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Plant row and soil factors influencing the microspatial patterns of plant-parasitic nematodes on sugarcane in Martinique(1)

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Summary - This study compares the microdistribution of plant-parasitic nematodes and sugarcane roots in relation to the row and some soil parameters on a ferrisol characterized by three degrees of hillock levelling. Soil and root samples were collected on a grid located between two rows of sugarcane. In the most levelled location, where carbon, nitrogen and potassium contents were the poorest, *Pratylenchus zeae* presented a spatial pattern related to the row. This was also observed with *Helicotylenchus erythrinae* in the three locations. On the contrary, *Criconemella onoensis* did not show a marked spatial pattern related to the row or root quantity in any of the situations. *Hemicriconemoides cocophillus* appeared to be distributed parallel to sugarcane rows in the direction of the slope. Spatial patterns were figured by graphical displays and analyzed using semi-variograms to confirm and characterize the observed patterns. The use of cross semi-variograms showed antagonistic distributions between *C. onoensis* and the other species which were more prominent in the levelled locations. In respect to hillock levelling intensity leading to variations of soil parameters, micro-spatial patterns and interactions among plant parasitic nematodes vary quantitatively and qualitatively.

Résumé - ***Influence du rang de culture et des facteurs édaphiques sur la micro-répartition spatiale des nématodes phytoparasites associés à la canne à sucre en Martinique*** - Le but de cette étude a été de comparer la micro-répartition de différentes espèces de nématodes phytoparasites et la densité racinaire de plants de canne à sucre, en relation avec le rang et certains paramètres édaphiques, sur un ferrisol caractérisé par trois niveaux de remodelage. Les échantillons de sol et de racine ont été prélevés sur une grille à maille régulière disposée entre deux rangs de canne à sucre. Dans la situation profondément remodelée, où les teneurs en carbone, azote et potassium sont les plus faibles, *Pratylenchus zeae* présente une structure spatiale liée au rang de canne. *Helicotylenchus erythrinae* montre cette répartition particulière dans les trois situations. Au contraire, *Criconemella onoensis* ne montre pas de distribution particulière vis-à-vis du rang et de la quantité de racine et ce, quelle que soit la situation. *Hemicriconemoides cocophillus* apparaît disposé en lignes parallèles au rang de canne, dans la direction de la pente. Les répartitions spatiales sont représentées graphiquement et analysées à l'aide de semi-variogrammes afin de confirmer et de caractériser les structures observées. L'utilisation de semi-variogrammes croisés montre des interactions antagonistes entre *C. onoensis* et les autres espèces. Ces interactions sont plus importantes dans la situation profondément remodelée. En fonction de l'intensité du remodelage et des variations consécutives des paramètres du sol, les répartitions et interactions entre nématodes phytoparasites varient quantitativement et qualitativement.

Key-words : *Criconemella onoensis,* edaphic factor, geostatistics, *Helicotylenchus erythrinae, Hemicriconemoides cocophillus,* hillock levelling, Martinique, microspatial structure, nematodes, *Pratylenchus zeae,* soil, sugarcane.

Spatial patterns of plant-parasitic nematodes in agricultural or natural ecosystems are influenced by both macro-distributional and micro-distributional components. The macro-distribution is governed by cropping history and by environmental parameters such as soil texture, soil moisture, and drainage pattern, which constitute major factors of habitat suitability. The micro-distributional attributes of a nematode population are strongly linked to the population's life history and feeding strategies (Ferris *et al.,* 1990). It is also well known that nematodes mostly occur in polyspecific communities and can interact with each other (Eisenback, 1993). The final outcome of these biological and edaphic influences results in varying degrees of aggregation in the spatial pattern of nematode populations (Ferris *et al.,* 1990).

In row crops, most management activities are oriented in the direction of plant rows (Noe & Campbell, 1985).

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They can affect soil properties (e.g., drainage pattern, porosity) and hence exert an influence upon macro-scale distribution of species (Norton & Niblack, 1991). A study of nematode micro-distribution in and between plant rows is necessary for understanding the relationship between nematodes, plants and soil, and for devising sampling protocols.

The present work is a preliminary investigation conducted in order to determine the most adequate sampling site between sugarcane rows for a future, more exhaustive study on nematodes and soil interactions.

The objectives of this research were : *i*) to compare the horizontal patterns of nematodes subjected to some environmental variables (plant roots, some physico-chemical soil characteristics, slope) on three related soil types of similar origin resulting from hillock levelling, *ii*) to study the influence of the row on the micro-distribution of plant-parasitic nematodes between two rows of sugarcane, and *iii*) to illustrate possible interactions among plant-parasitic nematode species.

In this study we use graphic representation and geostatistics to analyse basic data in order to find and describe spatial patterns of soil-dwelling nematodes. Because of the presence of autocorrelation among data sets, most of the traditional statistics, e.g., correlation coefficients are no longer valid. We thus propose to investigate the relationships between autocorrelated variables, such as nematode species, using cross semi-variance analysis.

Materials and methods

This study was conducted in the North East of Martinique (14° 43′ N, 60° 58′ W) on a permanent sugarcane area that has been in cultivation for more than 200 years and was partially levelled in the 1970s. The soil is an Ultisol (ferrallitic soil) developed on volcanic rocks. Hillock levelling consisted of mechanical land levelling to straighten the slopes and facilitate the mechanization of sugarcane harvest. This levelling of the meso-relief has brought to the surface B or C horizons which were initially located deeper in the soil (Chevignard *et al.*, 1987). In the field, levelled and non-levelled areas can be visually differentiated by the color of the outcropping layer (Munsell code). Non-levelled areas are called A, superficially-levelled area B and deeply-levelled areas C, related to their carbon content (Barret *et al.*, 1991).

In a sugarcane plot (Abricot, sugarcane cv. B5992, 9th ratoon), three micro-sites (1.92 m^2) were chosen less than 15 m apart and noticeably different in their soil parameters due to past hillock levelling. A sampling grid was located between two rows of sugarcane (separated by approx. 1.6 m). At each micro-site, 63 undisturbed samples were taken on a regular grid (1.6 m long × 1.2 wide) with a sampling interval of 20 cm. At each sampling point, soil and roots were collected, using a 5.5 cm diameter coring tool (volume = 237 cm^3) from 0-10 cm depth. Nematodes were extracted from the soil by the elutriation-sieving technique (Seinhorst, 1962) and from roots in a mist chamber (Seinhorst, 1950). Roots were separated from soil by wet sieving before elutriation and dried at 60 °C. Total nematodes density was expressed as the number of individuals per volume of 250 cm^3 (soil and roots) and root density was expressed as dry weight per 250 cm^3 soil.

With each core, a small volume of soil (*ca* 100 cm^3) was sampled for soil analysis. Organic carbon and nitrogen content were measured dry using a Nitrogen Carbon Sulfur Analyser NA 1500 (Carlo Erba Instruments). The cation exchange capacity (CEC) was measured with ammonium acetate at pH 7. The main cations (Ca, Mg, K and Na) were titrated with a flame spectrometer after exchange with ammonium acetate. Soil texture and pH were determined only on the central point of each grid.

The sampling points were graphically represented by squares whose size was proportional to the number of nematodes or root density (Thioulouse, 1989, 1990).

Semi-variograms were computed for each nematode species density using the program Var5 (Yost *et al.*, 1989). The program allows semi-variogram estimation and model fitting by a modified least square procedure (Cressie, 1985). Spatial correlation between different nematode species was assessed with cross semi-variogram analysis.

Results

COMPARISON OF PLANT-PARASITIC NEMATODE DISTRIBUTION AND ROOTING PATTERNS IN THE THREE LOCATIONS

The three sites were chosen accordingly to their specific soil parameters related to the past hillock levelling (Table 1). There were significant decreases in carbon, nitrogen, potassium and coarse sand content from location A to location C accompanied by increases in clay content, bulk density and carbon to nitrogen ratio. The saturation percentage (S/T) was higher in the deeply-levelled location. Hillock levelling created changes in soil chemistry that are still obvious after more than twenty years. Only the calcium levels were similar in each location. In these three locations, cation exchange capacity (CEC), pH, magnesium, sodium, and water content varied independently of hillock levelling. The slopes were fairly similar in the three locations with the rows in the direction of the slope.

At each site, the plant-parasitic nematode community comprised four main species : one endoparasite, *Pratylenchus zeae* Graham, 1951, and three ectoparasites, *Criconemella onoensis* (Luc, 1959) Luc & Raski 1981, *Helicotylenchus erythrinae* (Zimmermann, 1904) Golden, 1956, and *Hemicriconemoides cocophillus* (Loos, 1949) Chitwood & Birchfield, 1957. Besides these spe-

Table 1. *Mean and standard error (in parentheses) of physico-chemical parameters measured in each location (location A : non-levelled; location B : superficially-levelled; location C : deeply-levelled).*

Parameters	Location A	Location B	Location C
Munsell color	10 YR 5/8	7.5 YR 6/4	5 YR 6/6
Slope (degree)	8.25	9.64	8.81
pH H2O	5.62	6.09	5.90
pH KCl	5.58	6.12	5.73
clay %	46.64	54.19	65.90
fine silt %	17.16	14.29	21.03
coarse silt %	14.70	12.75	7.37
fine sand %	14.98	13.91	4.70
coarse sand %	6.52	4.86	1.00
Carbon %	2.493 *c* (0.084)	1.769 *b* (0.051)	1.423 *a* (0.075)
Nitrogen %	0.218 *c* (0.005)	0.137 *b* (0.004)	0.097 *a* (0.004)
C/N	11.33 *a* (0.17)	12.92 *b* (0.16)	14.59 *c* (0.26)
Bulk density g/cm^3	0.83 *a* (0.01)	0.88 *b* (0.01)	0.92 *b* (0.01)
Humidity %	32.54 *b* (0.43)	30.14 *a* (0.25)	35.12 *c* (0.46)
Ca meq %	6.29 *a* (0.20)	7.03 *a* (0.41)	6.15 *a* (0.17)
K meq %	1.07 *c* (0.04)	0.67 *b* (0.04)	0.51 *a* (0.02)
Na meq %	0.19 *a* (0.01)	0.23 *b* (0.01)	0.17 *a* (0.01)
Mg meq %	2.19 *b* (0.06)	1.83 *a* (0.05)	4.64 *c* (0.09)
CEC meq/100 g	15.13 *b* (0.25)	13.48 *a* (0.18)	14.52 *b* (0.19)
S/T %	64.51 *a* (1.29)	70.83 *a* (2.54)	80.02 *b* (2.05)

Means followed by a same letter within a line are not significantly different according to a Kruskal and Wallis test ($P < 0.05$).

Table 2. *Mean, standard error (in parentheses) and coefficient of variation [between angled brackets] of plant-parasitic nematode numbers per 250 cm^3 of soil in each location and roots weight.*

	Location A	Location B	Location C
H. erythrinae	239 *a* (59.90) [199]	415 *b* (58.85) [113]	134 *a* (25.21) [150]
H. cocophillus	683 *a* (64.72) [75]	572 *a* (67.07) [93]	531 *a* (65.22) [98]
C. onoensis	37 *a* (10.53) [226]	104 *a* (20.21) [154]	792 *b* (143.77) [144]
P. zeae	1211 *a* (73.18) [48]	1352 *a* (105.50) [62]	583 *b* (62.83) [86]
Roots (g)	0.57 *ab* (0.08) [116]	0.41 *a* (0.05) [106]	0.67 *b* (0.12) [145]

Means followed by a same letter within a line are not significantly different according to a Kruskal and Wallis test ($P < 0.05$).

cies, there was a low occurrence of *Paratrichodorus anthurii* Baujard & Germani, 1985, *Paratylenchus elachistus* Steiner, 1949 and *Xiphinema setariae* Luc, 1958.

Only *H. cocophillus* exhibited similar densities in the three locations (Table 2); while densities of *P. zeae* were higher in A and B locations than in the deeply-levelled C location. In contrast, densities of *C. onoensis* were higher in location C. The main differences in nematode communities appeared between the deeply-levelled location C, and the other two degrees of levelling (none or slight). The nematodes species can be ranked in decreasing order of density as *P. zeae* > *H. cocophillus* > *H. erythrinae* > *C. onoensis* in locations A and B while in location C the order is *C. onoensis* > *P. zeae* > *H. cocophillus* > *H. erythrinae*. These results are in accordance with other studies conducted on the effect of hillock levelling on a larger scale (unpubl.).

Root density was higher in location C than in location B, but only roots retained on a 0.2 mm sieve were collected.

Maps were used to describe nematode and plant rooting patterns. In location A, the nematode species *P. zeae* (Fig. 1) had a relatively homogenous spatial pattern and was not influenced by the proximity of sugarcane rows. In contrast, the density of *H. erythrinae* increased near sugarcane rows. No clear pattern was observed for the criconematids.

In location B, spatial patterns of all species were heterogenous. The influence of proximity to rows is specially obvious for the species *H. erythrinae* (Fig. 1) and to a lesser extent for *P. zeae*. The population of *H. cocophillus* appears also distributed parallel to sugarcane rows in the direction of the slope.

In location C, the spatial pattern of *C. onoensis* (Fig. 1) seems to be the opposite of that of the other species with a patch of high densities. Each species exhibited a very heterogenous density pattern.

Coefficients of variation were calculated for each nematode species. The lowest values were found with *P. zeae* and *H. cocophillus*. They were higher in the levelled location. The species *C. onoensis* and *H. erythrinae* had

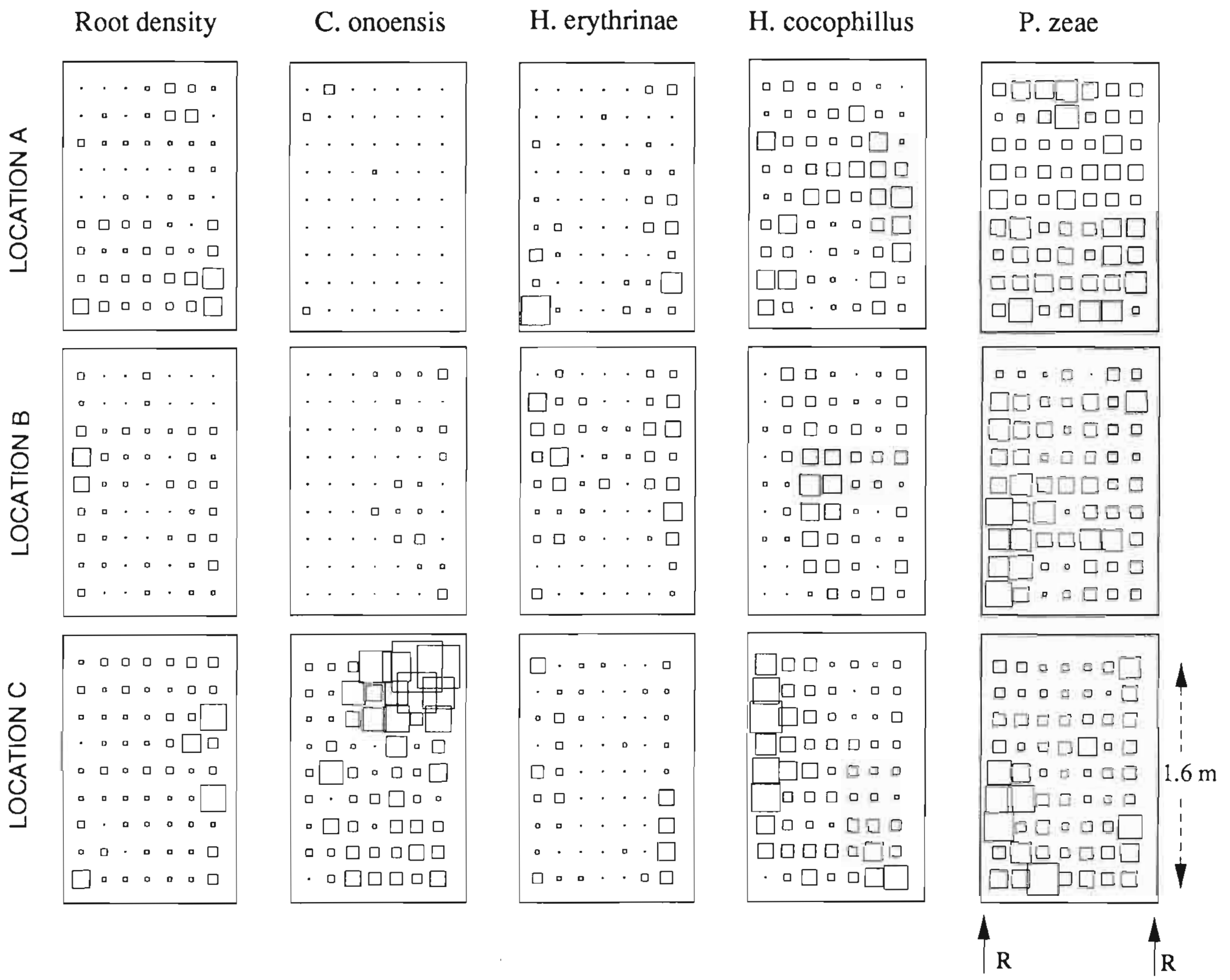

Fig. 1. *Graphic representation of the sampling area with square sizes proportional to the number of nematodes or root densities per 250 cm^3 in each location (R = position of sugarcane rows).*

the highest coefficients of variation, which confirms their very heterogenous spatial patterns previously observed on the maps.

From location A to C, root densities (Fig. 1) differed slightly and showed no marked spatial pattern, except in location B where root density was greater along the rows.

Although Fig. 1 gives a description of the species patterns, the spatial autocorrelation must be demonstrated. Spatial structures can be described through structure functions allowing to quantify the spatial dependency. In this study, we used the semi-variogram which is the structure function used in geostatistics (see Wallace & Hawkins, 1994 and Rossi *et al.*, 1996 for a review and a definition of the geostatistical terms). Spatial dependence was assessed by means of semi-variogram estimation. Once semi-variograms were estimated, a modified least square fitting procedure was used to fit a theoretical function to sample semi-variograms. Every species in all locations except *P. zeae* showed an increase of semi-variance with distance, which indicated autocorrelation (spatial dependence) among data sets, i.e., the variables are regionalized. On the contrary, in situation A, *P. zeae* exhibited a semi-variogram with 100 % nugget effect, indicating that there was not a structured pattern for the species distribution.

Parameters of semi-variogram models differ with nematode species and location (Table 3). The semi-variogram model for *C. onoensis* was linear in all locations, with *H. cocophillus* departing from this model in location A. The other two species fitted different models in each location.

Table 3. *Model parameters of theoretical semi-variograms of plant parasitic nematodes species.*

Nematode species	Location	Model	Nugget	Slope	Sill	Range
H. erythrinae	A	Linear	59056.0	27330.9		
	B	Spherical	89368.2		233592.9	5.8
	C	Exponential	14094.3		81336.3	39.2
P. zeae	A	100% nugget				
	B	Linear	281174.5	83290.2		
	C	Exponential	97373.8		758495.8	66.6
H. cocophillus	A	Spherical	127802.3		269887.6	5.2
	B	Linear	32851.5	121338.4		
	C	Linear	33906.9	55097.3		
C. onoensis	A	Linear	1717.3	940.7		
	B	Linear	13050.1	2385.94		
	C	Linear	79781.7	238558.8		

ROW INFLUENCE ON NEMATODES, ROOTS AND EDAPHIC FACTORS DISTRIBUTION

A statistical analysis (Kruskal and Wallis rank test) was performed to ascertain the symmetry of the sugarcane rows with nematode and root densities and with soil physico-chemical data. In a first hypothesis we assumed that symmetry exists, a situation which leads to four sets of sampling lines parallel to the sugarcane row (from the edge to the middle of the row). In a second hypothesis we considered that there is no symmetry, a situation which leads to seven sets of sampling lines. The results (Table 4) show that whatever the location and the number of sets, only *H. erythrinae* shows a significant preference near the rows. If only four sets of sampling lines parallel to sugarcane rows are considered, *P. zeae* exhibit significant higher densities along sugarcane rows only in location C on deeply-levelled soil. In location B, *H. cocophillus* shows higher densities between sugarcane rows, but this result reflects an aggregational property rather than a particular position with respect to the sugarcane row. There is a trend towards greater densities along rows in levelled locations compared to non-levelled location A.

Root densities are significantly higher along the row only in location B, while the same tendency is observed in locations A and C.

Concerning the physico-chemical components, at each location, the saturation percentage (S/T) was significantly higher between rows and the content in calcium, magnesium and sodium tended to be greater between rows (Table 5). More significant differences are observed if the seven sets of sampling lines are considered.

Table 4. *Plant parasitic nematode and roots position respect to sugarcane row in each location.*

	Location A		Location B		Location C	
	4*	7*	4*	7*	4*	7*
H. erythrinae	0.0002	0.0014	0.0001	0.0002	0.0001	0.0001
H. cocophillus	NS	NS	0.0128	0.0002	NS	0.0009
C. onoensis	NS	0.0283	NS	0.0001	NS	0.0035
P. zeae	NS	NS	NS	0.0096	0.0013	0.0034
Roots	NS	NS	0.0007	0.0025	NS	0.0130

* = sets of sampling lines;
Rank test of Kruskal and Wallis probability, NS = not significant.

Table 5. *Rank test of Kruskal and Wallis on physico-chemical parameters position in respect to, sugarcane row.*

Parameters	Location A		Location B		Location C	
	4*	7*	4*	7*	4*	7*
Carbon %	NS	NS	NS	NS	NS	0.0009
Nitrogen %	NS	NS	NS	0.0001	NS	0.0001
C/N	NS	NS	NS	0.0001	NS	0.0499
Bulk density g/cm^3	NS	NS	NS	NS	NS	0.0027
Humidity %	NS	0.0017	NS	NS	NS	0.0001
Ca meq %	0.0001	0.0003	NS	0.0001	0.0001	0.0001
K meq %	NS	NS	NS	NS	NS	0.0018
Na meq %	0.0297	0.0026	NS	0.0001	NS	0.0001
Mg meq %	NS	NS	NS	0.0075	0.0001	0.0001
CEC meq/100 g	NS	NS	NS	NS	NS	0.0397
S/T %	0.0002	0.0004	0.0093	0.0001	0.0044	0.0001

* = sets of sampling lines; NS = not significant.

INTERACTIONS AMONG NEMATODE SPECIES

Where hillocks were deeply levelled, *C. onoensis* distribution was dominated by a large patch located in a zone where the other species *H. cocophillus, H. erythrinae,* and *P. zeae* had their lowest densities (Fig. 1). Such a spatial segregation may reflect short-scale interactions among these species.

The presence of a negative spatial correlation between *C. onoensis* and the other species was assessed by means of the cross semi-variogram (Fig. 2). In location C, the cross semi-variance decreased with increasing distances thus revealing a negative spatial correlation between investigated variables. The *C. onoensis* high density patch is opposite to the other species high density patches. In location B the slope of the cross semivariogram is weaker, and even non existant in location A where the cross semi-variogram is " flat " (100 % nugget effect). The

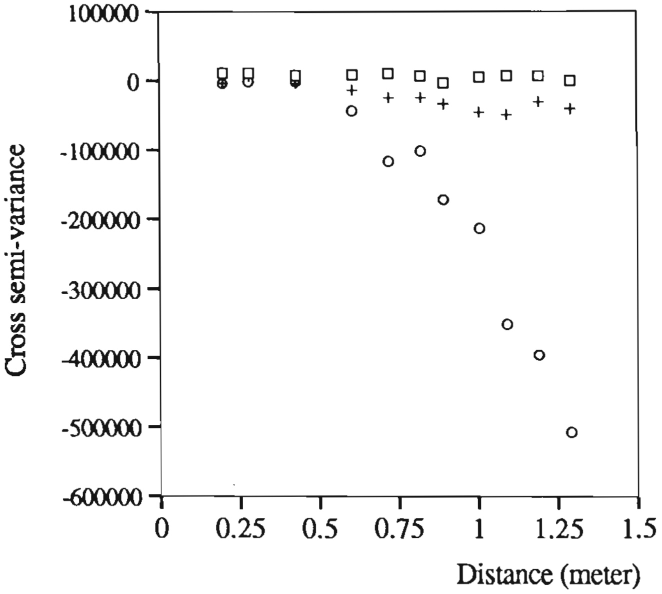

Fig. 2. *Cross semi-variograms for* Criconemella onoensis vs *sum densities of the other species in the different locations (Square = location A; plus sign = location B; circle = location C).*

cross semi-variograms indicate the absence of spatial correlation between *C. onoensis* and the other nematode species in locations A and B.

Discussion

Among the abiotic factors that govern nematode populations, moisture and temperature are generally considered to be most important (Norton, 1979). However Jones and Thomasson (1976) consider soil structure, and in particular the amount of inhabitable pore space, to be the prime soil properties affecting nematode communities.

In this study, the four nematode species presented marked spatial patterns in the three locations. The species *H. erythrinae* exhibited the same spatial pattern related to row and root density in all the locations. For this species, root resource seems to be one of the spatial determining factors.

The nematode *H. cocophillus* presented marked spatial patterns parallel to rows and in the direction of the slope, which can influence drainage, and water and nutrients flows. Topography has already been recognised as an important environmental parameter determining nematodes distribution (Barker & Nusbaum, 1971; Norton & Oard, 1981).

P. zeae and *C. onoensis* exhibited different spatial patterns, related to the intensity of hillock-levelling. The endoparasite *P. zeae* showed spatial patterns relate to rows only in deeply-levelled locations, where carbon, nitrogen, and potassium content were poorest. This species is able to complete its life cycle within the root. Individuals are released into the soil as the root decays and are able to penetrate immediately into freshly emerged roots from the base of the sugarcane clump. As with other strict endoparasitic nematodes, the soil phase of *P. zeae* is very restricted, so this species does not seem to be directly affected by soil properties but is influenced indirectly through the host plant response. In location A, where conditions are the best for plant growth, *P. zeae* spatial distribution is homogenous, while in the other locations this species seems concentrated along sugarcane rows, where root quantity is higher. Plant-parasitic nematodes are probably attracted by metabolic products or other factors originating from roots, such as roots exudates or CO_2 (Stolzy & Van Gundy, 1968; Klinger, 1972). In the three locations, roots attractants and their soil diffusates may be different due to clay and organic matter content and other environmental factors.

C. onoensis was less uniformly distributed than the other plant-parasitic nematodes in the sugarcane field. There were large variations in number between cane clump and the distribution within the root zone of individual cane was more variable than with other parasitic species. This may be due to biological factors. The locomotion of nematodes is generally by out-of-phase waves of muscle contraction in the dorsoventral plane, resulting in draconic (rather than snakelike) serpentine undulations. In contrast, in the criconematids the waves are in phase, so that movement is earthwormlike (Norton & Niblack, 1991). This different locomotion mode may contribute to the particular spatial patterns of *C. onoensis*. Nematodes movement is affected by soil moisture, texture, structure, compaction, and pore space (Jones & Thomasson, 1976). *C. onoensis* seems favored in location C where clay content and bulk density are higher than in the other locations. In addition, criconematids are sedendary ectoparasites which can stay up to a week feeding on the same cell (Hussey *et al.*, 1991), therefore eggs are laid in clumps by these pseudo-sedentary females, thus initiating a strongly aggregated spatial distribution. In thus case, soil properties may have a higher impact on *C. onoensis* than on other species because of its biological specificity.

Root quantities were lower in location B. That may be a local artefact due to fewer sugarcane clumps in the studied area, with row heterogeneity, or to root extraction technique. Previous studies conducted on hillock levelled fields show higher roots densities in location C than in location A. The location B should take an intermediate position (Barret *et al.*, 1991).

This study shows that soil properties, even in soils from the same origin, can exert a marked effect on the plant-parasitic nematode micro-spatial patterns. Soil density of *P. zeae* was greater along the sugarcane row in location C as already observed (Martin, 1967; Metha *et al.*, 1992). This may also be dependent on the continuous production of new roots in this zone. Nematode micro-distribution is primarily mediated by the distribution of food resource; for plant-parasitic nematodes, spacing, morphology, and physiology of the plant root system are primary determinants (Yeates, 1987; Ferris *et al.* 1990). Minimal or non-tillage practices in sugarcane fields may allow nematodes to remain in greater concentrations in the root zones and then promote a patchy distribution pattern (Barker & Campbell, 1981; Barker, 1985).

Similar tendency was already observed for other nematode species in a California vineyard (Ferris & McKenry, 1976). Noe and Campbell (1985) also found that in rows of tobacco crop plant parasitic nematodes were disposed in lines, with both high or low density, parallel to rows. Individual plants may support different nematode population densities (Goodell & Ferris, 1980). Within a field, nematode species and densities will vary widely among plants or even from one side of a plant to the other (Alby *et al.,* 1983), which can partly explain the assymetry observed between the two sugarcane rows in our study. This asymmetry appears more clearly in the deeply-levelled location C and thus for nematological and environmental data. This asymmetry is also the reflection of nematode aggregation characteristics due to individual host plant influences and edaphic properties.

Nematode density seems to be greater along sugarcane rows, in relation to root quantity. However, some soil chemical elements such as calcium, sodium, and magnesium appear to be in lower quantity along sugarcane rows. This peculiar distribution of cations may be due to the fact that roots are more numerous along the rows and regularly take up these cations for plant growth. Reuss *et al.* (1977, cited in Barker & Campbell, 1981) showed that nitrates distribution in agricultural fields where affected by the direction of crops rows.

The present results show that soil properties may be of importance in regulating nematode community spatial distribution. Location C, which corresponds to the lowest soil organic matter content, presents a nematode community in which spatial segregation seems strong among species. In opposition, this tendency decreases in location B and does not occur at all in location A. Although nematode competition is supposed to be weak, its members are constantly interacting with each other. Competition is usually the strongest between organisms that are most alike with respect to their physiological demands on the host (Eisenback, 1993). Nematode species may interact directly, as in the case of space competition among plant parasites within a root, or indirectly, if one species can decrease the suitability of the environment for colonization by other species (Freckman & Caswell, 1985).

The use of geostatistical analysis to study spatial distribution of plant-parasitic nematodes is very recent (Webster & Boag, 1992; Wallace & Hawkins, 1994; Robertson & Freckman, 1996; Rossi *et al.,* 1996) as is the use of cross semi-variograms to reveal antagonistic patterns between nematodes species (Delaville *et al.,* 1995). Using this tool, we observed that soil type influence the relationships between nematodes species and the spatial segregations among nematodes. It is known that competition can be modified by environmental factors (Eisenback & Griffin, 1987); we observed in this study that strong interactions appeared between *C. onoensis* and the other species only in deeply-levelled location where organic matter content was the poorest.

Conclusion

This study provided informations for greater consistency in nematode sampling nematodes in sugarcane, according to our objectives. In order to study relationships between nematodes and host-plant, sampling should be done along the rows. In contrast, to study relationships between nematodes and soil properties, sampling should be done in the middle of the space between rows were host-plant influence is supposed to be the lowest both on nematode populations and soil parameters.

The use of cross semi-variograms, when variables are regionalized, can be of great interest to show interactions among nematodes species and/or other variables e.g., *C. onoensis* against the other species in this study. This method can be used to look for relationship of nematodes with any environmental variables in term of spatial dependence. This relation can vary in respect to the environment at a very short scale, as observed here where antagonistic interactions among nematodes species were stronger in deeply-levelled soil.

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References

ALBY, T., FERRIS, J. M. & FERRIS, V. R. (1983). Dispersion and distribution of *Pratylenchus scribneri* and *Hoplolaimus galeatus* in soybean field. *J. Nematol.,* 15 : 418-426.

BARKER, K. R. (1985). Sampling nematode communities. *In :* Barker, K. R., Carter, C. C. & Sasser, J. N. (Eds). *An advanced treatise on* Meloidogyne, *Vol. 2.* Raleigh, USA, North Carolina State University Graphics : 3-17.

BARKER, K. R. & CAMPBELL, C. L. (1981). Sampling nematode population. *In :* Zuckerman, B. M., Mai, W. F. & Rohde, R. A. (Eds). *Plant parasitic nematodes, Vol. 3.* New York, Academic Press : 451-473.

BARKER, K. R. & NUSBAUM, C. J. (1971). Diagnostic and advisory programs. *In :* Zuckerman, B. M., Mai, W. F. & Rohde, R. A. (Eds). *Plant parasitic nematodes, Vol. 1.* New York, Academic Press : 232-239.

BARRET, P., CADET, P., FELLER, C. & ALBRECHT, A. (1991). Le remodelage des terres à la Martinique. 2. Variabilité intra-parcellaire du remodelage en relation avec la productivité végétale. *Cah. ORSTOM, Sér. Pédol.,* 26 : 105-113.

CHEVIGNARD, T., FELLER, C., ANDREUX, F. & QUANTIN, P. (1987). Le remodelage des terres à la Martinique. 1. Modification des propriétés de ferrisols et d'andosols cultivés en canne à sucre. *Cah. ORSTOM, Sér. Pédol.,* 23 : 223-236.

CRESSIE, N. (1985). Fitting variogram models by weighted least squares. *Math. Geol.,* 17 : 563-586.

DELAVILLE, L., ROSSI, J. P. & QUÉNÉHERVÉ, P. (1995). Microspatial structure of a sugarcane nematode community on an Ultisol in Martinique. *Nematologica,* 41 : 295 [Abstr.].

EISENBACK, J. D. (1993). Interactions between nematodes in cohabitance. *In :* Khan, M. W. (Ed.). *Nematode interactions.* London, UK, Chapman & Hall : 134-174.

EISENBACK, J. D. & GRIFFIN, G. D. (1987). Interactions with other nematodes. *In :* Veech, J. A. & Dickson G. W. (Eds). *Vistas on nematology.* Hyattsville, MD, USA, Soc. Nematologists Inc. : 313-320.

FERRIS, H. & MC KENRY, M. V. (1976). Nematode community structure in a vineyard soil. *J. Nematol.,* 8 : 131-137.

FERRIS, H., MULLENS, T. A. & FOORD, K. E. (1990). Stability and characteristics of spatial description parameters for nematode populations. *J. Nematol.,* 22 : 427-439.

FRECKMAN, D. W. & CASWELL, E. P. (1985). The ecology of nematodes in agroecosystems. *A. Rev. Phytopath.,* 23 : 275-296.

GOODELL, P. & FERRIS, H. (1980). Plant-parasitic nematode distributions in an alfalfa field. *J. Nematol.,* 12 : 136-141.

HUSSEY, R. S., MIMS, C. W. & WESTCOTT, S. W. (1991). Ultrastructure of food cells in roots parasitized by *Criconemella xenoplax. J. Nematol.,* 23 : 533-534 [Abstr.].

JONES, F. G. W. & THOMASSON, A. J. (1976). Bulk density as an indicator of pore space in soils usable by nematodes. *Nematologica,* 22 : 133-137.

KLINGLER, J. (1972). The effect of single and combinated heat and CO_2 stimuli at different ambient temperature on the behavior of two plant parasitic nematodes. *J. Nematol.,* 4 : 95-100.

MARTIN, G. C. (1967). Plant parasitic nematodes associated with sugarcane production in Rhodesia. *FAO Pl. Prot. Bull.,* 15 : 45-58.

MEHTA, U. K., SUNDARARAJ, P. & NATESAN, N. (1992). Horizontal and vertical distribution of *Pratylenchus zeae* for five consecutive years in a South Indian sugarcane field. *Afro-Asian J. Nematol.,* 2 : 67-73.

NOE, J. P. & CAMPBELL, C. L. (1985). Spatial pattern analysis of plant-parasitic nematodes. *J. Nematol.,* 17 : 86-93.

NORTON, D. C. (1979). Relationship of physical and chemical factors to populations of plant-parasitic nematodes. *A. Rev. Phytopath.,* 17 : 279-299.

NORTON, D. C. & NIBLACK, T. L. (1991). Biology and ecology of nematodes. *In :* Nickle, W. R. (Ed.). *Manual of agricultural nematology.* New York, USA, Marcel Dekker Inc. : 47-72.

NORTON, D. C. & OARD, M. (1981). Plant-parasitic nematodes in loess toposequences planted with corn. *J. Nematol.,* 13 : 314-321.

ROBERTSON, G. P. & FRECKMANN, D. W. (1996). The spatial distribution of nematode trophic groups across a cultivated ecosystem. *Ecology,* 76 : 1425-1432.

ROSSI, J. P., DELAVILLE, L. & QUÉNÉHERVÉ, P. (1996). Microspatial structure of a plant-parasitic nematode community in a sugarcane field in Martinique. *Appl. Soil Ecol.,* 3 : 17-26.

SEINHORST, J. W. (1950). De betekenis van de toestand van de grond voor het optreden van aanstasting door het stengelaaltje (*Ditylenchus dipsaci* (Kühn) Filipjev). *Tijdschr. Pl. Ziekt,* 56 : 292-349.

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

STOLZY, L. H. & VAN GUNDY, S. D. (1968). The soil as an environment for microflora and microfauna. *Phytopathology,* 58 : 389-399.

THIOULOUSE, J. (1989). Statistical analysis and graphical display of multivariate data on the Macintosh. *Computer Applic. Biosci.,* 5 : 287-292.

THIOULOUSE, J. (1990). Macmul and Graphmu : two Macintosh programs for the display and analysis of multivariate data. *Computers & Geosci.,* 16 : 1235-1240.

WALLACE, M. K. & HAWKINS, D. M. (1994). Applications of geostatistics in plant nematology. *J. Nematol.,* 26 : 626-634.

WEBSTER, R. & BOAG, B. (1992). Geostatistical analysis of cyst nematodes in soil. *J. Soil Sci.,* 43 : 583-595.

YEATES, G. W. (1987). How plants affect nematodes. *Adv. ecol. Res.,* 17 : 61-113.

YOST, R. S., TRANGMAR, B. B., NDIAYE, J. P. & YOSHIDA, N. S. (1989). *Geostatistical software for PC-DOS and MS-DOS.* Honolulu, HA, USA. Dept. Agron. Soil Sci., Univ. Hawaii, 31 p.