

# Identification of soil factors that relate to plant parasitic nematode communities on tomato and yam in the French West Indies

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## Abstract

A soil and nematode survey of tomato and yam crops was made in Martinique (French West Indies). Each sample was divided into two parts, one for the nematode study and one for the soil analysis. The coupling of the data was made using the coinertia analysis. For tomato plants which were grown from seeds, the nematode–soil relationships were very strong. For the two varieties of yams, *Dioscorea cayenensis-rotundata* and *D. alata*, whose infested seed tubers carry nematodes into the field, the relationships were weaker and depended on the yam variety. For *D. cayenensis-rotundata*, which was attacked by the endemic parasite *Pratylenchus coffeae*, the relationship between nematode community and soil type was strong. For *D. alata*, this relationship was weaker because it is mainly parasitised by the exotic species, *Scutellonema bradys*, which is exclusively introduced into the field with the seed tuber, whatever the soil type. Soil texture was the most important factor explaining the presence of some species. However, *Meloidogyne* spp. and the ectoparasitic species such as *Xiphinema* spp. were associated with light andosols; *Aorolaimus luci* needed, in addition, higher levels of organic matter. *P. coffeae* preferred any type of soil rich in organic matter and its abundance seemed influenced by calcium and magnesium content or pH. In contrast, *P. brachyurus* did not appear to be sensitive to any of the measured physico–chemical soil characteristics. © 1998 Published by Elsevier Science B.V. All rights reserved.

**Keywords:** Plant parasitic nematodes; Nematode–soil relationships; Coinertia analysis; Martinique; *Dioscorea* spp.; *Lycopersicon esculentum*

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## 1. Introduction

Plant parasitic nematodes have biological characteristics that distinguish them from other organisms that affect the growth of plants, viz, they are rela-

tively immobile and spend at least part of their life cycle within the soil matrix (Wallace, 1963). There, in the soil, they are dependent upon all events that happen in and on the field in which they live. As such, they are comparable to an agronomic factor, such as organic matter, and they can be managed in the same way, at the field scale (Greenland and Nye, 1959; Yeates, 1984). For example, fallowing can be used to increase the organic matter content of soil (Floret and Serpantié, 1993) and to reduce the number of nematodes (Ferris and Bernard, 1971;

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Netscher, 1985; Aung and Prot, 1990). Nematode abundance is highly dependent on the presence of the host plants. However, they are also influenced, to a greater or lesser extent, by most of the biological, chemical and physical components of the soil environment (Upadhyay et al., 1972; Jacq and Fortuner, 1979; Yeates, 1976, 1981; Cuc and Prot, 1992). As a result, there are soils or regions within soils that are unsuitable for particular nematode species and which, thus, contain fewer individuals or different nematode communities than more favourable environments. In the sugarcane fields in Martinique, when the lower soil horizons are brought to the surface, the balance between species in the community changes (Cadet and Albrecht, 1992). Generally, where low nematode numbers result from a biological cause, the soils are referred to as suppressive (Alabouvette, 1993; Stirling, 1991). Where they result from abiotic factors, the soils can be referred to as resistant (Amir and Alabouvette, 1993). For example, it is well known that *Meloidogyne* species are usually not abundant in clay soil (Kincaid, 1946). The term resistant soils could also include those in which crop damage is less than would be expected from the size of the nematode populations. Thus, for sugarcane, damage is less important in heavier soils than in sandy soils (Spaull and Cadet, 1990). This is not a result of fewer nematodes but rather a consequence of a slower rate of invasion of the roots by the nematodes, which allows sufficient time for the plant to develop its root system and, thus, to overcome subsequent injuries (Cadet et al., 1982).

It is well known that populations of plant parasitic nematodes can be controlled by growing resistant host plants. Nematode development can be prevented or limited by means of a genetic modification of the host (Berthou et al., 1989; Luc and Reversat, 1985). In a similar way, it seems possible that nematode populations could be controlled by modifying the abiotic components of their environment to create a resistant soil. So we can define mesological control as the reduction in size of the nematode populations, the change of the species balance in the communities and/or a reduction in the amount of root damage following the change in the abiotic environment (Cadet et al., 1994). For example, in South Africa and in West Africa, the same sugarcane varieties are cultivated on very similar sandy soils and they are

parasitised by the same species. But the composition of the ectoparasitic communities is different (Cadet and Spaull, 1985). In South Africa, it is dominated by *Xiphinema* and trichodorids whereas in West Africa, it is dominated by *Helicotylenchus*. Despite the fact that the West African ectoparasite community is much larger than that of South Africa, the damage to ratoon crops occurs only in South Africa (Spaull and Cadet, 1990). If we could change the balance between species in the South African community by increasing the proportion of *Helicotylenchus*, we would expect the damage to disappear in ratoon crops.

The influence of various types of soil on the distribution of nematodes has been reported by many authors (Castro et al., 1990; Norton, 1979, 1989; Prot and van Gundy, 1979). The aim of the present study is to identify the physico-chemical factors which, independently from the type of soil, are correlated to the nematode communities which parasitise tomato and yam crops in Martinique.

## 2. Material and methods

The survey was made in Martinique in the French West Indies. Seventy three tomato fields (150 m<sup>2</sup> to 1.5 ha) were sampled between the fruit initiation stage and the first yield. Three to five subsamples were collected in each field, roughly along a transect. Each subsample comprised an entire tomato plant with its root system and soil from the rhizosphere. Roots were cut into about 1-mm lengths and the nematodes extracted from a 30-g subsample in a mist chamber (Seinhorst, 1950). Each soil subsample was divided in two parts. The nematodes were extracted from each subsample by elutriation (Seinhorst, 1962). The level of infestation in the field was assumed to be equal to the average of the results obtained. For economical reasons, only one physico-chemical analysis was performed on a mixture of the subsamples to obtain the mean parameters of the field. The analyses performed on the soil samples were: Carbon (C), nitrogen (N), organic matter (OM), pH (water: pH<sub>O</sub> and KCl: pH<sub>K</sub>), soil texture (clay: Cla; fine silt: FS<sub>i</sub>; coarse silt: CS<sub>i</sub>; fine sand: FS<sub>a</sub>; coarse sand: CS<sub>a</sub>), total phosphorus (P<sub>2</sub>O), exchange capacity (CEC), calcium (Ca), magnesium

(Mg), potassium (K), sodium (Na), saturation coefficient (V%), wilting points (2.5: WP2; 3.0: WP3; 4.2: WP4).

For yam (*Dioscorea cayenensis-rotundata* (CR) and *D. alata* (AL), totaling 94% of the yam fields), samples were taken after the emergence of the new tubers. As mixed plantations were very frequent, yams were sampled by variety, even if they were located on adjacent rows. Two varieties were selected. For each variety, three to five subsamples of soil from the rhizosphere, roots and new tuber skin (from the proximal area) were collected in the same bag. In the laboratory, nematodes were extracted separately from each of the root and tuber samples, but the soil samples coming from the same field were mixed before soil analysis.

Three nematode species were found in the roots and tubers of yam: *Pratylenchus coffeae*, *Scutellonema bradys* and, very infrequently, *Meloidogyne* sp. (Kermarrec et al., 1987; Jatala and Bridge, 1990). These nematodes first multiply in the roots before invading the new tuber (Bridge, 1982; Cadet and Quénéhervé, 1994). In other words, if a root system is infested, the new tuber will also become infested. For the data analysis, only the highest infestation density observed in the yam roots or in the new tuber of each plant has been used.

From these results, six data tables were built. Each row represents one tomato field or one yam field. Columns represent nematode species or soil parameters. Thus, the six tables are:

- nematological table for tomato fields: 73 rows and 17 columns,
- pedological table for tomato fields: 73 rows and 20 columns,
- nematological table for *D. cayenensis-rotundata* fields: 63 rows and 12 columns,
- pedological table for *D. cayenensis-rotundata* fields: 63 rows and 20 columns,
- nematological table for *D. alata* fields: 89 rows and 12 columns,
- pedological table for *D. alata* fields: 89 rows and 20 columns.

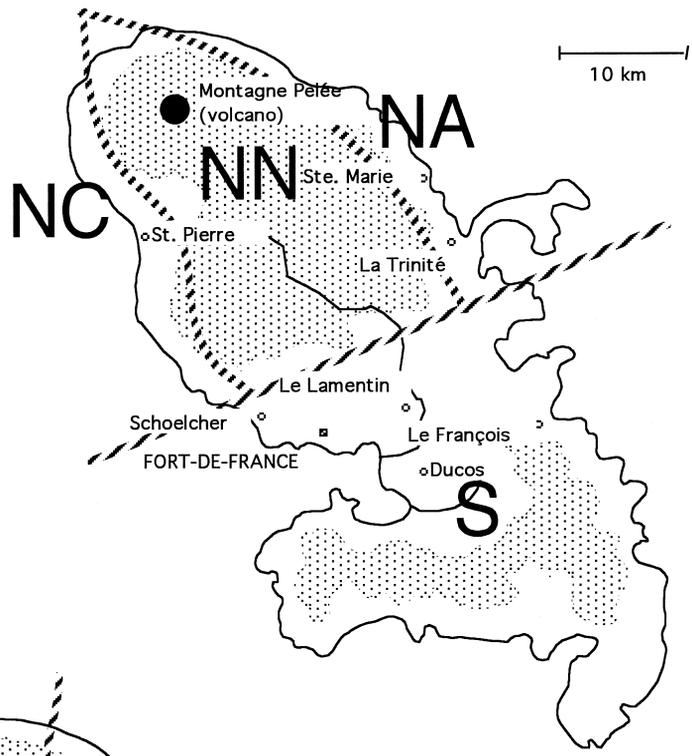
The abundance of nematode species or genera observed on these crops are listed in Table 1. The nematode numbers were transformed to  $\log(x + 1)$ . These data sets were first studied separately with Principal Components Analysis (PCA) on correlation matrix. For pedological data, PCA on correlation matrix is well adapted because variables are expressed in different units. To analyse the nematological data, we could have used Correspondence Analysis (CA), but we have preferred to use a PCA after logarithm transformation because of the very high

Table 1

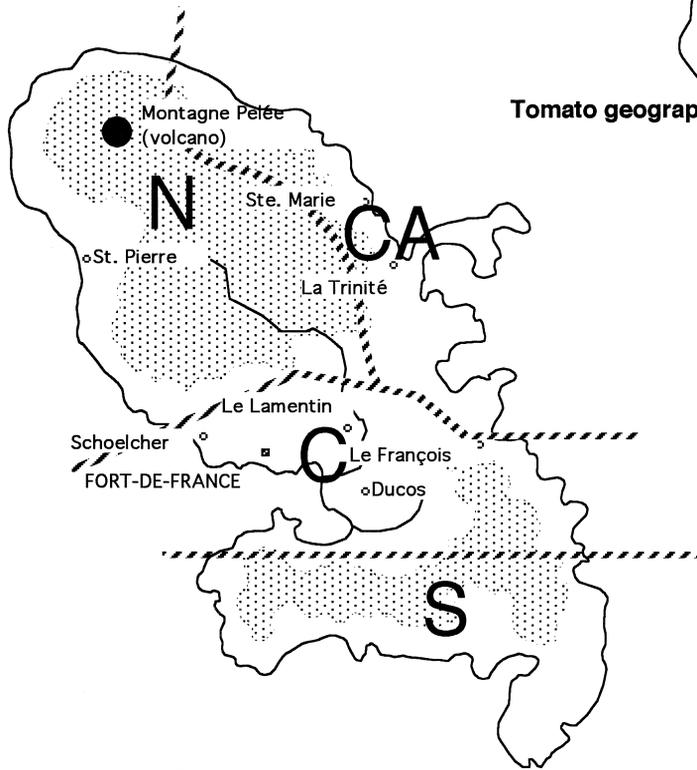
List of species and genera of plant parasitic nematodes found in yam and tomato crops in Martinique

Species	Code		Tomato		Yam	
	Soil	Root	Soil	Root	Soil	Root
<i>S. bradys</i>	Scus	Scur	–	–	+	+
<i>P. brachyurus</i>	Pras	Prar	+	+	–	–
<i>P. coffeae</i>	Pras	Prar	–	–	+	+
<i>Hoplolaimus seinhorsti</i>	Hops	Hopr	+	+	–	–
<i>Aorolaimus luci</i>	Aoro		+	–	+	–
<i>Hemicriconemoides cocophilus</i>	Hemi		+	–	+	–
<i>Meloidogyne incognita</i> and <i>arenaria</i>	Mels	Melr	+	+	+	+
<i>Criconemella ornata</i> and <i>onoensis</i>	Cric		+	–	+	–
<i>Helicotylenchus dihystrera</i> , <i>erythrinae</i> and <i>retusus</i>	Hels	Helr	+	+	+	–
<i>Rotylenchulus reniformis</i>	Rots	Rotr	+	+	+	–
<i>Telotylenchus ventralis</i>	Telo		+	–	–	–
<i>Longidorus</i> sp.	Long		+	–	–	–
<i>Paratrichodorus</i> sp.	Para		+	–	–	–
<i>Xiphinema</i> spp.	Xiph		+	–	+	–
<i>Tylenchorhynchus</i> sp. <sup>a</sup>	–		+	–	–	–

<sup>a</sup>Not used in the calculations.



Tomato geographic codes



Yam geographic codes

----- limits of areas

## TOMATO

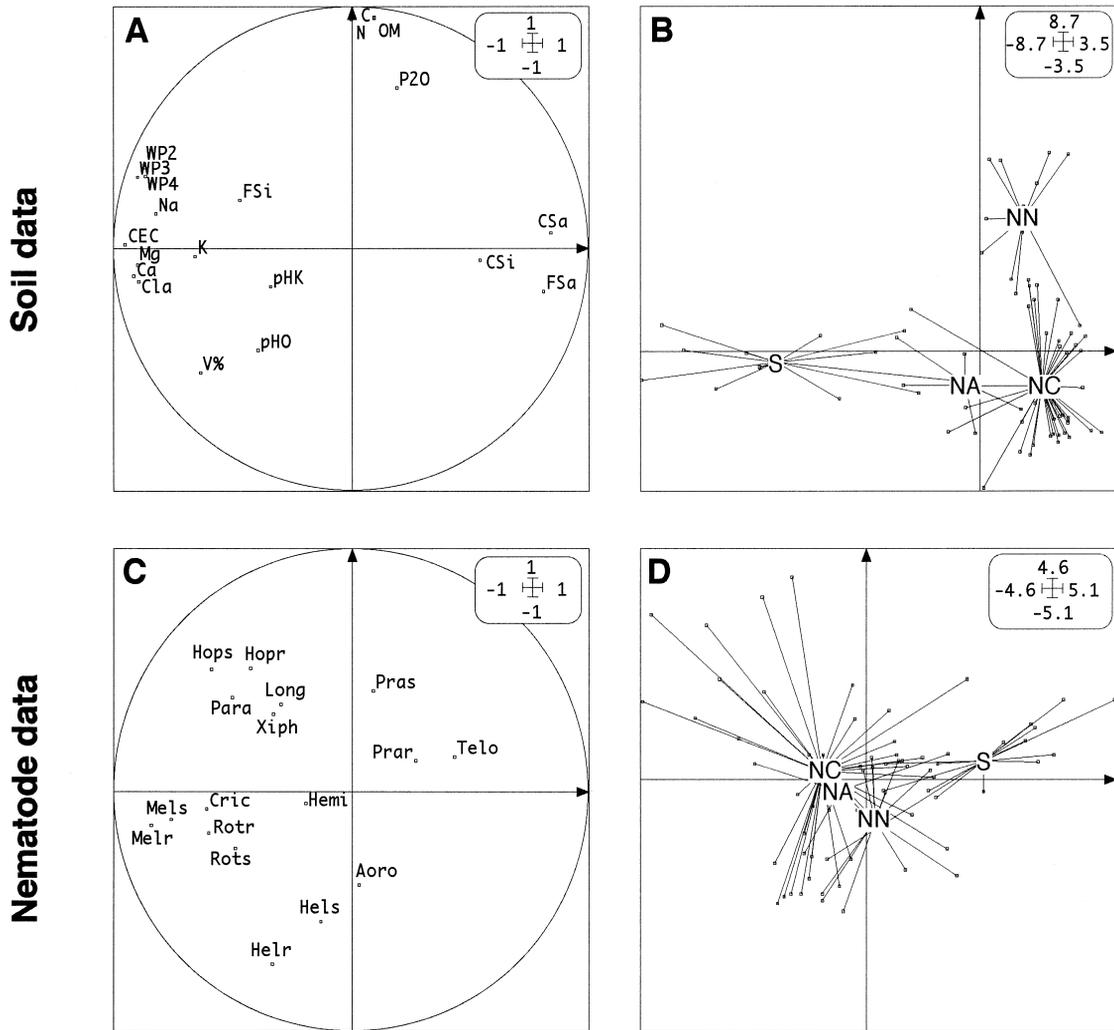


Fig. 2. Correlation circles and factor map (F1 × F2) of the PCA on pedological variables (A, B) and nematode species (C, D) for tomato fields. Nematode species codes are given in Table 1, and pedological variable codes are given in the text (Section 2). On the factor maps, the fields are grouped according to the region to which they belong on the island (see Fig. 1). Each field is linked to the gravity centre of the region, and these gravity centres are labeled with region codes.

variability of the number of nematodes. This high variability causes stability problems in CA and PCA is, therefore, preferable. The fauna and the soil data

were then coupled with coinertia analysis (Chessel and Mercier, 1993; Dolédec and Chessel, 1994). Computations and graphical displays were made with

Fig. 1. Geographical map of the Martinique showing tomato (above) and yam (below) crop zones defined on the island: (N) North; (NC) North Caribbean; (NN) North (Pelée Mountain); (NA) North Atlantic; (S) South; (CA) Centre Atlantic; (C) Centre.

the ADE-4 software (Thioulouse et al., 1995, 1997) and GraphMu (Thioulouse, 1989). On the factor maps, fields are grouped according to their geographical locality on the island (Fig. 1).

Interpreting the results of coinertia analysis rests on the following mathematical property: the covariance between the principal axes in the nematological and pedological spaces is maximum. Two important steps must be considered.

The comparison between the PCA and coinertia analysis factor maps shows which species and which variables are of interest: the most interesting ones are the ones which positions are different in the PCA factor map and in the coinertia analysis factor map.

The comparison between the nematological and the pedological coinertia analysis factor maps shows which species are correlated with which variables: the species with high factor scores are correlated with variables having a high factor score on the same axis and in the same direction.

### 3. Results

#### 3.1. Nematological and soil characteristics of the tomato fields

##### 3.1.1. Soil analysis

The results of the analysis of the 20 soil variables collected from each field were subjected to the PCA. On the correlation circle built with the first two factors (67% of the variability), the soil variables were distributed in three groups (Fig. 2A). One corresponding to proportions of sand (FSa and Csa) and coarse silt (CSi), a second group with variables corresponding to the finer particles, clay (Cla) and fine silt (FSi), as well as cations, exchange capacity (CEC) and WP. The third group was characterised by organic matter and the phosphorus content.

Points corresponding to the different fields were projected in the first factor map and named according to their position on the island (Fig. 2B). Fields

located in the south of the island (S), whose vertisols have a high clay content are separated from those located in the north of the island (NC, NA, NN), whose andosols contained a high proportion of sand (pumice stones). In this cloud, two groups could be distinguished: one corresponding to fields situated on the Pelée Mountain sides (NN), and one corresponding to fields located on the atlantic (NA) or caribbean (NC) coasts. The soils of the Pelée Mountain sides are rich in carbon as a result of previous volcanic eruptions, whereas more distant soils have lower carbon content.

##### 3.1.2. Nematological analysis

*Tylenchorhynchus* sp., which was only observed in one field, was removed from the fauna data before PCA. In the correlation circle, the different species were spread out in many groups (Fig. 2C). *Telotylenchus* (Telo) and *Pratylenchus* (Prar, Pras) were opposed to *Meloidogyne* (Melr, Mels) and *Rotylenchulus* (Rotr, Rots), both groups separated from *Helicotylenchus* (Hels, Helr) and *Aorolaimus* (Aoro). In the centre appeared *Hemicriconemoides* (Hemi).

In the factor map (Fig. 2D), fields located in the south (S) of Martinique were infested by *Pratylenchus* and *Telotylenchus*, but not with *Meloidogyne*. Fields in the north of the island were generally infested by a more diverse community, including mainly *Meloidogyne* and *Rotylenchulus*. In this cloud, plots corresponding to fields located on the hillsides of the Pelée Mountain (NN) were grouped, because of large populations of *Helicotylenchus* and *Aorolaimus*. The fields located on the coast (NA and NC) contained *Hoplolaimus* and *Xiphinema*.

#### 3.2. Soil and nematological characteristics according to the cultivated yam variety

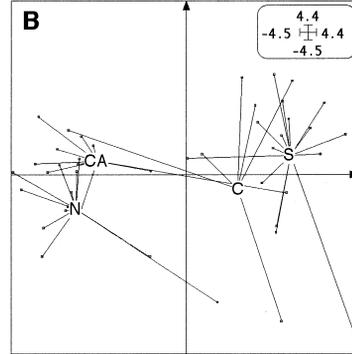
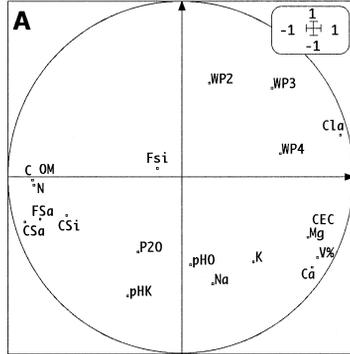
##### 3.2.1. *D. cayenensis-rotundata*

The simultaneous comparison of the correlation circle and factor map arising from the PCA of the soil data, showed that points corresponding to fields

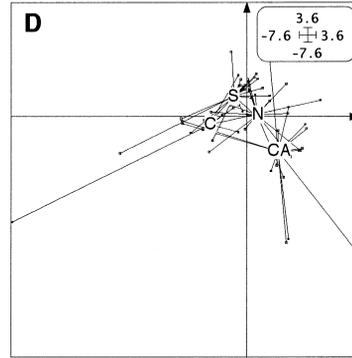
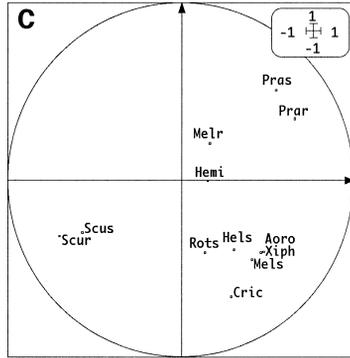
Fig. 3. Correlation circles and factor maps (F1 × F2) of the PCA on pedological variables (A, B, E, F) and nematode species (C, D, G, H) for the two varieties of yam: *D. cayenensis-rotundata* (A, B, C, D) and *D. alata* (E, F, G, H). Nematode species codes are given in Table 1, and pedological variable codes are given in the text (Section 2). On the factor maps, the fields are grouped according to the region to which they belong on the island (see legend to Fig. 2).

**D. cayenensis-rotundata**

**Soil data**

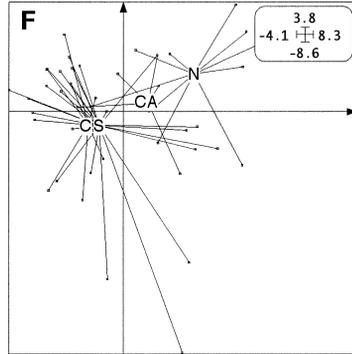
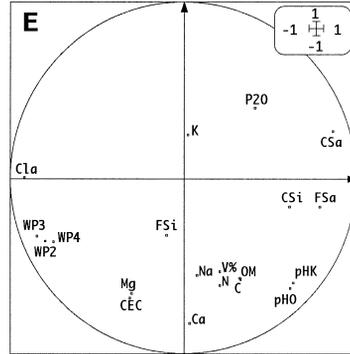


**Nematode data**

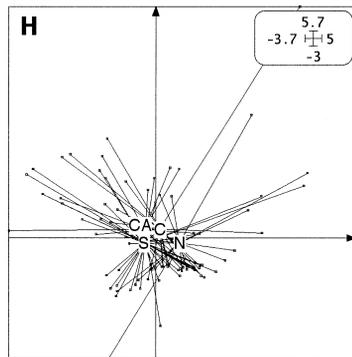
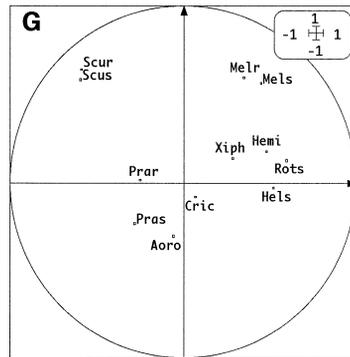


**D. alata**

**Soil data**



**Nematode data**



located in the centre (C) and the south (S) of the island, where the soil is more clayey, were opposed to fields located in the north and Atlantic centre (N and CA) because their soils are more sandy and rich in organic matter (Fig. 3A,B). On the nematological side, the factor map underlined the opposition between *Scutellonema* and *Pratylenchus* (Fig. 3C,D). A size effect appeared, because very few fields were infested by *S. bradys*. The points corresponding to fields infested with *P. coffeae* were grouped and a gradient of infestation in *P. coffeae* appeared from Atlantic centre (CA), to the south (S) where it was more abundant.

### 3.2.2. *D. alata*

A particle size gradient is shown by the soil data analysis. Points corresponding to clay fields in the south of the island are opposed to those corresponding to the few sandy pumice stone fields of the north (Fig. 3E,F), but the discrimination is not as sharp as for *D. cayenensis-rotundata*. Some fields in the south disturbed this repartition, due to the pH. On the second factor, the separation of the fields depended on phosphorus, potassium content and on calcium content.

There was a little obvious structure in the factor map resulting from the analysis of the nematological data (Fig. 3G,H). Points corresponding to the location of the different fields were, for the most part, in the centre of the map. They did not show a strong relationship with their geographical position on the island (compared to *D. cayenensis-rotundata*), but rather with the decreasing abundance of *S. bradys*, from the first to the third quadrant, and with the presence of *Meloidogyne*.

### 3.3. Nematode–soil relationships for tomato

The coinertia analysis did not induce major changes (Table 2) but it showed the strong relationships between nematode numbers and soil characteristics (Fig. 4). It confirmed the link between the pumice stones andosol of the north of the island and the presence of *Meloidogyne*, whereas *Pratylenchus* and, in particular, *Telotylenchus* were associated with the fields on the slopes of the volcano, which were very rich in organic matter. Conversely, *Helicotylenchus* which occupied all types of soil was positioned in the centre of the factor map.

Coinertia analysis produced an approximate mirror image of the factor map (Fig. 4A). It still showed the particle size gradient (clay–sand), and a gradient of decreasing amount of organic matter.

The factor map derived from the nematological data (Fig. 4C) rotated around the horizontal axis, to reinforce some relationships: between *Meloidogyne* and the pumice andosol, between *Aorolaimus* and soils rich in organic matter, between *Telotylenchus* and the clay soils. *Pratylenchus* (*P. brachyurus*) and *Helicotylenchus*, which were not affected by soil type, were located in the middle of the map. All other species were more abundant in light soil. In addition, for *Hoplolaimus* or *Longidorus*, their pH tended to be higher (and the organic matter content lower) than for *Criconemella* and *Rotylenchulus*.

Both factor maps established from fauna and soil data were similar to those of the PCA. The Monte Carlo test was highly significant: the 10,000 row permutations provided no inertia value higher than that obtained with the original (non-permuted) data (Fig. 6A).

Table 2  
Statistical characteristics of the coinertia analysis

		Correlation F1 (N) vs. F1 (S)	Correlation F2 (N) vs. F2 (S)	Conserved inertia (N)	Conserved inertia (S)
Tomato	PCA	−0.71	−0.47		
	Coinertia	−0.78	−0.79	99%	89%
<i>D. cayenensis-rotundata</i>	PCA	−0.44	−0.026		
	Coinertia	−0.78	−0.52	97%	82%
<i>D. alata</i>	PCA	−0.142	−0.04		
	Coinertia	−0.61	−0.54	57%	70%

First two columns: correlation between nematode (N) and soil (S) factors (F1 and F2) for PCA and coinertia analysis.

Last two columns: percentages of the PCA inertia conserved by the coinertia analysis. Coinertia analysis steadily improves the correlation between nematode (N) and soil (S) factors, while keeping most of the inertia taken into account by PCA.

## TOMATO

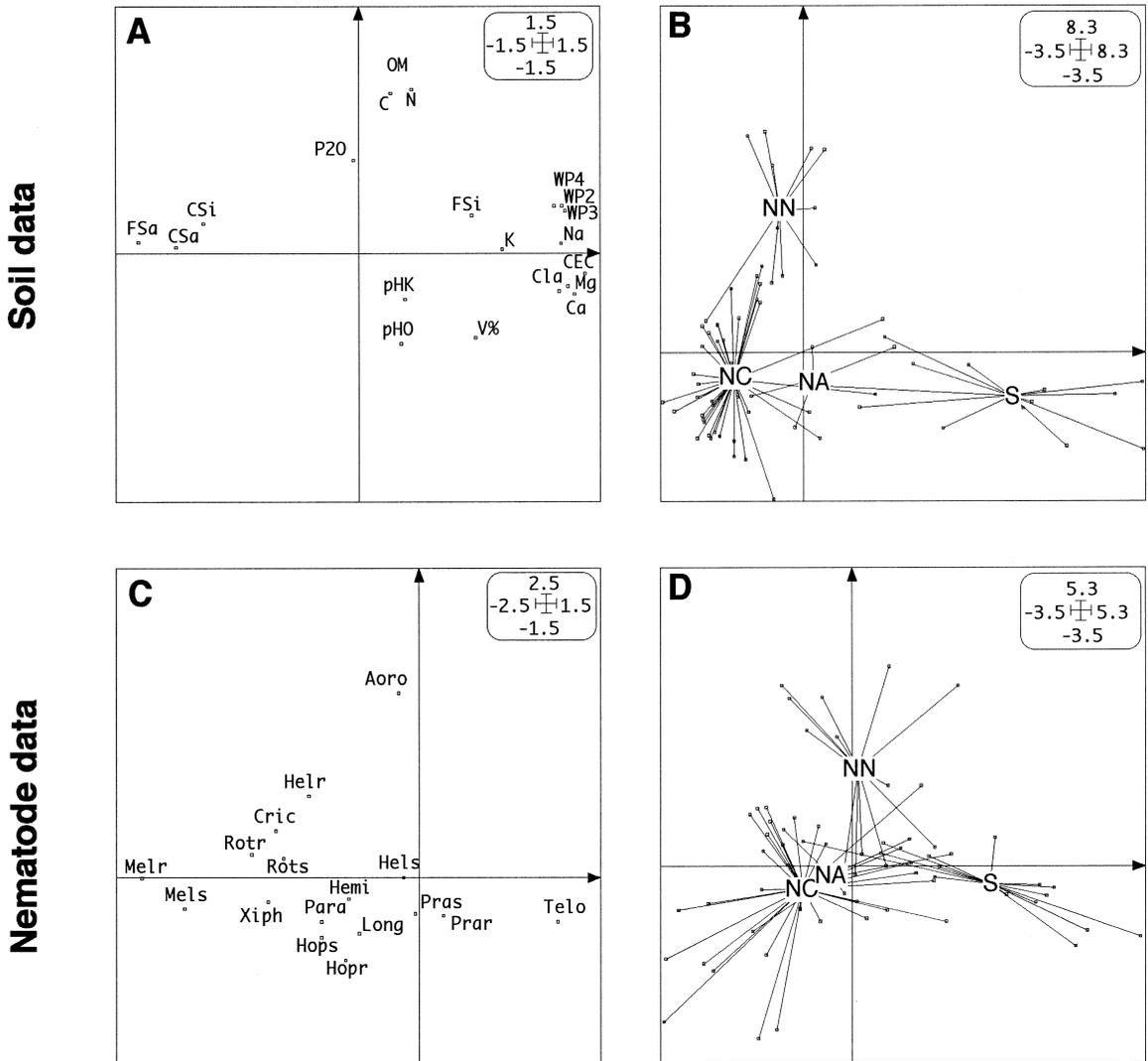


Fig. 4. Factor maps (F1 × F2) of the coinertia analysis on pedological variables (A, B) and nematode species (C, D) for tomato fields. Nematode species codes are given in Table 1, and pedological variable codes are given in the text (Section 2). On the factor maps, the fields are grouped according to the region to which they belong on the island (see legend to Fig. 2).

### 3.4. Nematode–soil relationships for the yam varieties

#### 3.4.1. *D. cayenensis-rotundata*

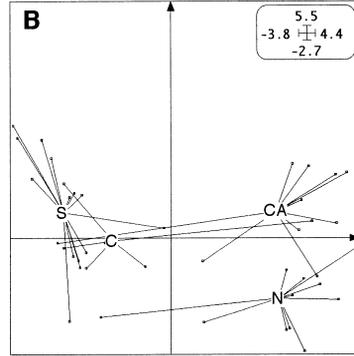
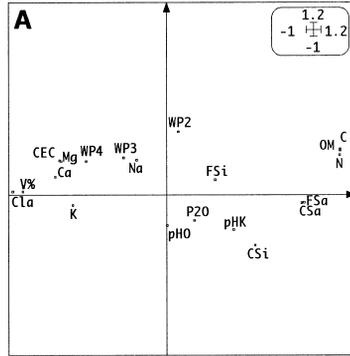
The map rotated on the vertical axis. The coinertia analysis restored the particle size gradient (Fig. 5A) and the gradients for calcium, magnesium, phos-

phorus and pH. The importance of organic matter is underlined. The north (N) and Atlantic centre (CA) samples contained a high proportion of organic matter and coarse particles, while the south (S) and centre samples (C) had a high proportion of clay particles (Fig. 5B).

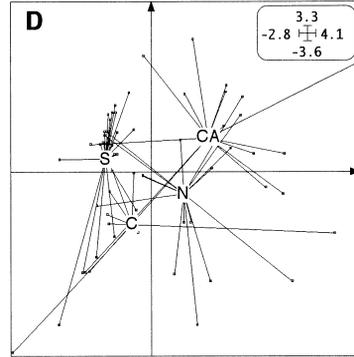
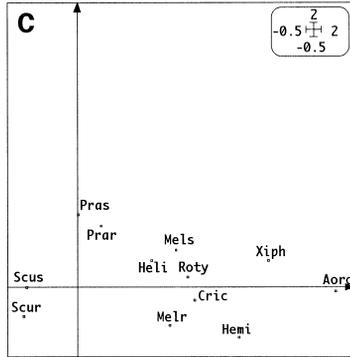
There were few changes in the factor map derived from the nematode data (Fig. 5C). *Aorolaimus*

**D. cayenensis-rotundata**

**Soil data**

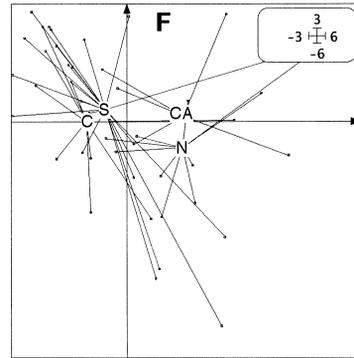
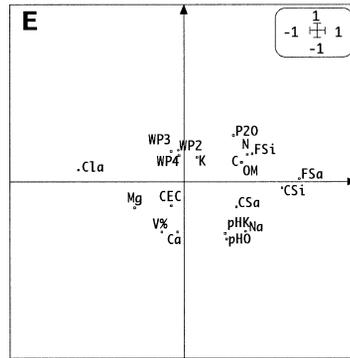


**Nematode data**

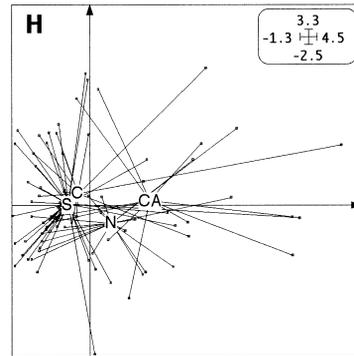
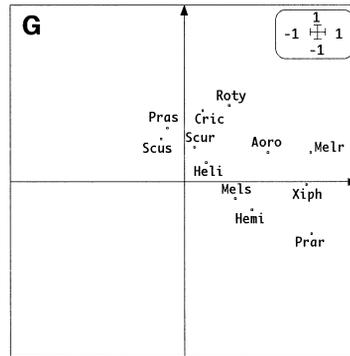


**D. alata**

**Soil data**



**Nematode data**



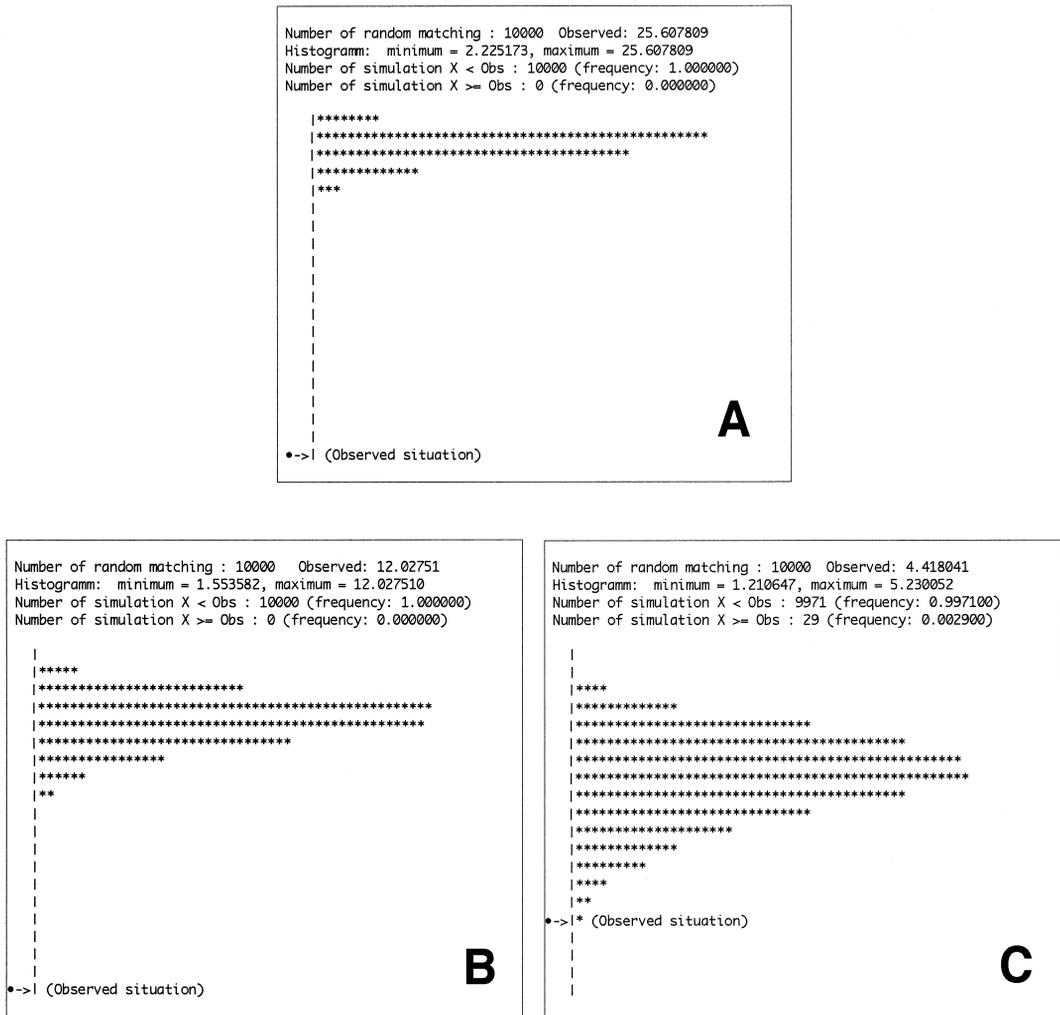


Fig. 6. Monte Carlo tests of the coinertia analysis for the tomato data (A), and each yam variety (B: *D. cayenensis-rotundata*, and C: *D. alata*). The observed situation point corresponds to the original coinertia analysis (with non-permuted rows). The value of the inertia for this situation is given in the first row. The histograms show the distribution of the criterion (total inertia) for the 10,000 analyses with randomly permuted rows.

moved on the map according to its association with andosol rich in organic matter. For *P. coffeae*, its presence in the soil was linked to a relatively higher exchange capacity, high rate of magnesium and calcium (Table 3) and lower pH. The relative positions

of geographical regions obtained in the pedological analysis is conserved in the nematological analysis (Fig. 5D).

The Monte Carlo test was highly significant ( $p < 10^{-5}$ , Fig. 6B).

Fig. 5. Factor maps (F1 × F2) of the coinertia analysis on pedological variables (A, B, E, F) and nematode species (C, D, G, H) for the two varieties of yam: *D. cayenensis-rotundata* (A, B, C, D) and *D. alata* (E, F, G, H). Nematode species codes are given in Table 1, and pedological variable codes are given in the text (Section 2). On the factor maps, the fields are grouped according to the region to which they belong on the island (see legend to Fig. 2).

Table 3

Average exchangeable calcium and magnesium (meq%) in the sample with low (–) and high (+) population of *P. coffeae*, for *D. alata* and *D. cayenensis-rotundata*

<i>P. coffeae</i>	<i>D. alata</i>		<i>D. cayenensis-rotundata</i>	
	–	+	+	–
Ca	5.7	5.6	4.9	4
Mg	2.9	2.6	2.3	1.8

### 3.4.2. *D. alata*

The factor map obtained after coinertia analysis of the soil variables described the soil particle size gradient, but by taking the finer particles (clay and fine sand) into account (Fig. 5E). There was a notable change in the position of two groups of variables, viz, the wilting point values, the importance of which decreased by slipping closer to the origin, and organic matter, which migrated to underline the relationship with *Aorolaimus*.

Almost all nematode species occupied different positions on the factor map were resulting from the coinertia analysis (Fig. 5G). *S. bradys* in roots was no longer a deciding factor and moved close to the centre of the map, far from *P. coffeae* in the field soils with low pH, high sodium content and poor in calcium and magnesium (Table 3).

There did not appear to be any obvious structures on the factor maps derived from the coinertia analysis of the nematological data or the soil data, except the opposition between the heavy soil of the south of the island and the lighter pumice stone soil of the north (Fig. 5F,H).

The Monte Carlo test by row permutation showed a spread out histogram (Fig. 6C). Among 10,000 permutations, 29 (0.29%) gave a result identical or superior to that obtained with the original (non-permuted) data set. This result, although still highly significant, is very different from the one obtained for *D. cayenensis-rotundata* (Fig. 6B).

## 4. Discussion

In Martinique, tomato and yam are often cultivated in the same areas, but generally, tomato fields

are more numerous in the north, whereas yam fields are more frequent in the south. Both crops are linked to the soil particle size gradient. This structure was maintained after coinertia analysis, but is less strong for *D. alata*. The study of the yam fields was characterised by an opposition between two nematode species: *P. coffeae* and *S. bradys*. This opposition derived from the different host–parasite relationships of the two most cultivated yam varieties: *D. cayenensis-rotundata* was attacked almost exclusively by *P. coffeae* and *D. alata*, was attacked in addition by *S. bradys* (Castagnone Sereno and Kermarrec, 1988).

These results add to those of others (Wallace, 1969; Cadet and Albrecht, 1992; Prot and van Gundy, 1981) that show soil texture plays an important role in explaining the relationships between soil and nematode species. In our study, these relationships appeared best in the parasitic nematode community of tomato, because the planting out of plants grown in a nursery avoided the introduction of nematodes with the planting material. The plants were attacked only by a nematode community already existing in the soil of the field. Obviously, if these nematodes were present in the soil, environmental conditions must have been favourable for their survival. For the tomato crop, most of the nematode species, such as *Meloidogyne*, preferred soils with coarse particles. Whereas for endoparasitic rootknot nematodes, the relationship appeared strictly dependant on soil particle size, for ectoparasitic species, chemical factors (pH, phosphorus) and, for *Aorolaimus*, organic matter may have a secondary influence on their abundance. *P. brachyurus* was present in all types of soil and thus did not appear to be influenced by the soil physico–chemical characteristics.

For yam, the nematode–soil relationships were the same as for the tomato and were issued mainly from the affinity of ectoparasitic species (or of *Meloidogyne*) for the light andosols, or from the affinity of *Aorolaimus* for the same soil but rich in organic matter. For *D. cayenensis-rotundata*, the species *P. coffeae* did not seem strongly linked to a specific soil texture, but appeared to be influenced secondarily by some soil chemical characteristics, such as calcium and magnesium or pH. This result can be explained because this species, even though it was often brought to the field in the yam seed tuber,

is found naturally in the field as an endemic species (Kermarrec et al., 1987). It can develop on other plants, such as, for example, banana, which is frequently grown in rotation with yam (Fargette and Quénéhervé, 1988; Fournet et al., 1990; Quénéhervé et al., 1995).

For *D. alata*, the nematode–soil relationship also exists because this variety is parasitised by the same nematode species as *D. cayenensis-rotundata*. But the relationship is weaker (as shown by coinertia analysis permutation test, Fig. 6C) because *D. alata* is also parasitised by *S. bradys*. As revealed by coinertia analysis, this species is not dependent from soil factors (shift toward the centre of the factor map, Fig. 5G). This situation can be explained by the origin of the infestation by *S. bradys*. This exotic species, which was introduced into Martinique in the 1970's, with the *D. alata* variety, was brought into the field within the seed tubers (Jatala and Bridge, 1990). It does not survive in the soil after the yam crop is harvested. In addition, *S. bradys* and *P. coffeae* rarely cohabit in the same tuber (Castagnone Sereno and Kermarrec, 1988), with the result that the corresponding variable (*P. coffeae* in the roots) was thrown in the opposite position on the coinertia factor map. The *P. coffeae*–soil relationships were expressed from its abundance in soil (variable *P. coffeae* in the soil). We found, in particular, an influence of pH, and sodium, calcium and magnesium content. The results obtained are not inconsistent because as the two varieties were not cultivated in exactly the same area, the lowest content of one element for *D. alata* was higher to the highest content of the same element for *D. cayenensis rotundata*.

The behaviour of *S. bradys* explains why the nematode–soil relationships for *D. alata*, were weak, as shown by the row permutation test. For *D. cayenensis-rotundata*, or for the tomato, the test was very highly significant. In these cases, nematode–soil relationships were very strong because all parasitizing nematodes carried out a part of their life in the soil. The validity of the results was reinforced by the fact that the same relationships were emphasised for the yam and the tomato surveys.

Twenty five years after *S. bradys* was introduced into Martinique, it is surprising that its cohabitation with *P. coffeae* in the tubers of *D. alata* was not

more frequent, as *P. coffeae* occurs naturally in the soil. To explain this phenomenon, we hypothesise that the presence of *P. coffeae* in the soil before planting gives a deciding advantage to this species. From the soil, it has the opportunity to invade the yam roots before *S. bradys*, which was found only in the seed tuber where it had first to multiply before migrating to the roots. Therefore, the roots constituted an intermediate centre of multiplication, which allowed the nematodes to "wait" for the emergence of the new tuber (Bridge, 1982; Cadet and Quénéhervé, 1994). If these roots are already occupied by *P. coffeae*, it is possible that *S. bradys* is unable to compete and to multiply. Thus, the new tubers are usually only infested by *P. coffeae*. On this basis, *S. bradys* could eventually disappear from Martinique. In addition, the reverse situation does not exist, that is to say *P. coffeae* in yam plants was never in competition with *S. bradys* which was not found in the soil, except for the females that leave the infested tuber after planting. However, the economic problem would not be resolved with the disappearance of *S. bradys* because *P. coffeae* causes equivalent damage (Acosta and Ayala, 1976).

The study revealed that the abundance of *P. coffeae* was linked to particular soil chemical characteristics such as pH, and sodium, calcium or magnesium content. The manipulation of these environmental abiotic factors is technically possible and could reduce the multiplication of *P. coffeae* during the period the yams are in the soil and thus reduce the damage caused after harvest during the storage period (Adesiyani et al., 1975; Cadet and Daly, 1996). This method of control can, however, only be considered for nematode species which are susceptible to chemical factors.

When soil texture is involved, cultural control methods could be developed. For example, the addition of organic matter to light textured soils infested with *Meloidogyne* is known to considerably decrease the damage caused by these parasites (Akhtar and Alam, 1993; Goswami and Meshram, 1991). Several hypothesis could explain this phenomenon, such as organic acid toxicity, development of predatory fungi and bacteria, antagonistic organisms. However, from our results the modification of the soil texture by the organic matter could be the principal factor.

## 5. Conclusion

It is worth to notice that in this study, the co-inertia analysis permutation tests reveal the peculiarity of nematode parasitism by showing a weaker relationship between an exotic nematode species and the soil variables. This method is a useful mathematical technique to identify relationships between the presence of some nematode species and physico-chemical characteristics of the soil. Manipulating certain chemical elements present in very low proportions in the soil, for example by the addition of chemical fertilizer, could influence nematode community by creating an unfavourable soil environment, without destroying the overall balance of the ecosystem.

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