three transects.

numbers were calculated for one dm^3 of soil. Six species were counted in the samples: *Pratylenchus zeae*, *Helicotylenchus erythrinae*, *Hemicriconemoides cocophilus*, *Paratylenchus elachistus*, *Xiphinema setariae* and *Paratrichodorus anthurii*).

Several different analyses were performed on the soil sample. Organic carbon (C) and nitrogen (N) were measured on dried soil with a CHN Carlo Erba Model 1106 auto-analyser. The measurements of pH were done on soil suspensions with a soil:solution ratio of 1:2.5. The soil granulometry (mechanical analysis) was determined by sifting (200, 50 and 20 μm mesh sieves) and sedimentation (5 and 2 μm), after destruction of organic matter by hydrogen peroxide treatment and soda dispersion. The following parts were also obtained: coarse sand (SG, 200 to 2 000 μm), fine sand (SF, 50 to 200 μm), coarse silt (LG, 20 to 50 μm), fine silt (LF, 5 to 20 μm) and clay (A, less than 2 μm). For this study, clay and fine silt have been grouped together because of the difficulties in the dispersion of silt in this type of soil. The total phosphorus was determined by colourimetric titration (PELLOUX *et al.*, 1971). The cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+) were titrated with a flame spectrophotometer after exchange with ammonium acetate.

Statistical analysis

The results are grouped in two tables, with the sampling points as rows in both tables and the nematode counts as columns of the first table and the pedological results as colums in the second.

The data have been analysed by the co-inertia (or co-structure) method (CHESSEL & MERCIER, 1993; DOLÉDEC & CHESSEL, 1994). This method belongs to the "data coupling" approach, which enables two tables of data to be analysed simultaneously. In the fields of agronomy and ecology, these two tables often correspond to a table of environmental data and a floro-faunistic table. Numerous methods have been suggested to analyse such data (see a review by CHESSEL & MERCIER, 1993), one of the simplest, from the theoretical point of view being the co-inertia method. Already described by TUCKER (1958) under the name of inter-battery factor analysis, this method has been presented as an alternative to canonical analysis (GITTINS, 1985), and generalized to any type of table (quantitative, qualitative, or contingency) by MERCIER (1991).

The geometrical interpretation is simple. Classical methods (PCA: principal components analysis, CA: correspondence analysis, and MCA: multiple correspondence analysis) aim at summarizing a table by searching orthogonal axes on which the projection of the sampling points (rows of the table) have the highest possible variance. This characteristic ensures that the associated graphs (factor planes) will best represent the initial results. To extract information common to both tables, canonical analysis searches successive pairs of axes (t_i and u_i, one for each table) with a maximum correlation. By using the covariance instead of the correlation as a criterium, co-inertia analysis maximizes both the correlation and the projected variance on axes t and u:

$$\operatorname{cov}(t_i, u_i) = \operatorname{cor}(t_i, u_i) \sqrt{\operatorname{var}(t_i) \operatorname{var}(u_i)}$$

This ensures that the axes will have both a good correlation between one other (like canonical analysis axes) *and* a real meaning for each of the two tables (like PCA and CA axes). Two sets of factor scores are obtained for the sampling points: scores of the rows "seen by the environmental variables" and scores of the rows "seen by the species". These scores can be used to draw classical factor maps. We also obtain factor scores for environmental variables and for species, that help interpreting the preceding graphics. See CHESSEL & MERCIER (1993) or DOLÉDEC & CHESSEL (1994) for a more detailed explanation of the use of these scores.

Moreover, a randomization test can be used to check the significance of the co-structure in equivocal situations. This method consists in performing many times a random permutation of the rows of both tables, followed by the re-computation of the analysis. Comparing the results obtained in the normal analysis with the results obtained after randomization provides an estimation of the probability of finding the observed situation in the absence of relationships between environmental variables and faunistic data.

Computations and graphical displays were obtained using the computer programs ADE (CHESSEL & DOLÉDEC, 1993) and GraphMu (THIOULOUSE, 1989).

RESULTS

Single transect analysis

Soil variables

The analysis of the variation of the pedological variables along the three transects enables two groups of variables to be distinguished (fig. 2). The first group includes carbon, C:N ratio, phosphorus, some textural elements (clay and fine silt, fine and coarse sand) and potassium, which change according to the levelling and the type of transition between the different areas. The second group of variables is independent of the levelling process: pH water, pH KCl, coarse silt, "mineral" cationic exchange capacity, calcium, magnesium and sodium.

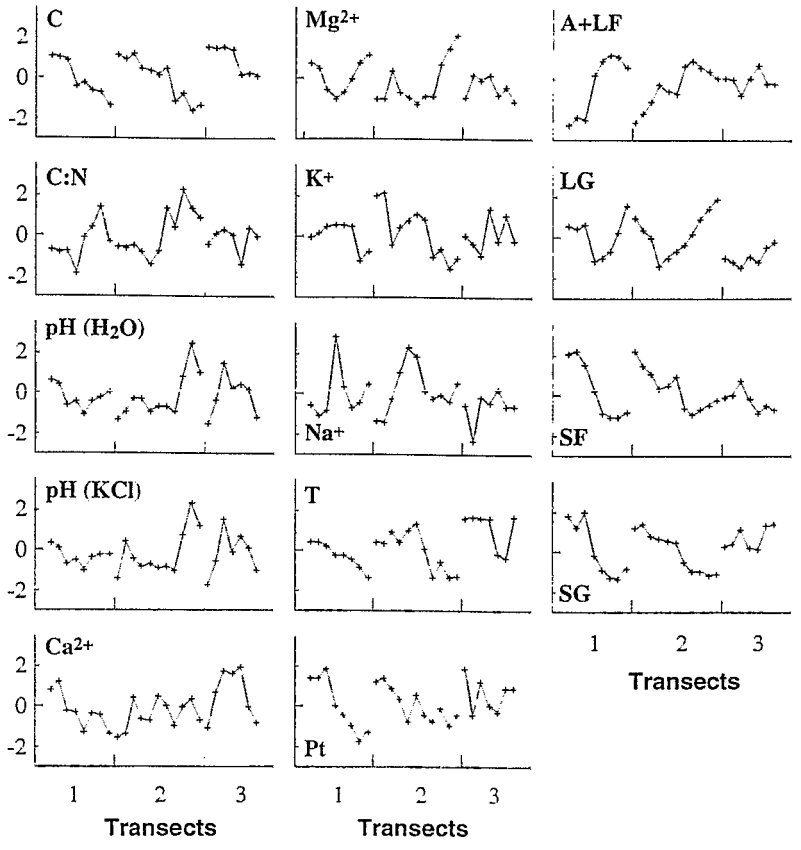

FIG. 2. – Representation of the standardized values of the 14 soil variables along each sampling point of the three transects (see legend to Table I).

Nematological variables

The six nematode species are split into two groups : *P. zeae*, *H. erythrinae*, *H. cocophilus*, which are present in large numbers and *P. elachistus*, *X. setariae*, *P. anthurii* which are always sparsely represented (fig. 3). Along the first two transects, the density of *Hemicriconemoides* increases, whereas along the second and the third transects, the density of *Pratylenchus* decreases.

Global analysis of the three transects

Figure 4 shows the results of the PCA of the pedological variables (table I) and of the CA of the nematode data (table II). In the upper part of the figure the F1 X F2 factor planes for the columns are represented, i.e. the correlation circle of the 14 soil variables (PCA) and the factor map of six nematode species (CA). In the lower part, the F1 X F2 factor planes of the rows are shown, with the three transects represented separately.

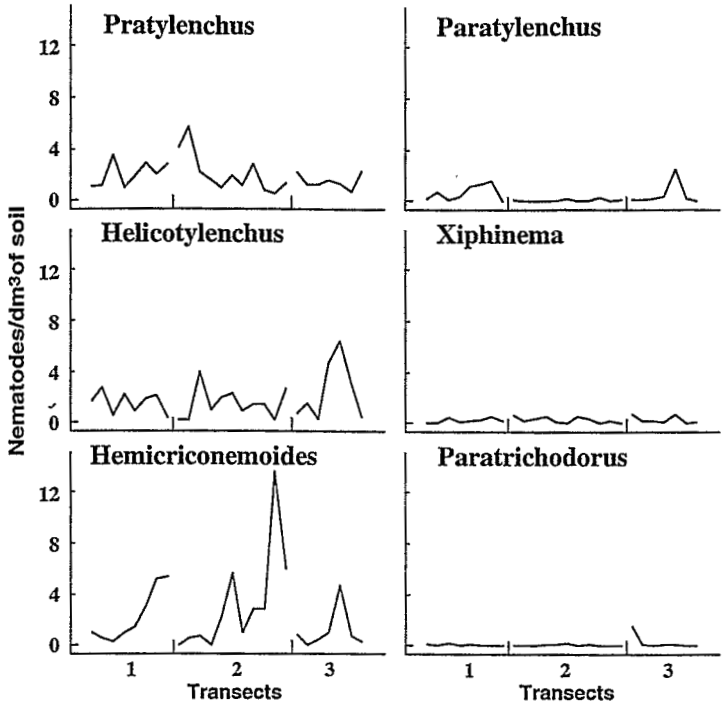

FIG. 3. – Representation of the six nematode species abundances ($\times 10^{-3}$) along the three transects.

Analysis of the soil results

In the correlation circle defined by factors 1 and 2 (which describe 48% and 19% respectively of the total variability of the table), the first factor is mainly explained by the variables associated with the levelling process: organic matter and particles sizes. Carbon (related to organic matter content) and fine and coarse sand proportions (located towards the first axis negative values) are opposed to the C:N ratio (which represents the organic matter "quality") and silt and fine soil particles (located towards the positive values of the first axis). Among the chemical components, the opposition between magnesium and phosphorus or potassium is clear. The second factor is explained by the content of exchangeable chemical components (Ca^{2+} and Na^{+}), which are not linked with the levelling process.

For the first two transects, the points corresponding to the samples, projected in the F1 × F2 factor plane, are approximately arranged according to their order along the transect. Points 11 to 13 and 21 to 26 at the beginning of these transects, correspond to layer A, rich in organic matter and more sandy, whereas points 15 to 18 and 28 to 2b at the end of the transects, correspond to the outcrop of layer C, poor in organic matter and comprising finer particle sizes.

The variations of Na^{+} content, linked to the second factor, do not correspond to a simple gradient. Points 31 and 37, corresponding to the third transect ends, appear

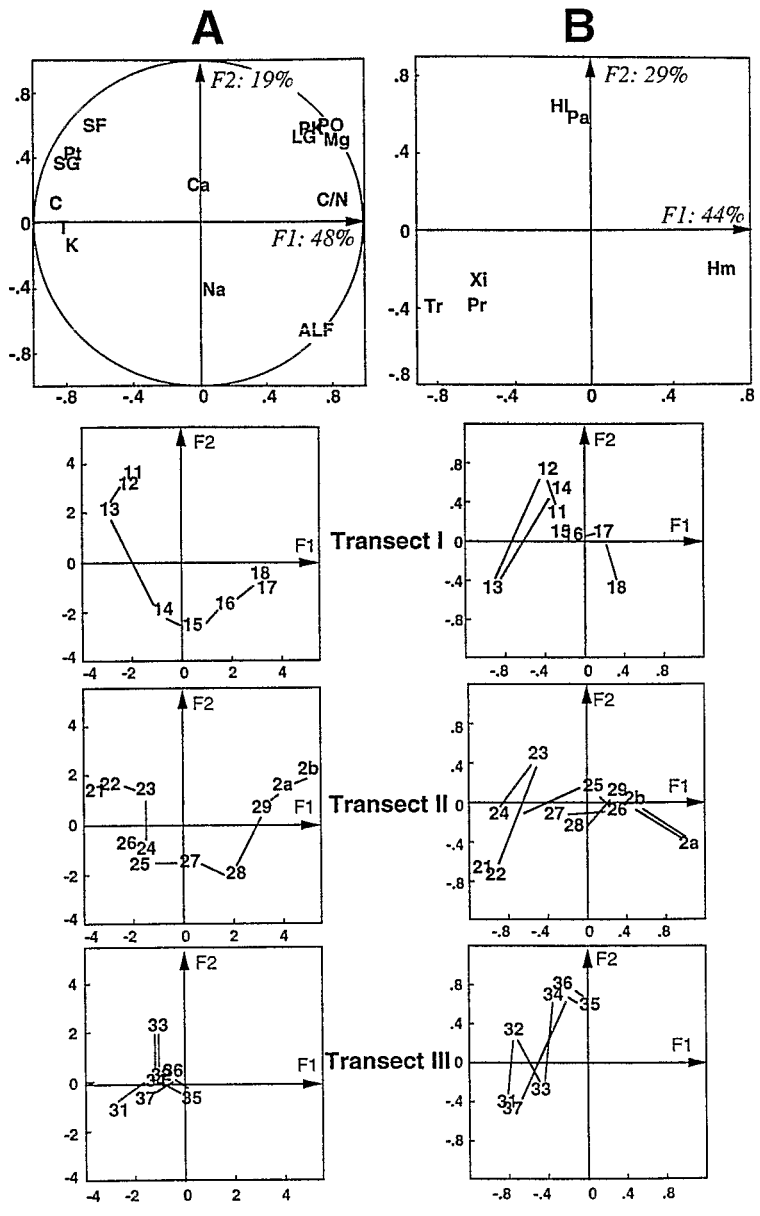

FIG. 4. – Results of the soil data PCA (1A) and of the nematological data CA (1B). Top: F1 × F2 factor planes of the columns (PCA correlation circle of the soil variables and CA factor plane of the six nematode species). Bottom: F1 × F2 factor planes of the rows (left = PCA, right = CA) ; the three transects have been represented separately and sampling points are numbered 11 to 18, 21 to 2b and 31 to 37; cf. table legends.

towards the negative values of F2, and have a higher calcium content than points 32 to 36, located in the middle, and appearing towards the positive values of F2.

Analysis of the nematological results

In the F1 × F2 factor plane (73% of the total variability of the table) the nematodes are split into three groups (fig. 4), each one containing a species able to persist at high densities. On the first axis, *Hemicriconemoides* is opposed to a group including *Pratylenchus, Xiphinema* and *Paratrichodorus*, whereas on the second axis, *Helicotylenchus* and *Paratylenchus* are opposed to the other species. In this factor plane also, the projections of the points corresponding to the samples are organised approximately according to the sampling order along the first two transects. For points 11 to 15 and 21 to 24, the populations of *Pratylenchus* are high, whereas those of *Hemicriconemoides* are low (A layer) and the converse for points 16 to 18 and 28 to 2b, located at the other end of transects 1 and 2 (C layer).

Some points of the three transects move towards the positive values of the second factor because they correspond to samples containing high numbers of *Helicotylenchus*. This is particularly true for the samples taken near the middle of the third transect, in the transition area between layers A and C.

Co-inertia analysis

The coupling of the tables produces new factors, which allow the study of the soil and fauna tables by projecting variables and sampling points in the new F1 × F2 factor planes. Fig. 5 represents these new maps.

The soil variables are arranged in a pattern similar to that observed in the initial PCA, except for Ca^{2+}, which moves from the positive to the negative values of F2. This analysis increases the similarity between the transect scores from the soil results and those from the nematological results. For the first two transects, the link with the first factor (correlated with the levelling) is obviously reinforced. For the third transect, the inversion of the "soil transect" around axis 1, brings it nearer to the "nematological transect".

Figure 6 shows the comparison of the first two axes of the initial analyses (PCA and CA) with the corresponding axes of the co-inertia analysis. The cluster of points obtained with CA and PCA first factor is similar to that obtained with co-inertia analysis, and the correlation between them is high: 0.81. However, the co-inertia analysis slightly increases this correlation to 0.87, while keeping 99% of the CA inertia and 96% of the PCA inertia.

For F2, these values are respectively 97% and 69%. The coupling considerably increases the correlation, as shown by the rearrangement of the points in the factor plane. The permutation test is highly significant ($p < 0.001$) for F1 and significant ($p < 0.05$) for F2.

DISCUSSION AND CONCLUSION

The similarity of the factor scores of samples in the separate analysis of the soil and fauna tables shows that there is, in both cases, a pronounced structure. Both F1s reflect obvious gradients for transects 1 and 2. The second factor underlines the

TABLE I. – *Physico-chemical parameters measured at each sampling point along the three transects. (C: carbon (‰) ; C:N: carbon:nitrogen ratio ; PO: pH water ; PK: pH KCl ; Ca: calcium (meq/%) ; Mg: magnesium (meq/%) ; K: potassium (meq/%) ; Na: sodium (meq/%) ; T: sum of basis (meq/l) ; Pt: total phosphorus (‰) ; A + LF: clay + fine silt (%) ; LG: coarse silt (%) ; SF: fine sand (%) ; SG: coarse sand (%)).*

	C	C/N	PO	PK	Ca	Mg	K	Na	T	Pt	A + LF	LG	SF	SG
11	20.23	11.58	6.21	5.51	7.39	3.27	0.67	0.23	13.52	0.35	62.1	6.9	20.6	10.2
12	19.99	11.35	6.07	5.37	7.81	3.08	0.74	0.16	13.42	0.35	64.8	6.7	21	8.5
13	19.22	11.44	5.35	4.85	6.21	2.25	0.87	0.19	13.16	0.38	64.2	7	18.2	10.7
14	12.1	9.41	5.48	5	6.1	1.94	0.91	0.66	12.3	0.27	79.5	4.5	12.3	4.8
15	13.01	12.71	5.05	4.67	5	2.17	0.89	0.34	12.3	0.24	84.7	4.7	7.4	2.8
16	10.8	13.64	5.5	5.07	6.05	2.67	0.87	0.21	11.99	0.21	86.4	5.2	6.5	1.7
17	10.47	15.56	5.63	5.13	5.93	3.27	0.23	0.24	11.38	0.16	86	6.5	6.4	1.5
18	6.9	12.28	5.8	5.15	4.94	3.55	0.39	0.36	10.41	0.19	82.1	8.3	7.6	3
21	20.5	11.85	4.9	4.42	4.7	1.9	1.45	0.13	13.52	0.34	63.4	7.5	21.2	8.5
22	19.41	11.76	5.17	5.54	4.94	1.93	1.51	0.12	13.37	0.35	66.2	6.6	17.7	9.1
23	20.8	12	5.59	5.02	6.89	2.98	0.52	0.27	14.34	0.32	70.3	6.1	16.1	7.4
24	16.97	11.34	5.58	4.77	5.71	2.16	0.84	0.43	13.42	0.29	76.3	4.1	12.8	7.1
25	16.4	10.24	5.16	4.86	5.66	1.98	0.98	0.59	14.44	0.22	74	4.7	13.4	6.8
26	15.32	11.43	5.31	4.74	7.01	1.73	1.11	0.53	15.05	0.3	73.3	5.2	15.5	6.5
27	17.15	15.41	5.31	4.78	6.51	2.04	1	0.32	12.91	0.24	82.7	5.6	8.5	3.8
28	8.11	13.68	5.14	4.68	5.39	2	0.31	0.27	10.41	0.22	84.7	6.4	6.9	2.5
29	10.19	17.06	6.33	5.76	6.37	3.21	0.44	0.29	11.79	0.26	82.4	7.4	8.1	2.6
2a	5.46	15.42	7.4	6.75	6.83	3.81	0.08	0.25	10.47	0.21	80.9	8.1	9.1	2.1
2b	7.17	14.51	6.44	6.03	5.68	4.3	0.27	0.37	10.57	0.24	78.6	8.8	10.3	2.2
31	22.84	12.13	4.75	4.23	5.23	1.95	0.69	0.23	15.49	0.38	78.8	4.7	10.9	6.1
32	22.25	13.08	5.53	4.93	7.2	2.83	0.54	0	15.6	0.24	78	4.4	11.5	6.3
33	22.67	13.38	6.77	6.23	8.43	2.63	0.33	0.28	15.49	0.34	72.7	4	14.5	8.4
34	21.92	12.95	5.92	5.25	8.22	2.81	1.2	0.24	15.44	0.27	78.8	4.8	10.5	5.8
35	15.13	10.2	6.07	5.71	8.62	2.05	0.61	0.33	12.41	0.25	83	4.4	7.4	5.7
36	15.73	13.6	5.87	5.35	6.38	2.35	1.07	0.22	12.11	0.32	77	5.4	9	8.9
37	14.89	12.83	4.97	4.65	5.53	1.84	0.61	0.22	15.54	0.32	77	5.8	8.1	9.1

TABLE II. – *Number of individuals per dm³ of soil at the different sampling points along the three transects for six nematode species. (Pr* = Pratylenchus zeae, *Hl* = Helicotylenchus erythrinae, *Hm* = Hemicriconemoides cocophilus, *Pa* = Paratylenchus elachistus, *Xi* = Xiphinema setariae *and Tr* = Paratrichodorus anthurii.*)*.

	Pr	Hl	Hm	Pa	Xi	Tr
11	1 112	1 668	984	208	80	172
12	1 172	2 732	536	724	80	0
13	3 524	564	280	164	492	176
14	1 000	2 240	960	360	160	0
15	1 880	900	1 440	1 140	180	100
16	2 920	1 840	3 060	1 360	340	0
17	2 060	2 140	5 220	1 640	560	0
18	2 820	400	5 380	0	180	0
21	4 100	240	80	100	680	80
22	5 720	240	540	0	180	0
23	2 220	3 940	700	20	360	0
24	1 620	980	80	0	600	160
25	1 000	1 920	2 220	0	160	160
26	2 000	2300	5 620	180	0	200
27	1 140	900	1 000	0	600	80
28	2 800	1 420	2 820	0	380	160
29	800	1 440	2 860	320	80	80
2a	580	240	13 580	0	240	0
2b	1 360	2 660	5 940	100	20	0
31	2 204	760	836	160	744	1 552
32	1 288	1 504	24	160	192	160
33	1 256	304	504	180	180	4
34	1 580	4 660	960	400	120	160
35	1 380	6 420	4 640	2 520	700	160
36	700	3 100	740	240	80	80
37	2 280	520	280	80	100	80

originality of transect 3. In these conditions, it is not surprising that the results of the co-inertia analysis are close to the results of the initial analyses. This confirms the existence of a strong relation between the soil observations and the abundance of some nematode species.

The biological interpretation of this link is unclear, but it results mainly from organic matter and particle size gradients corresponding to the regular variations in the abundance of two nematode species, *H. cocophilus* and *P. zeae*. This confirms previous results (CADET & ALBRECHT, 1992) that areas rich in organic matter harbour high populations of *H. cocophilus* whereas areas poor in organic matter harbour low populations (and conversely for *P. zeae*). Compared to the spatial study mentioned previously, the analysis along transects shows that this transition is progressive. Consequently, it is not an exceptional phenomenon, happening at random, but rather a real quantitative linkage. It is the lateral variation of soil structure that "induces" the inversion of the population balance in the nematode community.

Other studies have shown the relations between abiotic factors and the frequency or the abundance of nematode species. DE PELSMAEKER & COOMANS (1987) observed that *Globodera* is more abundant in soils rich in organic matter.

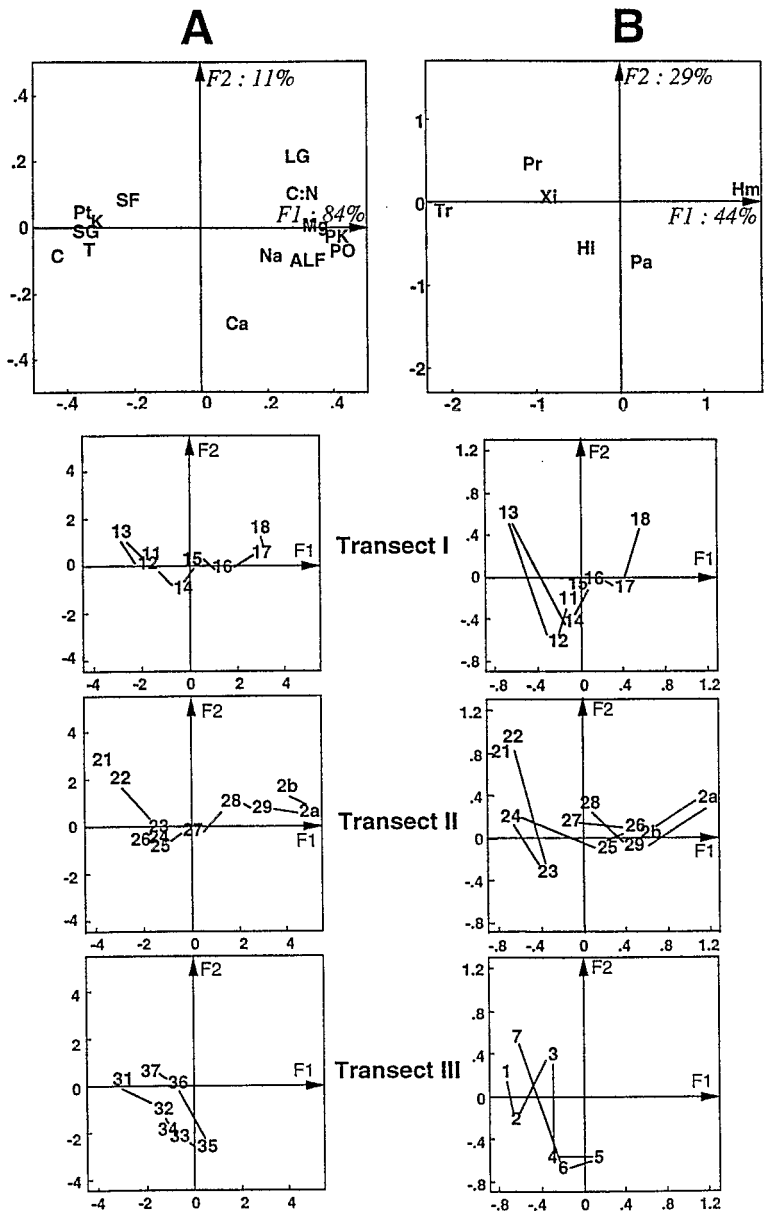

FIG. 5. – Co-structure analysis. Top: F1 x F2 factor planes of the columns (A: soil variables; B: nematode species). Bottom: F1 x F2 factor planes of the rows (cf. figure 2 and tables legends).

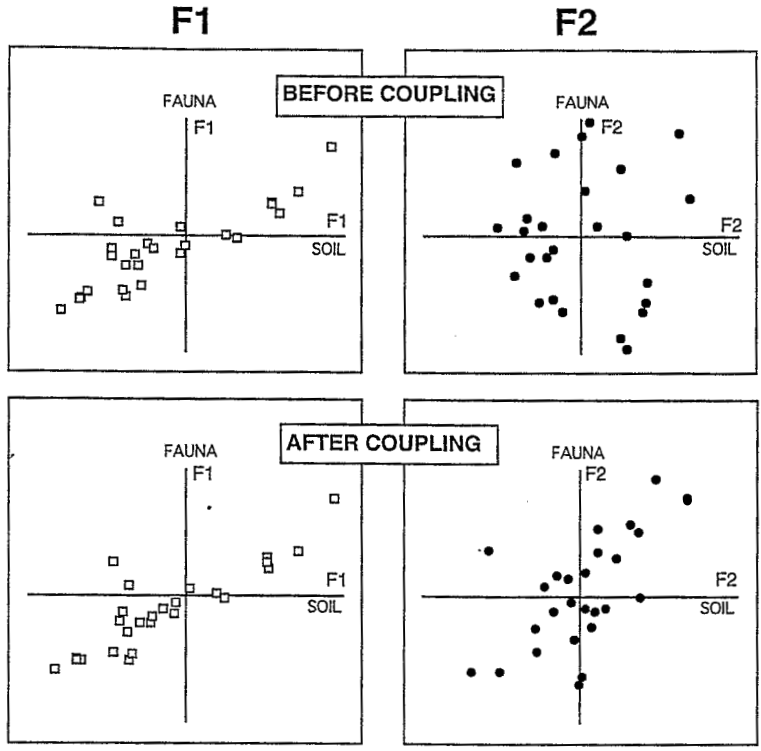

FIG. 6. – The projections before and after coupling of the first (□) and second (●) factor scores of the analyses of soil and nematological data. Before coupling: the first factor of CA has been plotted against the first factor of PCA (left) ; the second factor of CA has been plotted against the second factor of PCA (right). After coupling: the first factor of the co-inertia analysis of nematological data has been plotted against the first factor of the co-inertia analysis of soil data (left) ; the second factor of the co-inertia analysis of nematological data has been plotted against the second factor of the co-inertia analysis of soil data (right).

However, differences can appear between species of the same genus. These authors showed that *P. penetrans* is usually associated with soil of high pH whereas *P. crenatus* is found in soils of low pH. This relation between pH and the distribution of nematode species has been observed frequently but usually at a geographic scale too large to be validated (NORTON, 1989). Our observations show that pH preferences are present on a smaller scale of a few tens of centimeters and, thus, in an area that can otherwise be considered as homogeneous. For example, the abundance of *P. zeae* is inversely proportional to pH, and changes between two samples that are only 1.6 m apart.

As well as a relationship between *H. cocophilus* and soil organic matter, the co-inertia analysis underlines the importance of some chemical factors, such as phosphorus, which also seem to be linked to the fluctuations of *H. cocophilus* and *P. zeae* populations. There are other relationships which appear discontinuously along

the transects ; for example, the presence of low populations of *Helicotylenchus* and *P. zeae* corresponds to places where basic elements, particularly Ca^{2+}, are low.

The present analysis identifies the elements which covary with the nematode populations but it gives no indication about their modes of action leading to the modification of the species balance in the nematode community. These mechanisms should be analysed in the future under controlled artificial conditions. Understanding these mechanisms is necessary for a mesological control method for nematodes which would involve the modification of soil elements to shift the population balance in the nematode community and reduce its pathogenicity. This offers many possibilities, particularly avoiding the creation of an "ecological vacuum", as would be caused by most of the chemical control methods based on the non-specific elimination of the nematodes.

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