

**POPULATION DYNAMICS OF *MELOIDOGYNE INCOGNITA*
AND INFESTATION LEVELS BY *PASTEURIA PENETRANS* IN A NATURALLY
INFESTED FIELD IN MARTINIQUE**

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ABSTRACT

Ciancio, A., and P. Quénéhervé. 2000. Population dynamics of *Meloidogyne incognita* and infestation levels by *Pasteuria penetrans* in a naturally infested field in Martinique. *Nematropica* 30:77-86.

The population dynamics of *Meloidogyne incognita* juveniles (J2) in association with the parasite *Pasteuria penetrans* was studied in a field in Martinique. Data obtained at three-week intervals for one year were analyzed to study the relationship between J2 density and endospore infestation levels. Six crop sequences were evaluated in five replicates. They were: resistant tomato—okra—fallow—cabbage; susceptible tomato—okra—fallow—cabbage; bean—pepper—fallow—cabbage; eggplant—fallow; cucumber—velvetbean—fallow—cabbage; fallow—pepper—cabbage—fallow—cabbage. The J2 densities showed fluctuating trends, frequently synchronous with fluctuations of endospore infestation. The highest J2 numbers observed ranged between 1 000 and 1 500 nematodes/100 g of soil in the first four crop sequences, and between 150 and 250 J2/100 g of soil in the last two. The highest percentages of nematodes with adhering endospores ranged between 50 and 70%. The resistant tomato crop showed a sharp decrease in the nematode density at the end of the crop sequence, with a similar synchronous decrease of the endospore infestation. This trend was also observed during the fallow periods in the other treatments. Susceptible crops allowed a sharp increase of the J2 densities. During these periods of population growth, the concomitant increase of the endospore infestation levels was interrupted with fast growing J2 densities. In the last two crop sequences, the J2 densities progressively decreased because of the non-host status of velvetbean and of a longer fallow, respectively. When all the pooled data from the six treatments were considered, a significant linear correlation was observed between J2 densities and the corresponding endospore infestation values ($P < 0.001$). This relationship appeared related to the density of females releasing J2 and/or endospores in the soil. All pooled mean densities also followed the Gutenberg-Richter power law distribution, indicating the occurrence of chaotic effects influencing their dynamics. Although chaos implies non-predictability of J2 numbers and endospore infestation dynamics, it also suggests that large-scale fluctuations may induce local nematode suppression by *P. penetrans*.

Key words: Biological control, crop cycle, endospore, infestation, *Meloidogyne incognita*, parasitism, *Pasteuria penetrans*, rotation.

RESUMEN

Ciancio, A. y P. Quénéhervé. 2000. La dinámica de poblaciones de *Meloidogyne incognita* y el nivel de infestación por *Pasteuria penetrans* en un campo en Martinica. *Nematropica* 30:77-86.

En el presente estudio se ha seguido la dinámica poblacional de larvas de segundo estadio (J2) de *Meloidogyne incognita* asociadas al parásito *Pasteuria penetrans* en un campo en Martinica. Muestras efectuadas cada tres semanas se analizaron para estudiar la relación entre la densidad de J2 y su infestación por endosporas. Seis secuencias de cultivos han sido evaluadas durante un año con cinco repeticiones, cada una con la siguiente alternancia: tomate resistente—okra—descanso—coliflor; tomate susceptible—okra—descanso—coliflor; frijol—pimiento—descanso—coliflor; berenjena—

descanso—coliflor; pepinillo—pica-pica—descanso—coliflor; descanso—pimiento—coliflor—descanso—coliflor. La densidad de las J2 se caracterizó por fluctuaciones, frecuentemente sincronizadas con las fluctuaciones de infestaciones por endosporas. Las densidades más altas de J2 se observaron entre 1 000 y 1 500 nematodos por 100 g de suelo en las cuatro primeras secuencias de cultivo y entre 150 y 250 J2 por 100 g de suelo en las últimas dos. El porcentaje más alto de nematodos con endosporas adheridas varió entre 50 y 70%. El tomate resistente Carmido mostró una marcada disminución en la densidad de los nematodos al final del ciclo, con una disminución similar y sincronizada de la infestación por endosporas. Esta tendencia ha sido también observada durante el período de descanso en los otros tratamientos. En los cultivos susceptibles se observó un incremento muy elevado de las densidades de los juveniles. Durante estos períodos de crecimiento poblacional, el crecimiento correspondiente de los niveles de infección por endosporas se interrumpió con crecimientos rápidos de las densidades de J2. En las últimas dos secuencias, las densidades de J2 disminuyeron progresivamente debido a la no hospedancia del pica-pica y por el descanso más largo, respectivamente. El análisis conjunto de todos los datos de los seis tratamientos reveló una correlación lineal significativa entre las densidades y los niveles de infestación por endosporas correspondientes ($P < 0.001$). Esta relación pareció depender de la densidad de las hembras que liberan J2 y/o endosporas en el microcosmo del suelo. Todas las densidades promedio de J2 también siguieron la distribución exponencial de Gutenberg-Richter, indicando la presencia de efectos caóticos que afectaron sus dinámicas. Aunque caos implique no predicción del número de J2 y dinámica de infestación de endosporas, también sugiere que grandes fluctuaciones pueden inducir una supresión local de nematodos por *P. penetrans*.

Palabras claves: Control biológico, endospora, infestación, *Meloidogyne incognita*, parasitismo, *Pasteuria penetrans*, rotación, secuencia de cultivo.

INTRODUCTION

Since the first investigations and the re-description of *Pasteuria penetrans* Sayre & Starr as an obligate microbial antagonist of root-knot nematodes, this bacterium has shown potential for biological control of nematodes in pot tests and in other controlled conditions (Mankau, 1980; Minton and Sayre, 1989; Sayre and Starr, 1985; Sayre and Starr, 1988; Stirling, 1984). Studies conducted in fields naturally infested with *P. penetrans* and other related forms showed that these nematode pathogens persist in soil, regulating the densities of susceptible host populations to variable extents, with few interactions with other soil inhabitants and no adverse environmental impact (Atibalentja *et al.*, 1998; Bird and Brisbane, 1988; Ciancio, 1995; Davies *et al.*, 1990; Chen and Dickson, 1998).

Host development is essential for *P. penetrans*, which is strictly dependent on

the nematode biology for its own development and growth. It exhibits specific nematode preferences because of a narrow host range (Davies *et al.*, 1988; Oostendorp *et al.*, 1990; Stirling, 1985). Moving hosts are required which intercept activated endospores, previously released by decaying parasitized females. Additional properties of resting infective endospores such as resistance to desiccation and high temperatures led to efforts to develop practical soil treatments through *in vitro* mass cultivation and production (Bishop and Ellar, 1991; Williams *et al.*, 1989). To date these attempts have been unsuccessful.

Passive adhesion of endospores to the nematode cuticle initiates germination and vegetative growth of the parasite (Sayre and Starr, 1988; Sturhan *et al.*, 1994). The adhesion process is not affected by storage of endospores in dry or wet soil (Oostendorp *et al.*, 1990). Epidemiological data from West Africa showed that propagule

interception and host adhesion were influenced by soil texture and host plant, and that the most favorable conditions were encountered in sandy soils with a low clay content (Mateille *et al.*, 1995).

The aim of this study was the quantification of the *P. penetrans* adhesion process in soil and the evaluation of the parasite impact on a *Meloidogyne incognita* (Kofoid and White) Chitwood population during one year in a tropical environment. We estimated changes of the juveniles (J2) numbers in soil and determined the fraction encumbered with endospores in a naturally infested field. A factorial combination of crop sequences and host plants was tested in order to evaluate the effects of host and non-host plants on the degree of *P. penetrans* nematode infestations.

MATERIALS AND METHODS

Soil samples were taken at three week intervals in a field naturally infested with *M. incognita* and *P. penetrans* located at Le Carbet, Martinique at an agricultural training station of the Ministry of Agriculture. The field was chosen due to its long history of vegetable production (>20 years), with the previous cropping period of 8 months with eggplant (*Solanum melongena* L. cv Kalenda). The soil was alluvial developed on volcanic premices with more than 20% silt and pH of 6.4. The climate was humid-tropical with a mean monthly temperature of 28°C. Each plot consisted of six beds 2.5 m long and 15 m². Soil samples consisted of 12 cores (2 cm diam × 20 cm deep) collected for each plot in the root zone. The 12 cores from each plot were mixed and nematodes were extracted from 250 cm³ of soil by the elutriation-sieving technique (Seinhorst, 1962). Results were expressed as nematode numbers per 100 g of dry soil (105°C, overnight). The endospores of *P. penetrans* were counted on 50 nematodes

hand picked from the sieved soil suspension, and the endospore infestations were scored as percentage of nematodes with adhering endospores.

Six crop sequences, selected on the basis of the most common local varieties, were evaluated in five replicates: 1) resistant tomato, *Lycopersicon esculentum* cv. Carmido—okra, *Abelmoschus esculentus* L. cv. Emerald—fallow (9 weeks)—cabbage, *Brassica oleracea* L. cv. Fortuna; 2) susceptible tomato cv. Caraibo—okra cv. Emerald—fallow (9 weeks)—cabbage cv. Fortuna; 3) bean, *Phaseolus vulgaris* L. cv. Contender—pepper, *Capsicum annuum* L. cv. Narval—fallow (9 weeks)—cabbage cv. Fortuna; 4) eggplant cv. Kalenda—fallow (9 weeks)—cabbage cv. Fortuna; 5) cucumber, *Cucumis sativus* L. cv. Calypso—velvetbean, *Mucuna pruriens* L. var. *utilis*—fallow (9 weeks)—cabbage cv. Fortuna; 6) fallow (18 weeks)—pepper cv. Narval—cabbage cv. Fortuna—fallow (9 weeks)—cabbage cv. Fortuna. Tomato cv. Carmido is a nematode resistant variety and velvetbean is a non-host crop used in the tropics to reduce nematode densities in soil. The remaining crops were all susceptible to *M. incognita*.

To allow a reconstruction of the two time series closer to the continuous fluctuations expected between each sampling time, data were interpolated using a cubic spline method with second derivative (SAS, 1988). The distribution of all the mean densities was fitted using the Gutenberg-Richter (G-R) power law distribution,

$$N_D = k \frac{1}{D^x}$$

with N_D = the total numbers of observations per density class of dimension D , x = coefficient (usually ≤ 1) and k = constant (Gutenberg and Richter, 1956).

RESULTS

At the end of the previous eggplant crop and just before initiating the experiment, population density of *M. incognita* was 1171 J2/100 g dry soil, with 50.1% of the nematodes with adhering *P. penetrans* endospores. During the period of study the J2 densities showed alternating peaks, usually corresponding to the presence of susceptible host plants and frequently synchronous with infestation levels (Fig. 1). The highest nematode densities observed ranged between 1 000 and 1 500 J2/100 g soil in the first four crop sequences, and between 150 and 250 J2/100 g soil in the last two. The highest levels of J2 with adhering endospores ranged between 50 and 70%. The mean annual densities and infestations varied between 60-396 J2/100 g soil and 19.4-30.7%, respectively (Table 1).

A significant correlation was obtained between the nematode density and the *P. penetrans* infestation levels when all observations were pooled and computed ($r = 0.35$, $P < 0.001$; $n = 108$; Fig. 2). When each crop sequence was examined individually, significant correlations were also found between densities and infestations in crop sequence 3 ($r = 0.555$, $P < 0.05$), crop sequence 5 ($r = 0.698$, $P < 0.001$) and crop sequence 6 ($r = 0.657$, $P < 0.01$). When all the mean densities from the six plots were considered, they appeared to follow the Gutenberg-Richter power law distribution ($r^2 = 0.947$; $k = 2571.05$; $x = 1.008$, Fig. 3).

Crop sequence 1. The resistant tomato cv. Carmido supported low nematode population growth, followed by a sharp final decrease with a concomitant and similar drop of the endospore infestations (weeks 1 to 18). The following crop, okra cv. Emerald grown in weeks 18 to 36, was a very good host. The nematode population displayed a sharp, bell-shaped growth pattern. The endospore infestation levels ini-

tially followed a similar trend which was interrupted after three weeks. This peak was followed by two fluctuations, the first one contemporary to the highest J2 peak (week 30), the second one occurring during fallow, when the nematode population densities in soil became nearly undetectable (weeks 39 to 45). Subsequent synchronous growths of J2 density and endospore infestations were observed during the final cabbage crop (Fig. 1A).

Crop sequence 2. The susceptible tomato Caraibo supported rapid growth of J2 densities interrupted by an initial drop that was synchronous with an infestation peak (weeks 9-12). The nematodes decreased sharply by the end of the crop (week 18). In the following weeks, the J2 increased rapidly on okra until declining six weeks before the end of the crop sequence (week 30). The endospore infestations increased synchronously with densities until week 27, and then declined 3-6 weeks after J2 density decreased (weeks 27-42). Nematode densities and *P. penetrans* endospore infestations declined to very low levels during the subsequent fallow period, and then increased by the end of the crop sequence on cabbage (Fig. 1B).

Crop sequence 3. The nematode populations fluctuated during the initial bean crop, followed by near exponential increase on pepper with a synchronous increase in endospore infestation level (week 30). Both variables declined during the following fallow and increased again on cabbage (Fig. 1C).

Crop sequence 4. Fluctuations of density and infestations were observed during the first 10 weeks on eggplant cv Kalenda. Densities peaked at weeks 15-18 and then declined before the end of the crop and until planting of cabbage. In contrast to nematode densities, endospore infestations increased until declining sharply in week 45 (Fig. 1D).

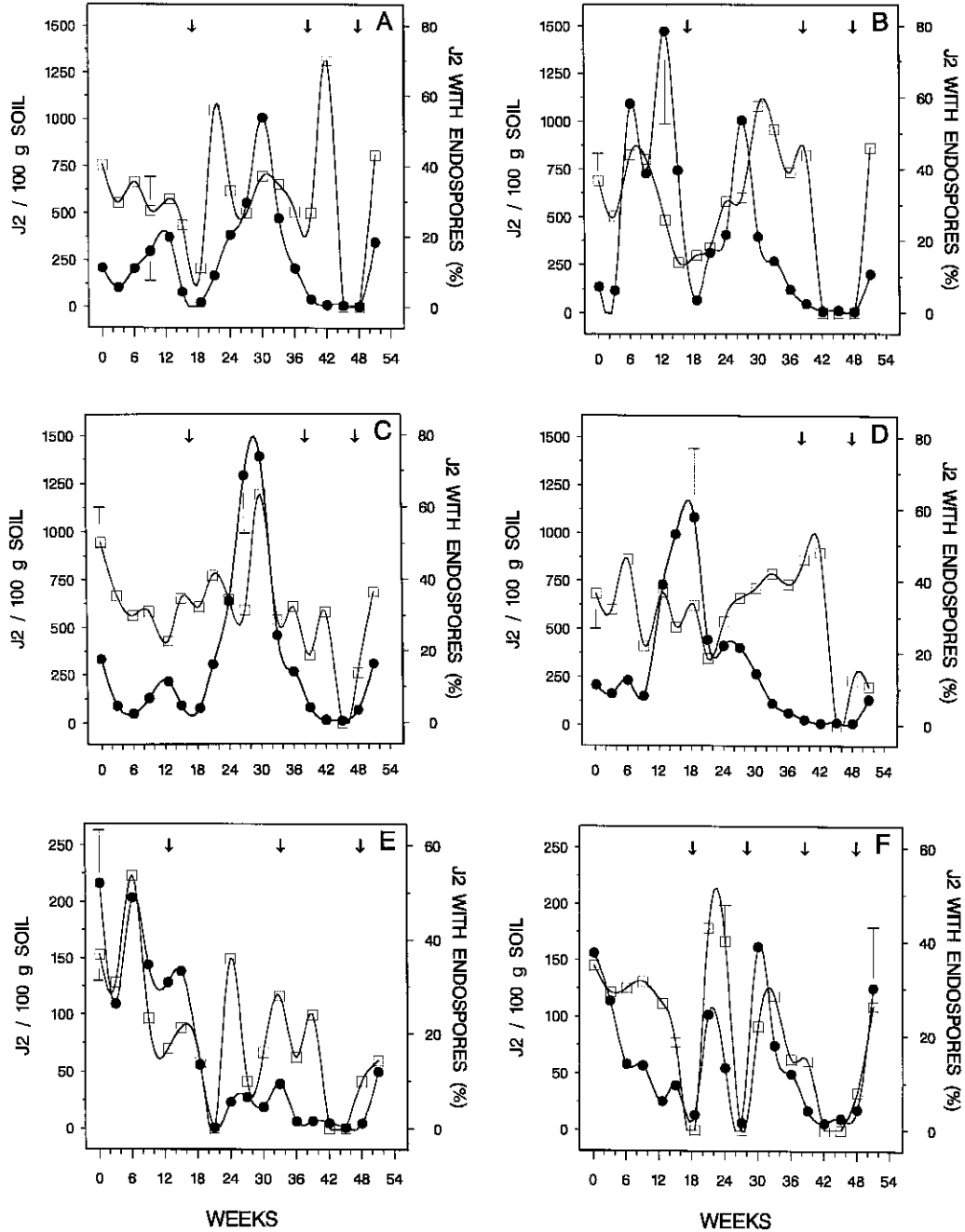


Fig. 1. Changes in population densities of second stage juveniles (J2) of *Meloidogyne incognita* per 100 g of soil (dot) and percent infestation by adhering *Pasteuria penetrans* endospores (square) in a naturally infested field in Martinique. Data show the mean values of five replicates for the six crop sequences examined. Vertical bars show the maximum SE unit values observed in each time series. A-F: Crop sequence from 1 to 6 and crops (marked by arrows) as shown in Table 1.

Table 1. Overall yearly means of *Meloidogyne incognita* J2 densities and percentages of infestation by endospores of *Pasteuria penetrans* for each cropping sequence.

Crop sequence	Variable	Initial values	Mean	SE
1				
Resistant tomato, cv. Carmido—okra cv. Emerald—fallow—cabbage cv. Fortuna	J2 density ^a	208	250	59.9
	Endospore infestation ^c	40.4	30.7	4.0
2				
Susceptible tomato cv. Caraibo—okra cv. Emerald—fallow—cabbage cv. Fortuna	J2 density	136	396	102.4
	Endospore infestation	36.8	29.1	4.2
3				
Bean cv. Contender—pepper cv. Narval—fallow—cabbage cv. Fortuna	J2 density	331	322	95.7
	Endospore infestation	50.4	31.6	3.1
4				
Eggplant cv. Kalenda—fallow—cabbage cv. Fortuna	J2 density	209	303	77.1
	Endospore infestation	36.4	30.6	3.1
5				
Cucumber cv. Calypso—velvetbean var. <i>utilis</i> —fallow—cabbage cv. Fortuna	J2 density	216	65	16.9
	Endospore infestation	36.8	19.4	3.3
6				
Fallow—pepper cv. Narval—cabbage cv. Fortuna	J2 density	156	60	12.0
	Endospore infestation	34.8	20.4	3.3

^aJ2 / 100 g soil.^c% of J2 with adhering endospores

Crop sequences 5 and 6. The last two sequences resulted in nematode population densities below 250 J2/100 g soil. In crop sequence 5, the J2 numbers progressively decreased on cucumber, with a sharp and identical fluctuation of endospore infestations (weeks 1-21; Fig. 1E). Nematodes remained below 50 J2/100 g of soil during the non-host velvetbean crop and fallow, and increased again on cabbage. Crop sequence 6 showed synchronous trends with remarkable similarities and marked growth of both variables on pepper and cabbage (weeks 18-24 and 30-33). The J2 increased on the second cabbage

crop, with a concomitant and identical trend for endospore infestation (Fig. 1F).

DISCUSSION

The nematode population density and endospore infestation trends were frequently characterized by synchronous fluctuations with near similar amplitudes, and they were more evident at densities lower than 200-300 J2/100 g soil. (Fig. 1). The correlations between J2 densities and endospore infestations suggest a strong link between nematodes and *P. penetrans*. Synchronous trends were also observed

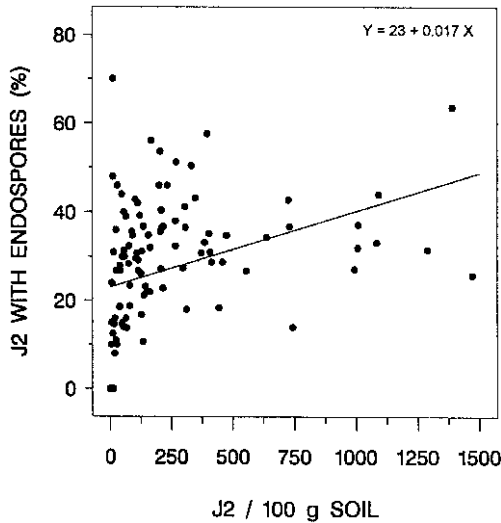


Fig. 2. Relationship between the densities of second stage juveniles (J2) of *Meloidogyne incognita* and the percent of nematodes with adhering *P. penetrans* endospores in a naturally infested field in Martinique.

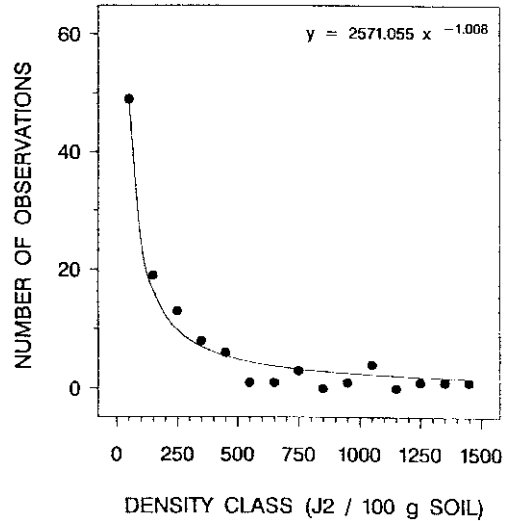


Fig. 3. Gutenberg-Richter distribution per density class of the population densities of *Meloidogyne incognita* observed after pooling the data from all crop sequences.

during fallow and cabbage in all the crop sequences. The parallel trends might result from the density of females in the plant root systems, because both J2 and *P. penetrans* endospores are released by female nematodes into the soil. A residual density of maturing endospores from previous parasitism could only have affected the beginning of this trend. However, synchrony occurred in some crop sequences or on certain crops, often characterized by a one-two week delay of endospore infestations, and probably due to the time required for the majority of endospores to mature and become infective.

In general, at low nematode densities the relationship between *M. incognita* and *P. penetrans* was linear (synchronous). At higher nematode densities, other factors increasingly regulated endospores and nematodes, with a progressive appearance of non-linearity characterizing their interaction at density values in the order of 1 000-1 500 J2/100 g soil. These factors included

plant host status, density dependence of nematodes, and stochastic disturbances related to the soil environment. With the exception of cucumber, all susceptible plants allowed near exponential nematode growth, with J2 frequently declining before the end of the crop. In the two last crop sequences however, the peak nematode densities on susceptible crops occurred during a short 6-week period, with a maximum density corresponding only to a fraction of the values observed from the other crop sequences. A decline occurred on cucumber which is ordinarily a highly susceptible host. In these two crop sequences a nematode suppressive effect was present; however, *P. penetrans* infestations were generally less than 50% and not directly related to nematode decline.

In the first crop sequence the resistant tomato Carmido permitted modest nematode population growth, probably due to resistance breaking near the warmer soil surface and/or overall low nematode

reproduction or residual eggs hatching in soil. On the following okra crop, the divergence between nematode density and endospore infestation observed at weeks 24-30 resulted from the sharp J2 exponential growth (weeks 18-30) induced by high food availability from a good host for *M. incognita*. The drop of endospore infestations observed at week 24 may have resulted from a lower probability of endospore attachment due to less time spent by J2 in the soil before root penetration. At this time, release of endospores into soil was insufficient to maintain high infestation levels, allowing a significant fraction of nematodes to avoid intercepting endospores. Conversely, the large numbers of endospores subsequently released in soil and the low nematode numbers during the next fallow may have produced the endospore infestation peak (up to 70% of J2) observed at weeks 39-45 (Fig. 1A).

The highest nematode growth rates on susceptible hosts were observed at initial density values below 100 J2/100 g of soil; at higher initial values the population growth was lower or negative due to intraspecific competition (Seinhorst, 1966; Fig. 1D-F). This dynamic was not influenced by *P. penetrans*, since the expected nematode growth on susceptible hosts were, in part, observed. This trend suggests that at very low host densities *P. penetrans* was not regulating or suppressing the host population, and nematodes escaped infestation resulting in maintenance of the pathogen's nutritional source. The parasite effects were mainly observed at higher J2 density values, with anticipated nematode declines or interrupted growth trends (Fig. 1B, D).

Continuous cropping with susceptible host plants was considered essential to build up soil suppressiveness by increasing *P. penetrans* infestation levels in the tropics (Madulu *et al.*, 1994). How many years are required to observe a soil suppressiveness

induced by *P. penetrans*, however, is unknown. In a two year study in perennial kiwi plantations, a trend toward reduced *Meloidogyne* spp. numbers was observed by the end of the sampling period, with a contemporary increase of J2 encumbered with endospores (Verdejo-Lucas, 1992). In Florida, *P. penetrans* was observed in *Meloidogyne* spp. suppressive soils and acted as a significant biological control agent (Weibelzahl-Fulton *et al.*, 1996). Our data are in partial agreement with these observations but, although the previous history of the field is well known, no general trends toward higher endospore infestation levels were observed. In the last two cropping sequences, the infestation levels remained low and appeared unrelated to any residual suppression induced by the previous crop history. This observation suggests that a cropping period lasting several years is required to reach a suppressive state in soil or that nematode suppression could be favored by reducing the *P. penetrans* mortality or any dispersal factors limiting the endospores survival or efficiency in soil.

The time spent in soil by the J2 before reaching a suitable feeding site may also affect the endospore loads. The endospore infestation by *P. penetrans* is a dimensionless number and differs from the real density of endospores in soil. High infestation levels (>60% of J2) might be expected when high endospore numbers are present. The same can also be obtained with lower endospore density if nematodes migrate in soil for a longer time. Conversely, low infestation levels may be observed with high (>1 000 J2/100 g soil) nematode numbers, in presence of high endospore densities, if the J2 require only a few hours to reach and penetrate the roots. Thus, the relative numbers of endospores available for attachment per moving nematode and the time spent in soil by the J2 may be more significant than absolute endospore num-

bers. For efficient biological control, high infestation levels (>60%) must be observed in the field together with high host densities. In these conditions it seems possible to expect natural host suppression due to the parasite reproduction. In our study, this situation was apparently observed only on pepper in crop sequence C, when the nematode population density decreased rapidly in mid cycle (Fig. 1C).

The G-R distribution is generally used in seismology to describe the frequencies of natural phenomena like earthquakes, in which the highest catastrophic energies are rare. The G-R distribution is generally considered as an indicator of non-linearity and chaos, and relates the frequency of an event to its dimension. These dynamics can be represented as systems in which a small difference in the initial values of a group of variables can yield very large final changes.

The G-R distribution of the pooled mean nematode densities suggests that chaotic or non linear components may be influencing the nematode dynamics. This observation is in agreement with the fluctuating trends of J2 and the differences of nematode densities from sequences characterized by similar susceptible crops. Detecting determinism in the factors governing the nematode and the bacterial parasite dynamics may be possible only *a posteriori*, since forecasting is impeded by the presence of chaotic components. This situation was previously demonstrated to occur even in the simplest theoretical population models (May, 1976). The distribution observed is also similar to the negative binomial distribution already observed for the numbers of endospores attached per infested J2 of cyst or root-knot nematodes (Chen and Dickson, 1997; Atibalentja *et al.*, 1998). Although a one-year data series represents only a narrow portion of the long term dynamics occurring in a natural ecosystem, chaotic factors suggest that a

further degree of complexity is present in the soil microcosm.

One of the possible explanation for the G-R distribution of J2 densities is that extreme nematode numbers do not last for long periods in soil due to density dependence, host damage, reproductive potentials or natural antagonism, and that the most frequently encountered nematode densities remain far from maxima. In chaotic systems the initial conditions greatly affect the final outcome, even when the initial differences, in this case nematode population densities, are small. Our study suggests that large-scale trends might drive the host and parasite fluctuations far from any equilibrium region, with real possibilities of temporary nematode suppression.

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