

# Microspatial structure of a plant-parasitic nematode community in a sugarcane field in Martinique

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## Abstract

The spatial pattern of four species of plant-parasitic nematodes in a sugarcane crop in Martinique was analysed using geostatistics. Aggregation of populations was first described with the variance to mean ratio and Morisita's index. The indices showed that nematodes had clumped distributions. Geostatistical analysis demonstrated that the nematode data were autocorrelated and allowed a fine description of the species density patterns. Correspondence analysis was used to ordinate the data and showed the presence of an antagonism between *Criconemella onoensis* and the other species. A cross semi-variogram indicated a negative cross correlation between the pattern of *Criconemella onoensis* and the pattern of the sum of the other species present at the study site.

**Keywords:** Nematode community; Microspatial structure; Soil; Geostatistics; Sugarcane

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## 1. Introduction

Assessing the spatial variability of nematode community is useful in understanding the ecology of the species encountered and their population dynamics in relation to their habitat and food resources. Furthermore, from an economical point of view, the knowledge of existing patches of plant parasites should allow to define more efficient sampling strategies perhaps necessary to apply tailored inputs.

Ferris et al. (1990) defined two components in the spatial pattern of plant-parasitic nematode populations: (i) a macro-distributional component occurring at the field scale; (ii) a micro-distributional component occurring at a smaller spot scale. The macro-distribution is affected by (i) environmental parameters such

as soil texture, soil moisture or drainage pattern that constitute major factors of habitat suitability and (ii) external factors such as cropping history and selection pressure of differential host plant distribution. The micro-distribution is linked to life history and feeding strategy of the different species. However, nematode micro-distribution is primarily mediated by food resource distribution. Thus the spatial pattern of plant-parasitic species is strongly affected by host plant spacing (Ferris et al., 1990), root system architecture (Quénéhervé, 1990) and plant physiology (Yeates, 1987). These combined phenomena lead to the presence of more or less clumped distributions for most of the soil dwelling nematodes.

Traditional methods for spatial pattern analysis are based on the calculation of frequency distributions and indices of dispersion (Elliot, 1971; Campbell and Noe, 1985).

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Methods based on frequency distributions consist in fitting a discrete probability distribution to sample count frequency data to indicate whether the distribution is random or not. Agreement with Poisson distribution is used to indicate a random spatial pattern. Contagious spatial patterns are often well described by the negative binomial model (reviewed by Campbell and Noe, 1985).

Another approach uses indices of dispersion. Various indices have been proposed as measures of spatial aggregation. Among them, the variance to mean ratio is compared with 1 with a  $\chi^2$  test to indicate departure from randomness (Elliot, 1971). This index is less than 1 for a regular distribution, equal to 1 for a random pattern and higher than 1 for a clumped pattern. The variance to mean ratio increases with increasing aggregation but is affected by sampling unit size and the total number of individuals in the sample (Elliot, 1971).

Taylor's (1961, 1984) power law is based on the non-linear relationship between sample mean and variance. The method yields an index of dispersion that is a quantitative measure of population aggregation (Boag and Topham, 1984; McSorley and Dickson, 1991) and can be used to determine normalizing transformations (Merny and Déjardin, 1970; Duncan et al., 1989). The use of that index may be costly in terms of time and labor as it requires repeated estimates of mean and variance.

Comparing aggregation tendency of populations with largely diverging mean densities implies the use of an index insensitive to variation in mean density. Morisita (1971) has developed such an index of dispersion independent of the sample mean and the total number of individuals in samples ( $x$ ) but which is strongly linked to the total number of sampling units. It is defined as

$$I_s = n \left( \sum_{i=1}^n (Z_i^2) - \sum_{i=1}^n Z_i \right) / \left[ \left( \sum_{i=1}^n Z_i \right)^2 - \sum_{i=1}^n Z_i \right]$$

where  $n$  is the number of sampling units and  $Z_i$  the count for the  $i$ th sampling unit.

Morisita's index is a good comparative index of dispersion for samples containing the same number of sampling units. It equals 1 for random distributions, is less than 1 for regular distributions and greater than 1 for clumped distributions. Departure from randomness can be tested by comparison with a  $\chi^2$  value (Elliot, 1971).

Both frequency distribution methods and indices of aggregation provide limited information on the spatial pattern since information on the actual location of samples with respect to each other is ignored. The number of patches (if any), their shapes, the presence of density gradient and other characteristics of the distribution pattern remain unknown (Nicot et al., 1984; Debouzie and Thioulouse, 1986).

The available literature indicates that animal populations currently exhibit spatial pattern at various scales (see review in Liebhold et al., 1993). Several authors used geostatistics to examine the spatial pattern of nematodes at the field scale (Webster and Boag, 1992; Robertson, 1994; Wallace and Hawkins, 1994). Robertson (1994) showed the presence of a spatial structure of various nematode feeding groups ranging from 2 to 75 m. The resulting vast ranges of spatial dependence justify the use of geostatistics to quantify spatial autocorrelation over a wide range of scales, in contrast to conventional methods (dispersion indices), which are limited to sampling unit scale (Nicot et al., 1984).

If the observation made at one spot gives information regarding the values of a neighbouring point, the variable is said to be spatially dependent, i.e. regionalized or autocorrelated. In this case, classical statistics are no longer appropriate and specific methods, such as geostatistics should be applied. The geostatistics were primarily developed in geology (Matheron, 1963) and used later in soil science (Burgess and Webster, 1980a,b). Their application in soil ecology is even more recent (Robertson, 1987; Webster and Boag, 1992; Wallace and Hawkins, 1994; Rossi et al., 1995). The semi-variogram is the central tool of geostatistics. It quantifies both the scale and the intensity of the spatial variation and is the basis for optimal interpolation by kriging. The kriging estimation technique allows values at unsampled site to be estimated and hence, to draw accurate isarithmic maps of the considered variable in the sampled area.

Furthermore, autocorrelation among data carries statistical problems. The relationship between two autocorrelated variables cannot be investigated through the Pearson correlation coefficient because sample independence is not met if data are spatially correlated. Legendre (1993) underlines that in the case of two positively autocorrelated variables, the confidence interval around the Pearson correlation coefficient is underestimated by the classical method.

Estimation of the cross semi-variogram constitutes a way of investigating spatially cross correlated variables, i.e. co-regionalized variables. Its shape reveals the presence of a cross correlation, either negative (negative slope of the cross semi-variogram) or positive (positive slope of the graph).

The aim of the present work was to describe the spatial pattern of a plant-parasitic nematode community in a sugarcane field at the fine scale of the inter-row spacing. Geostatistics were used in addition to conventional approaches based on aggregation indices.

## 2. Materials and methods

Most studies using dispersion indices (Shaukat and Khan, 1993) and geostatistics (Webster and Boag, 1992) in relation to nematode distribution in soil have been conducted either on bare soils just before replanting or after harvest, or with plants of sufficiently high density that their root systems may be regarded as entirely mixed up. Another point to mention is the necessity of using plants which are either in pure stands or where there is an even mix of species in order to avoid misinterpretation of results due to nematode host specificity. When considering cultivated plants the parameter to consider first is the space between plants, this being especially the case with perennials.

In northeast Martinique, the plant-parasitic nematode community of sugarcane crop cv. B5992 in the ninth ratoon was investigated between two sugarcane rows. The soil type is an Ultisol (ferrallitic soil) developed on volcanic ashes. A regular grid (1.6 m long, 1.2 m wide) with a sampling interval of 20 cm was located between two sugarcane rows (separating distance 1.2 m) where 63 (9 × 7) undisturbed samples were taken. At each sampling spot, soil and roots were collected using a 5.5 cm diameter coring tool (volume 237 cm<sup>3</sup>) in the 0–10 cm soil layer. Roots were separated from soil by wet-sieving before elutriation. Nematodes were extracted from the soil by the elutriation–sieving technique (Seinhorst, 1962) while a mist chamber (Seinhorst, 1950) was used to extract the nematodes from the roots. Nematode density was expressed as the number of individuals per 100 cm<sup>3</sup> soil + roots.

### 2.1. Correspondence analysis

Correspondence analysis (CA) was used for ordination of nematode data and to investigate the relationships between the different species. Data analysis was performed using ADE 3.6 software developed by the University of Lyon I (France) (Chessel and Dolédec, 1992).

### 2.2. Graphical displays

Sampling points were displayed graphically using squares, the sizes of which were proportional to the numbers of nematodes using GRAPHMU software written by J. Thioulouse (1989, 1990) (Fig. 1).

### 2.3. Geostatistics

The central tool of spatial analysis with geostatistics is the semi-variogram which describes the evolution of the semi-variance with the inter-sample distance.

The semi-variance is estimated using the formula

$$\gamma(h) = 1/2M(h) \sum_{i=1}^{M(h)} \{ [Z(x_i) - Z(x_i + h)]^2 \}$$

where  $M(h)$  is the number of sample pairs at each distance interval  $h$  and  $Z(x_i)$  and  $Z(x_i + h)$  are the values of the variable at any two places separated by distance  $h$ .

The semi-variogram is the plot of the semi-variance against the distance. Its shape indicates whether the variable is spatially dependent. The more alike the values separated by a given distance, the lower the semi-variance. Thus, generally the semi-variance increases with increasing distance as similarity between points decreases. If the variable is not spatially dependent, the semi-variance fluctuates around the sample variance and the semi-variogram is 'flat'.

A theoretical model is fitted to the semi-variogram calculated from sample values. The model must be positive definite (Armstrong and Jabin, 1981; McBratney and Webster, 1986) and generally only authorized functions are used in semi-variogram modelling (for a review see Webster, 1985). There are two classes of models, bounded and unbounded models. In bounded models, the semi-variance increases with increasing distance until it reaches a certain value (the sill variance) for a given distance interval (the range,

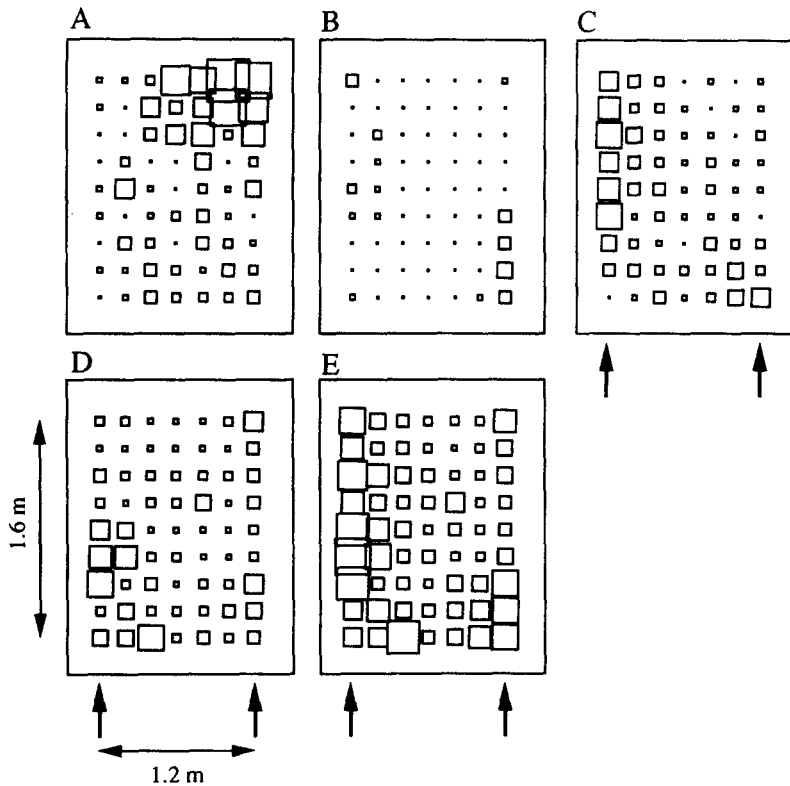


Fig. 1. Maps of the sampled plot with square sizes proportional to the number of nematodes per 100 cm<sup>3</sup> soil at each sampling point. (A) *Criconemella onoensis*; (B) *Helicotylenchus erythrinae*; (C) *Hemicriconemoides cocophillus*; (D) *Pratylenchus zeae*; (E) sum of *Helicotylenchus erythrinae*, *Hemicriconemoides cocophillus* and *Pratylenchus zeae*. Arrows indicate the direction of the sugarcane rows.

a). Points separated by a distance larger than the range are statistically independent. For distances larger than the range the semi-variance remains fixed, leading to a plateau in the semi-variogram. The intercept of the semi-variogram is generally a non-zero value called the nugget variance ( $C_0$ ). It accounts for measurement errors (human nugget) and variability due to unseen patterns (occurring at scales shorter than the minimum inter-sample distance). The sill variance minus the

nugget variance is the spatial variance (C). This term accounts for the part of the total variance that can be modeled by the spatial structure. In unbounded models, the semi-variance does not reach a plateau and appears to increase without limit.

The simplest unbounded model is the linear model where the semi-variance increases with distance and is modeled by the following linear relationship

$$\gamma(h) = C_0 + wh \text{ for } h > 0$$

Table 1  
Sample statistics and cluster indices from samples of plant-parasitic nematodes

Species	Mean	Variance	Variance to mean	Morisita's index
<i>Criconemella onoensis</i>	316.7	208370.8	119.9*	3.04*
<i>Helicotylenchus erythrinae</i>	53.4	6405.1	284.19*	3.20*
<i>Hemicriconemoides cocophillus</i>	212.3	42871.8	201.9*	1.93*
<i>Pratylenchus zeae</i>	233.2	39771.5	404.24*	1.72*

Means are expressed in numbers of nematodes per 100 cm<sup>3</sup> soil. Asterisks indicate significant clumped distribution ( $P < 0.05$ ).

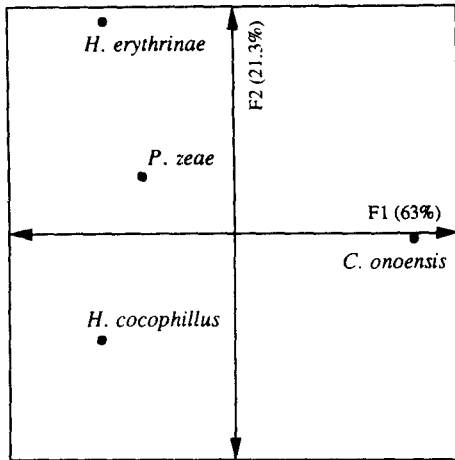


Fig. 2. Plane of first two axes of CA. The first axis represents 63% of the total inertia and the second 21.3%.

$$\gamma(h) = 0 \text{ for } h = 0$$

where  $h$  is distance,  $C_0$  is the nugget variance and  $w$  is slope. A straight line is fitted to the observed values, the intercept being the nugget variance ( $C_0$ ).

In this study we met bounded sample semi-variograms which were modeled by the exponential model. Its formula is

$$\gamma(h) = C_0 + C[1 - \exp(-h/r)] \text{ for } h > 0$$

where  $r$  is a distance parameter that defines the spatial scale of the variation. The sill is approached asymptotically and there is no strict range. Therefore, a common rule of thumb is to regard the effective range as  $a' = 3r$  which is the distance at which the semi-variance reaches approximately  $C_0 + 0.95C$  (Webster, 1985).

Once the semi-variogram model is determined, the kriged estimate of a variable  $Z$  at location  $X_0$  is calculated using the formula

$$Z^*(x_0) = \sum_{i=1}^n \lambda_i Z(x_i)$$

where  $\lambda_i$  represents weights applied to each of the  $i$  neighboring samples  $Z(x_i)$ . The weights  $\lambda_i$  are chosen to ensure (i) absence of bias and (ii) minimum estimation variance. The weights  $\lambda_i$  are derived from a set of equations determined by the semi-variogram model and the location and orientation of the sample points

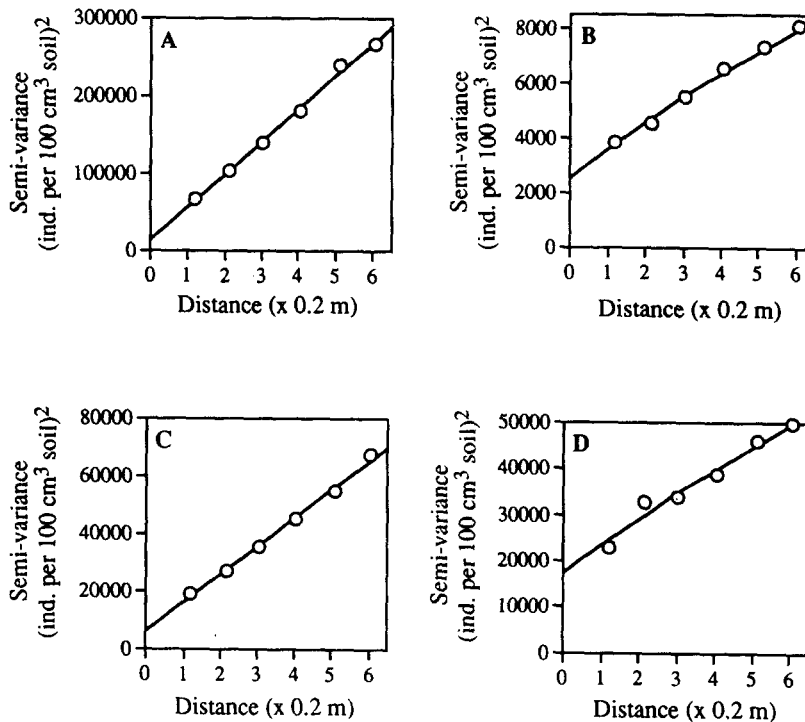


Fig. 3. Semi-variograms for plant-parasitic nematode density per 100 cm<sup>3</sup> soil. (A) *Criconebella onoensis*; (B) *Helicotylenchus erythrinae*; (C) *Hemicriconemoides cocophillus*; (D) *Pratylenchus zaeae*. Distance unit is the minimum inter-sample distance (20 cm).

Table 2  
Model parameters of theoretical semi-variograms of four plant-parasitic nematode species

Species	Model	$C_0$	Slope	$C$	$C + C_0$	$r$	Range
<i>Criconemella onoensis</i>	Linear	14203.2	42436.5	–	–	–	–
<i>Helicotylenchus erythrinae</i>	Exponential	2510.4	–	14510.7	17021.2	13.1	39.3
<i>Hemicriconemoides cocophillus</i>	Linear	6037.4	9808.6	–	–	–	–
<i>Pratylenchus zeae</i>	Exponential	17338.3	–	135360.9	152699.2	22.3	66.9

$C_0$  and  $C$  are expressed in (number of nematode per 100 cm<sup>3</sup> soil)<sup>2</sup>;  $r$  and the range are expressed in distance units of 20 cm.

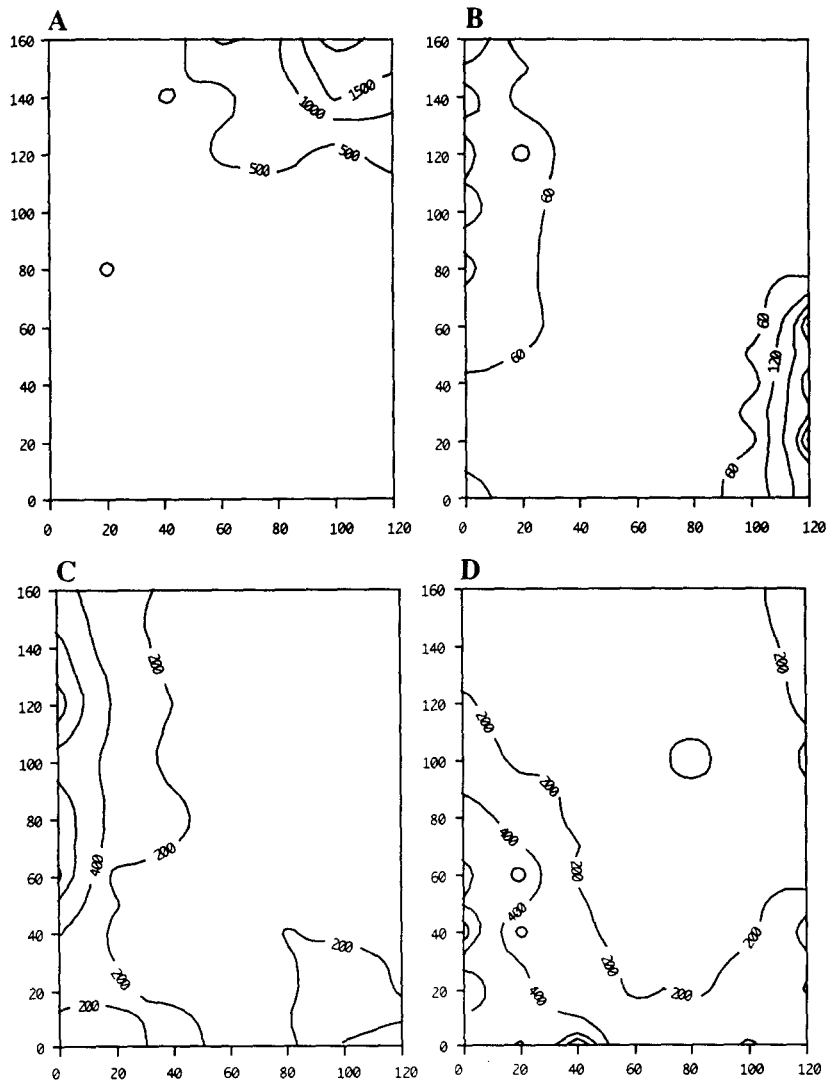


Fig. 4. Contour maps of the estimates by kriging of the nematode density per 100 cm<sup>3</sup> soil. (A) *Criconemella onoensis*; (B) *Helicotylenchus erythrinae*; (C) *Hemicriconemoides cocophillus*; (D) *Pratylenchus zeae*.

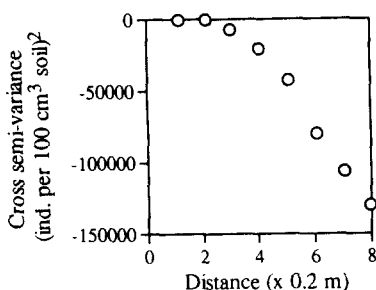


Fig. 5. Cross semi-variogram for *Criconemella onoensis* and the sum of the other species. Distance unit is the minimum inter-sample distance (20 cm).

relative to each other and the points where estimation is needed.

Kriged estimates of soil volume can be made for unsampled points of the same size as those on which measurements were done (punctual kriging) for larger blocks of a given area (block kriging). The advantage of kriging is to provide minimum estimation error (estimation variance) that can be used to build maps of estimate reliability.

Spatial correlation (i.e. coregionalization) between pairs of variables was evaluated with cross semi-variance analysis. Cross semi-variance between the variables  $V$  and  $W$  is estimated using the formula

$$\gamma_{vw}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [V(x_i) - V(x_i + h)] [W(x_i) - W(x_i + h)]$$

where  $N(h)$  is the number of data pairs separated by distance  $h$ .

The cross semi-variogram is the plot of cross semi-variance against the distance  $h$ . It shows the same features as the semi-variogram except that cross semi-variance may be negative if there is a negative correlation between variables.

In this study, the semi-variograms were computed for each species using the program VAR5 (Yost et al., 1989), part of a geostatistical package developed by the University of Hawaii. VAR5 provides both semi-variogram and an automatic fitting procedure based on modified least squares procedure (Cressie, 1985). Cross semi-variograms between different nematode densities were calculated again with VAR5 in order to find possible spatial correlation between species distributions.

### 3. Results

At the study site the plant-parasitic nematode community comprised four main species: one endoparasite, *Pratylenchus zeae* (Graham, 1951) and three ectoparasites, *Criconemella onoensis* (Luc, 1959) Luc and Raski, 1981, *Helicotylenchus erythrinae* (Zimmermann, 1904) Golden, 1956 and *Hemicriconemoides cocophillus* (Loos, 1949), Chitwood and Birchfield, 1957 (Table 1). The three species *Paratrichodorus anthurii* (Baujard and Germani, 1985), *Paratylenchus elachistus* (Steiner, 1949) and *Xiphinema setariae* (Luc, 1958) were encountered at very low density (respectively 1.1, 0.4 and 0.6 individuals per 100 cm<sup>3</sup> soil) and were not taken into account in the analysis.

The variability of the recorded density in each sample unit was high and led to high variance values (Table 1) which are common in nematology. The variance to mean ratios were significantly higher than 1 ( $P < 0.05$ ,  $\chi^2$  test, see Elliot, 1971) indicating clumped spatial distributions for each species (Table 1). Morisita's index of dispersion was calculated (Table 1) and this also showed the aggregative nature of the species pattern ( $P < 0.05$ ).

The first axis of the CA accounted for 63% of the total variance. Along this axis, the density of *C. onoensis* was opposed to that of the other species (Fig. 2). A description of nematode density patterns was obtained by simple graphical displays (Fig. 1). These illustrate (Figs. 1(A)–1(D)) the spatial pattern of each species density. Fig. 1(E) shows the pattern of the sum of the species that are opposed to *C. onoensis* along the first axis.

Semi-variograms were estimated for each species and theoretical models were fitted (Fig. 3). For each species, the semi-variance increased in an almost linear way with increasing distance. The resulting positive slopes indicated that the variables were spatially structured. A linear model was fitted to sample semi-variogram for *C. onoensis* and *Hemicriconemoides cocophillus* while an exponential model was more suitable for sample semi-variogram of *Helicotylenchus erythrinae* and *Pratylenchus zeae* density. Parameters of the models are given in Table 2.

Values of the different variables were estimated at points located on a grid with a 10 cm side superimposed on the sampling scheme. At each point, estimates were

done by punctual kriging and these were used to draw the contour maps displayed in Fig. 4.

Results of the CA indicate an opposition between *C. onoensis* and the other plant-parasitic species. The cross semi-variance analysis was used to investigate further the spatial co-occurrence between that species and the others. The cross semi-variance tended to decrease with increasing distance since each semi-variance value was negative (Fig. 5). This shape revealed the presence of a consistent negative relationship between the density of *C. onoensis* and that of the other species.

#### 4. Discussion

In the sugarcane field investigated, each species had a significantly clumped spatial distribution at the scale of the sampling unit size. In view of the size of the surface investigated (63 sampled points over 1.2 m × 1.6 m), these patterns correspond to the micro-distributional component of the spatial distribution proposed by Ferris et al. (1990). *Criconemella onoensis* had the largest variance to mean ratio but Morisita's index was higher for *Helicotylenchus erythrinae*. This difference in aggregation assessment is due to the differences in species density, the variance to mean ratio being influenced by the total number of individuals in the sample (Elliot, 1971). In contrast, Morisita's index is only influenced by the number of sampling units and therefore must be preferred as a method of comparing species aggregation if densities vary.

However, aggregation indices provide limited information because they are restricted to the sampling unit scale. Other methods are needed if investigations are to be extended to larger scales, geostatistics being one of these. At the scale of the sampled plot, simple graphical displays showed the presence of complex spatial patterns of plant-parasitic nematode species. Further, the semi-variograms demonstrated the consistency of these structures. Kriging provided estimates of species density at points where no samples were taken, thus allowing accurate contour mapping of the variable through the whole sampled area.

Correspondence analysis showed that the major source of data heterogeneity (63% of the total variance) is explained by an opposition between *C. onoensis* and the other species (Fig. 2). Comparison of the

pattern of *C. onoensis* (Figs. 1(A) and 4(A)) and the distribution of the other species (Fig. 4(E)) suggests the presence of antagonistic patterns. The population of *C. onoensis* is essentially concentrated in the upper right part of the plot where the density of the other species is lowest. The consistency of this negative relationship was demonstrated by the cross semi-variogram that exhibits a negative slope (Fig. 5).

It is generally recognized that micro-distribution of nematodes is governed by food resource patterns and the feeding strategy of the species.

The feeding strategy of *C. onoensis* and some other criconematids is unusual in that they behave as sedentary ectoparasites. They may stay up to 1 week feeding on the same cell (Hussey et al., 1991) and consequently all eggs are deposited at the same location, thus leading to highly clumped distributions. In contrast, other plant-parasitic species move throughout the soil and their eggs can be more evenly distributed. These biological specificities are of importance in understanding micro-distributional patterns of the nematode community. The particular feeding strategy of some criconematids may explain the spatial pattern (Fig. 1(A)) characterized by a strong patch, although *Helicotylenchus erythrinae* appears to be more aggregated. However, the opposed distributions observed between *C. onoensis* and the other species remain unexplained. One hypothesis may be that the presence of small patches in which *C. onoensis* occurs at high density results from strong competition with other plant-parasitic species. However, caution is needed, possible competitive interactions must be demonstrated and species behavior better documented.

Since the sampled area was small, the relative size of the support of observations may be considered as large (total surface of the 63 samples: surface of the plot = 7.8%). However, reducing within-sample variability using smaller sampling units would increase measurement errors associated with nematode sampling, extraction and counting. The result would be increased nugget variance.

From a practical viewpoint, the existence of highly structured pest populations throughout the field complicates the design of sampling schemes intended to determine population size. Designing optimal sampling schemes is possible after the semi-variogram has been established (McBratney and Webster, 1981). Therefore, armed with the semi-variogram, one may deter-



mine the actual pattern of the pathogen, apply tailored input of pesticide and determine an optimal sampling scheme.

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