

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 zae* presented a spatial pattern related to the row. This was also observed with *Helicotylenchus erythrinae* in the three locations. On the contrary, *Criconebella onoensis* did not show a marked spatial pattern related to the row or root quantity in any of the situations. *Hemicriconebellus 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 zae* présente une structure spatiale liée au rang de canne. *Helicotylenchus erythrinae* montre cette répartition particulière dans les trois situations. Au contraire, *Criconebella 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. *Hemicriconebellus 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 : *Criconebella onoensis*, edaphic factor, geostatistics, *Helicotylenchus erythrinae*, *Hemicriconebellus cocophillus*, hillock levelling, Martinique, microspatial structure, nematodes, *Pratylenchus zae*, 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 feed-

ing 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 m²) 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 m 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 cm³) 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 cm³ (soil and roots) and root density was expressed as dry weight per 250 cm³ soil.

With each core, a small volume of soil (ca 100 cm³) 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 zaeae* Graham, 1951, and three ectoparasites, *Criconebella onoensis* (Luc, 1959) Luc & Raski 1981, *Helicotylenchus erythrinae* (Zimmermann, 1904) Golden, 1956, and *Hemicriconebellodes 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 H ₂ O	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 ($P < 0.05$).

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. zaeae* 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 de-

Table 2. Mean, standard error (in parentheses) and coefficient of variation [between angled brackets] of plant-parasitic nematode numbers per 250 cm³ of soil in each location and roots weight.

	Location A	Location B	Location C
<i>H. erythrinae</i>	239 a (59.90) [199]	415 b (58.85) [113]	134 a (25.21) [150]
<i>H. cocophillus</i>	683 a (64.72) [75]	572 a (67.07) [93]	531 a (65.22) [98]
<i>C. onoensis</i>	37 a (10.53) [226]	104 a (20.21) [154]	792 b (143.77) [144]
<i>P. zaeae</i>	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 ($P < 0.05$).

creasing order of density as *P. zaeae* > *H. cocophillus* > *H. erythrinae* > *C. onoensis* in locations A and B while in location C the order is *C. onoensis* > *P. zaeae* > *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. zaeae* (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. zaeae*. 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. zaeae* and *H. cocophillus*. They were higher in the levelled location. The species *C. onoensis* and *H. erythrinae* had

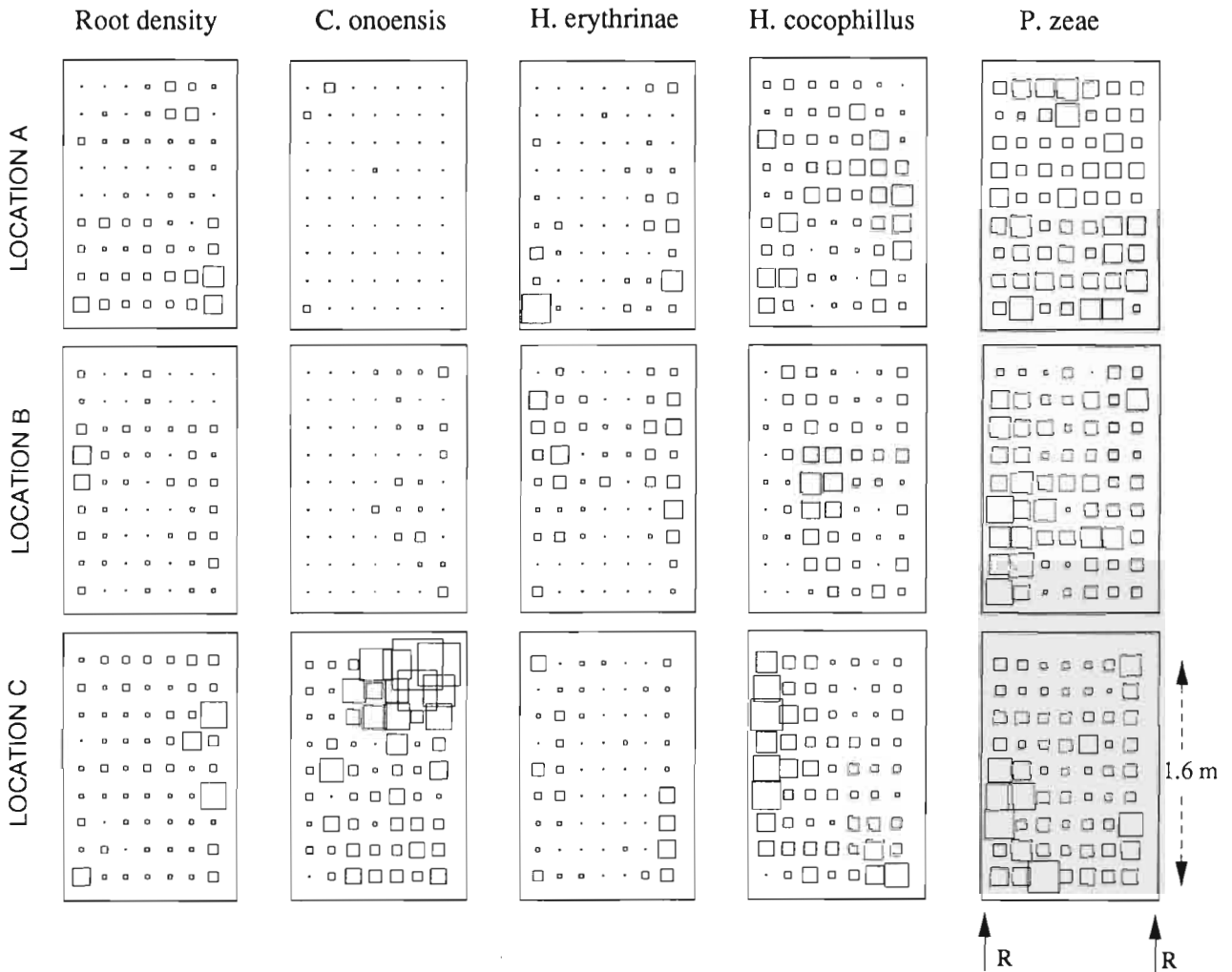


Fig. 1. Graphic representation of the sampling area with square sizes proportional to the number of nematodes or root densities per 250 cm³ in each location (R = position of sugarcane rows).

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 estima-

tion. 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. zaeae* 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. zaeae* 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.

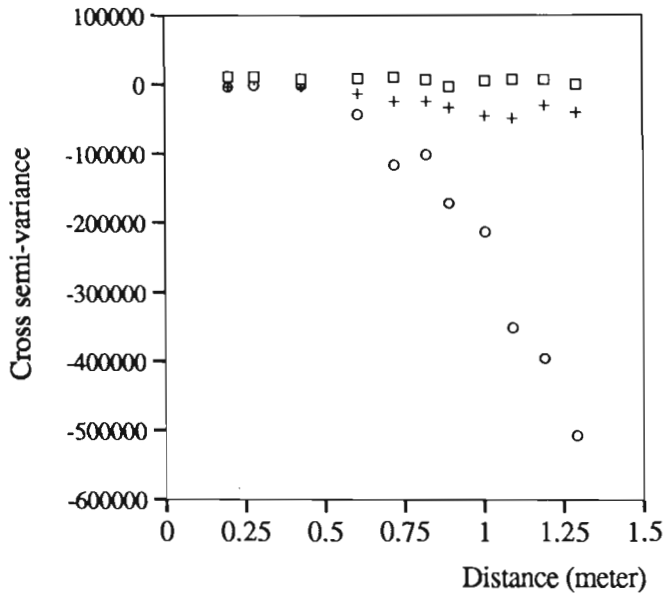


Fig. 2. Cross semi-variograms for *Criconemella onoensis* vs sum densities of the other species in the different locations (Square = location A; plus sign = location B; circle = location C).

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. zaeae and *C. onoensis* exhibited different spatial patterns, related to the intensity of hillock-leveling. The endoparasite *P. zaeae* 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. zaeae* 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. zaeae* 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 CO₂ (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 sedentary 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. zaeae* 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 asymmetry 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 where 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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