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Temporal study of natural populations of Heterorhabditid and Steinernematid nematodes in horticultural crop soils

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Summary – The dynamics of natural populations of entomopathogenic nematodes in horticultural crop soils were studied via monthly sampling of eight sites in Catalonia (NE Spain) over 14 months. Entomopathogenic nematodes were found at six of the eight sites and they continued to be detected regardless of the agricultural practices carried out at the sites. During the study these sites were ploughed, which destroyed the natural habitat of the nematodes, then left fallow for several months, but this did not have any significant effect on the presence of the nematodes. However, some seasonal fluctuations were observed with lower populations during the hotter summer months. This seasonality also appeared to affect the vertical distribution: the nematodes migrated to deeper layers during summer, presumably to avoid the damaging effects of temperature and lack of humidity. The results of this study show that natural populations of entomopathogenic nematodes are capable of persisting and surviving for a long time in the soil, by adapting to the fluctuating and adverse conditions of their habitat.

Résumé – ***Etude temporelle des populations naturelles de nématodes Heterorhabditides et Steinernematides dans les sols horticoles*** - La dynamique des populations de nématodes entomopathogènes dans des sols horticoles a été étudiée par des prélèvements mensuels en huit sites de Catalogne (nord-est de l'Espagne) pendant 14 mois. Ces nématodes entomopathogènes ont été détectés dans six des huit sites et ont continué à l'être quels qu'aient été les traitements agricoles pratiqués sur ces sites. Pendant cette étude, les sites ont été labourés, détruisant ainsi l'habitat naturel des nématodes, puis laissés en jachère pendant plusieurs mois, sans que la présence des nématodes n'en paraisse affectée. Cependant, une influence saisonnière peut être observée, la présence des nématodes étant plus faible pendant les mois d'été où la température est élevée. Cette influence saisonnière apparaît également affecter la répartition verticale des nématodes qui migrent vers les couches plus profondes du sol, vraisemblablement pour éviter les effets néfastes de la température et du manque d'humidité. Les résultats de cette étude montrent que les populations naturelles de nématodes entomophathogènes sont capables de persister et de survivre dans le sol pendant de longues périodes en s'adaptant aux conditions fluctuantes et adverses de leur habitat naturel.

Key-words: ecology, entomopathogenic nematodes, Heterorhabditidae, persistence, Steinernematidae, vertical distribution.

Entomopathogenic nematodes of the families Steinernematidae and Heterorhabditidae are obligate and lethal parasites of insects. They possess many of the attributes of an ideal biological control agent as they have a wide host spectrum, are environmentally safe, can be produced in large-scale bioreactors, are easily applied, and are compatible with most chemical pesticides. These organisms are used as biological control agents of different insect pests in diverse climatic conditions. By using the *Galleria* trap method (Bedding & Akhurst, 1975), it is possible to estimate the occurrence of entomopathogenic nematode species in the soil, and this technique has been used in many parts of the world (Poinar, 1990). García del Pino and Palomo (1996) observed a wide distribution of these nematodes in Catalonia (Spain). However, none of these studies examined the population dynamics of the nematodes. A few temporal studies of natural populations of heterorhabditid and steinernematid nematodes (Hominick & Briscoe, 1990), and of their dynamics in cultivated soils (Glazer *et al*, 1996; Sturhan, 1996) have been published. As stated by Hominick and Reid (1990), the study of population dynamics of entomopathogenic nematodes is fundamental to understanding their persistence, distribution, and effect on insect populations and for the development of predictive models for control programmes.

In this study, we investigated the dynamics of natural populations of steinernematid and heterorhabditid nematodes through a temporal survey lasting 30 months with monthly sampling during a 14-month period at eight horticultural crop sites. The presence of these nematodes and their vertical distribution were analysed in relation to the environmental and agricultural conditions throughout the four seasons in which they were studied.

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Materials and methods

The presence of entomopathogenic nematodes was monitored in eight sites (P1 to P8), each with an area of approximately 50 m^2, situated in horticultural fields in Baix Llobregat (Catalonia, Spain). The samples were taken monthly from September 1990 to October 1991, and on separate occasions during August 1992 and January 1993.

At each site, each sample was composed of three sub-samples taken at 1 to 3 m intervals. The status of the crop growing at that time was noted. Each sub-sample consisted of 1 kg of soil taken from a 1 m^2 area, at a depth of 5-20 cm. The three sub-samples were pooled and placed in a plastic bag for transport to the laboratory, where the nematodes were extracted through a modification of the "*Galleria*-trap" method (Bedding & Akhurst, 1975). The sample was divided into three equal fractions, approximately 1 kg each, and these were placed in plastic containers of 1 dm^3 capacity with six late instar *Galleria mellonella* larvae at the bottom of each container. When necessary, the samples were moistened to allow mobility of nematodes. The containers were kept at a temperature of 23 ± 2 °C and sealed to prevent desiccation of the sample. After 7 days, the *Galleria* larvae were recovered and partially dissected to test for the presence of entomopathogenic nematodes. To quantify the presence of nematodes at every site, the three fractions of each sample containing nematodes were recorded.

The climatic data was recorded throughout the survey, including minimum, maximum, and mean air temperatures and rainfall. The soil at the eight sites was analyzed for granulometry and fertility. During the survey, no nematicides were applied to the soil, and it was not disinfected. However, it was impossible to prevent the application of other chemical pesticides (insecticides, fungicides, etc.).

To study the vertical distribution of natural populations of entomopathogenic nematodes, depth sampling was carried out by boring during the months of April 1991, August 1991, October 1991, and January 1993, only in those fields where nematodes had been detected during the monthly samplings. Depth sampling consisted of ten soil samples, each 3 cm in diameter and 30 cm deep, extracted by using a gouge auger. Each core sample was divided into 5 cm long sections. Each section was placed in a Petri dish 9 cm in diameter and labelled for transport to the laboratory. The "*Galleria*-trap" method was used by adding four late instar *G. mellonella* larvae in each dish for extracting the nematodes. The dishes were kept at 23 ± 2 °C and covered with a plastic bag to prevent desiccation. After 7 days, the larvae were recovered and partially dissected to detect the presence of nematodes, and the number of larvae parasitized by nematodes was recorded at each depth.

Results

The granulometry analysis indicated that the sampled soils were loam or silt loam. The fertility analysis revealed that their salinity and pH range were adequate for nematodes survival and that they had a high organic matter content (see Table 1).

The climatic conditions that we recorded -viz., minimum, maximum and mean monthly air temperatures and monthly precipitation during the 14 months of the study- are given in Fig 1. A clear seasonality was present with a minimum winter temperature of 1.2 °C, but the average monthly minimum temperature in winter did not drop below 5 °C and the montly

Table 1. *Granulometry and fertility analyses of the soils sampled.*

	Granulometry analysis					Fertility analysis				
	Fine sand (0.05 - 0.5 mm)	Coarse sand (0.5 - 2 mm)	Silt (0.002 - 0.05 mm)	Clay (<0.002 mm)	Classif. USDA*	E. C. (dS/m)	pH	O. M. (% p/p)	P (mg./kg.)	K (mg./kg.)
P1	13.61	14.99	60.95	24.06	L-S	0.52	8.01	3.84	147.70	907.51
P2	15.04	16.61	60.87	22.52	L-S	0.42	8.10	3.41	106.12	725.45
P3	34.65	36	51.21	12.79	L-S	0.60	8.16	2.43	50.97	624.14
P4	29.78	37.97	42.36	19.67	L	0.51	7.98	4.58	137.94	864.65
P5	31.34	33.54	48.38	19.08	L	0.40	7.99	3.16	49.49	299.46
P6	30.32	34.35	44.49	21.16	L	0.77	7.51	4.10	101.34	487.37
P7	9.25	11.14	59.97	28.89	L-C-S	0.77	8.16	3.25	55.72	386.57
P8	12.93	13.23	61.57	25.20	L-S	0.60	8.18	2.44	48.80	258.71

* L : Loam, S : Silt, C : Clay

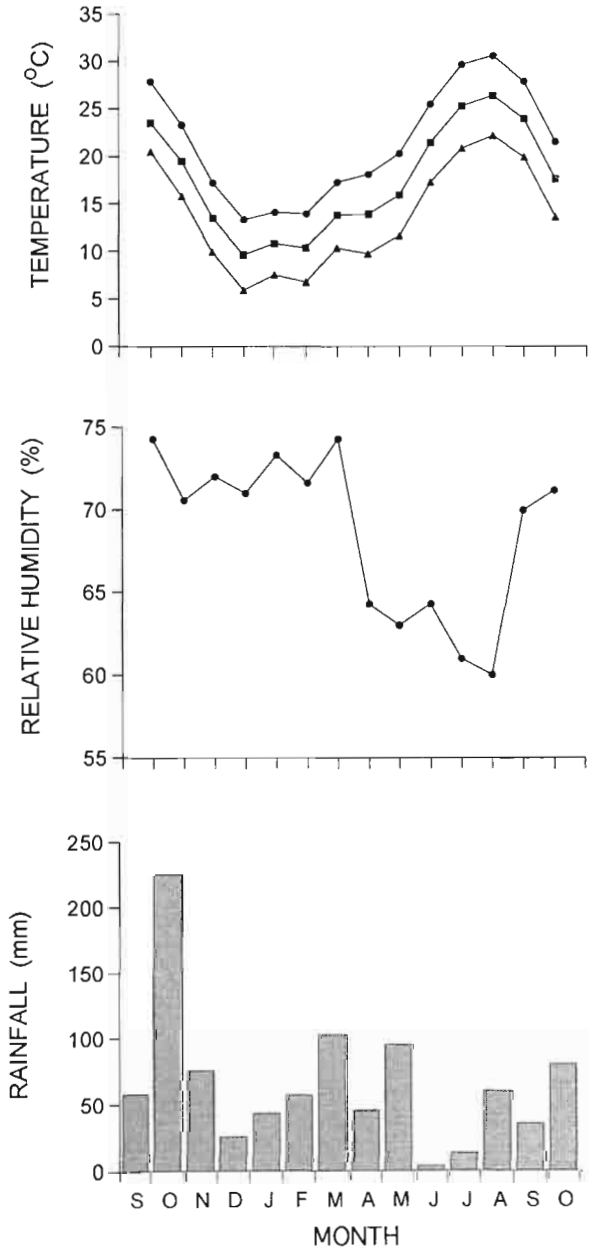

Fig. 1. *Climatic conditions in the sites sampled. Temperature reported as monthly maximum (●), minimum (▲), and mean (■) temperatures.*

mean temperature in winter was approximately 10 °C. During the summer, the maximum temperatures were up to 33 °C, although the average monthly maximum did not exceed 30.5 °C. The characteristic seasonality of the Mediterranean region was also evident in the recorded rainfall, with minimum precipitation in June and July (3.6 and 13.3 mm, respectively).

In two of the eight sites sampled (P7 and P8) no entomopathogenic nematodes were found during the entire period of the study. These two sites were not included in the subsequent calculations or figures.

In five of the six sites with entomopathogenic nematodes, nematodes belonging to the family Heterorhabditidae, *i.e.*, *Heterorhabditis bacteriophora,* Poinar, 1976, were observed, while only site P3 contained nematodes belonging to the family Steinernematidae, *i.e.*, *Steinernema feltiae* (Filipjev, 1934). During the survey, no changes were observed in the species originally detected at any of the sites analysed.

The graphic representation of the number of sites and the number of samples containing entomopathogenic nematodes during the 14 months of the survey (Fig. 2) reveals some seasonal fluctuations in the occurrence of nematodes throughout the year, which could be related with the seasonality of the environmental parameters described above (Fig. 1).

Observing the results for each of the sites during the study, we see that the presence of the entomopathogenic nematodes is variable (Fig. 3). In only two sites (P3 and P5) were the nematodes detected regularly, regardless of the agricultural practices being carried out on the sites at the time of the successive samplings. At site P3, at the time when the natural population of the nematode *S. feltiae* was detected, a crop of tomato plants harboring a potential supply of insect hosts was under cultivation. After two months (September and October) the crop was dug out and the site was left in this condition for two more months (November and December). After this, the field was ploughed, which altered the structure of the soil and destroyed the habitat that had been protecting the nematodes, thus exposing them to the effects of harmful agents (solar radiation, desiccation, etc.). The field remained fallow for 3 months (February to April), which means that the land was not watered for more than 6 months. As there was no crop during this period, the insect supply probably was minimal. After this, the land was ploughed again and then left fallow for another 3 months (June to August). Throughout this time, every monthly sample yielded nematodes until July and August, when none were detected. In September the land was sowed and the entomopathogenic nematodes reappeared and they were also detected in October. On the next two separate samplings (August 1992 and January 1993), no nematodes were detected in August 1992, but they reappeared in January 1993, 15 months after their last detection (October 1991). A similar trend was observed in site P5 (Fig. 3) with natural populations of *H. bacteriophora.*

The vertical distribution of entomopathogenic nematodes in the soil is shown in Fig. 4. The percentage of larvae parasitized by nematodes in relation to depth

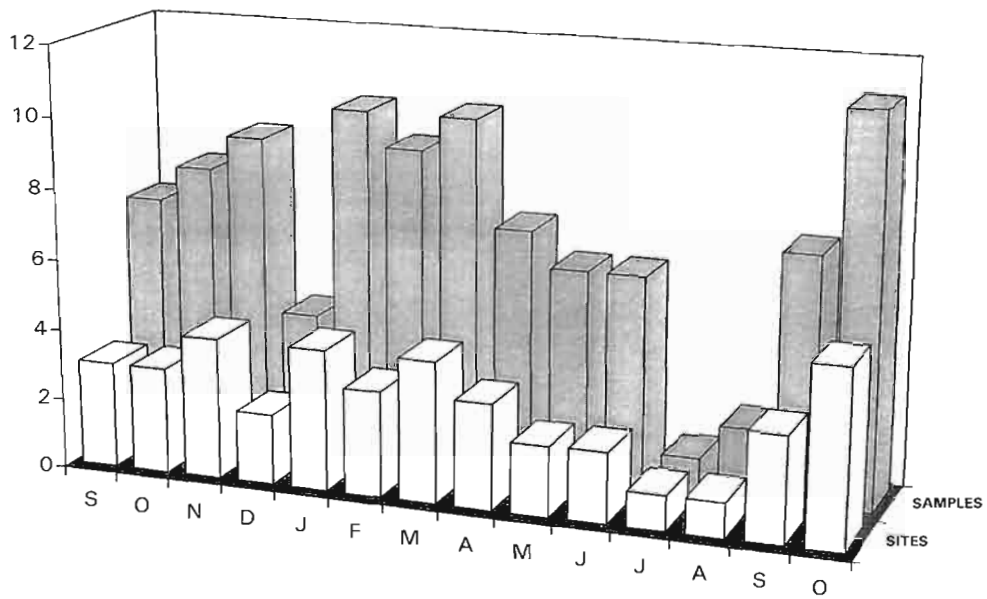

Fig. 2. *Number of sites and number of samples containing entomopathogenic nematodes during the 14 months of the survey.*

was calculated from all the samples taken during the four seasons of the study in those fields where nematodes were present. We assumed that the number of infected larvae found by sampling was related to the actual number of nematodes that were present in the soil (Mráček, 1982). The results relating to the two species of nematodes found (*H. bacteriophora* and *S. feltiae*) are presented as two separate graphs, as their dispersive behaviour and persistence are different, which causes different vertical distributions. Although for both species the greatest numbers of nematodes were detected between 5 and 10 cm depth, in the aggregate they have a significantly different vertical distribution (χ^2 = 13.10, *d.f.* = 5, P = 0.0224). *H. bacteriophora* is present in greater numbers at greater depths and in smaller numbers (6% of the *Galleria* larvae parasitized) near the surface (0-5 cm depth) (Fig. 4). On the contrary, *S. feltiae* is mostly present in the upper zones and there are less nematodes at greater depths: 9% of parasitized larvae at 20-25 cm and 5% at 25-30 cm depth (Fig. 4). Fig. 5 shows the vertical distribution of the entomopathogenic nematodes, measured as the percentage of *Galleria* larvae parasitized by nematodes at each depth, for every season and for every field studied. Separate statistical analyses were made for sites with entomopathogenic nematodes from the family Heterorhabditidae and for site P3 with the steinernematid nematode *S. feltiae*. In both cases, there was a statistical difference in the vertical distributions during the different seasons (χ^2 = 154.8, *d.f.* = 15, $P \leq 0.0001$ for *H. bacteriophora* and χ^2 = 342.4, *d.f.* = 15, $P \leq 0.0001$ for *S. feltiae*).

Discussion

There are very few studies on the temporal development of natural populations of entomopathogenic nematodes. In the present study, in some sites the nematodes were regularly detected in the soil throughout the entire period of the study (with the exception of the summer months), while in other sites their occurrence was more variable. Besides seasonal effects, this variability can be attributed to various intrinsic and extrinsic factors, and it may also depend on the abundance of the nematodes. The most significant extrinsic factors were abiotic factors, such as temperature, humidity, structure, and organochemical characteristics of the soil (Kaya, 1990), and biotic factors, such as cultivation cycle of the host and presence of antagonists (Poinar & Jansson, 1986 *a,b;* Epsky *et al.*, 1988; Kim *et al.*, 1988; Gilmore & Potter, 1993). Intrinsic factors may also play a major role in the observed variability in the occurrence of entomopathogenic nematodes. Various authors have shown that infective juveniles of the nematodes go through non-infective stages in order to stagger their infectiousness as a survival strategy (Bednarek &

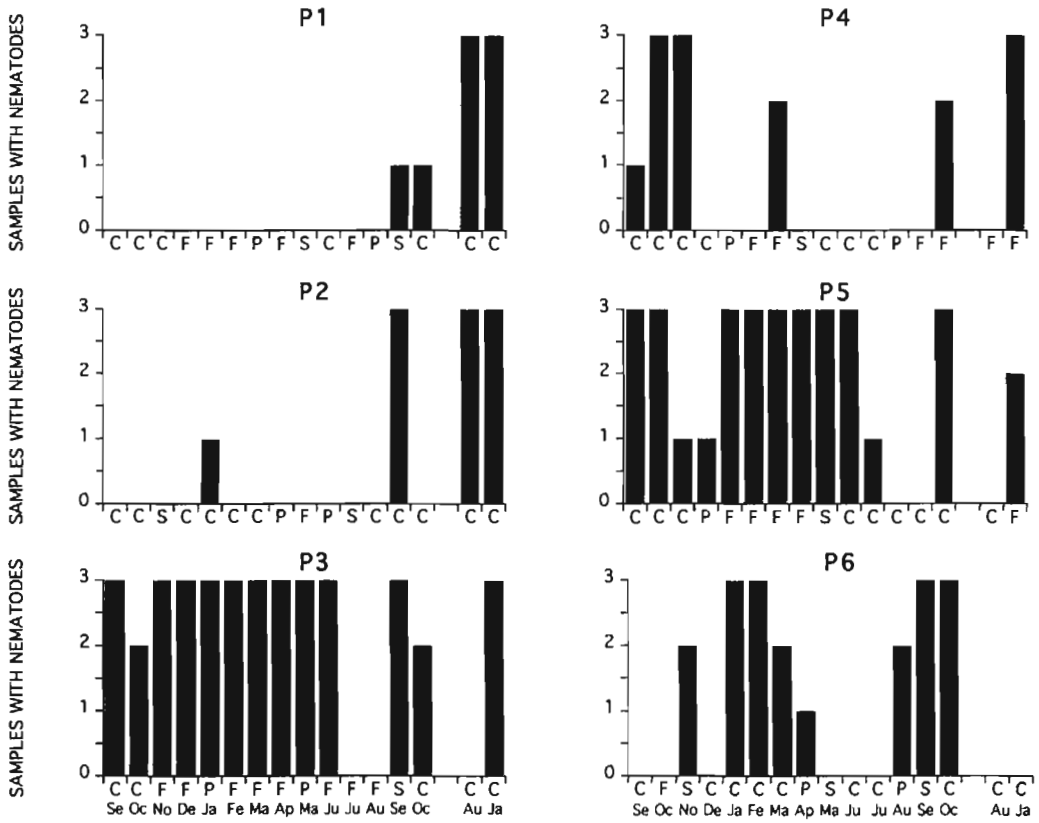

Fig. 3. *Presence of nematodes in each of the sites during the study, and current agricultural practices at the sites: (C) crop present, (F) fallow, without crop, (P) ploughed, (S) sowed. (n = 3 per sampling date).*

Nowicki, 1991; Fan & Hominick, 1991; Kaya & Gaugler, 1993; Bohan & Hominick, 1996 *a,b*).

The seasonal fluctuations observed in the populations of entomopathogenic nematodes in the Mediterranean region consist in a decrease of the population levels during the summer months, which is largely due to the higher temperatures. Hominick and Briscoe (1990) found no evidence of a seasonal component in the occurrence of the nematode *S. bibionis* (= *S. feltiae*), in a survey carried out over 28 months in Southern England, where the temperatures during July and August vary between 14.5 and 22 °C with a mean temperature of 17 °C. By contrast, in our study the mean temperature was 26.5 °C and the maximum temperature was 30.5 °C during the same period. This absence of seasonality in the occurrence of nematodes in the northern European countries has also been observed by Sturhan (1996) in Germany, who found the highest number of infective juveniles in June and August, which is quite the opposite of our results. These various observations suggest that the presence or absence of a seasonal fluctuation in the population levels of entomopathogenic nematodes, and the nature of such a seasonal fluctuation if it exists, depend on the climatic conditions of the locality where the nematodes are present. As various authors have already observed (Burrman & Pye, 1980 *a,b*; Molyneux, 1985; Kung & Gaugler, 1991), temperature has an effect on the speed of depletion of nutritive reserves, therefore on the persistence and survival of infective juveniles in the soil. Moreover, temperature affects other environmental factors such as humidity, and biotic factors such as presence and population levels of predators and pathogens of the infective juveniles, which leads to a lesser survival of these nematodes in the soil.

In agricultural soils, cultural practices periodically destroy the soil structure and the plant cover. The

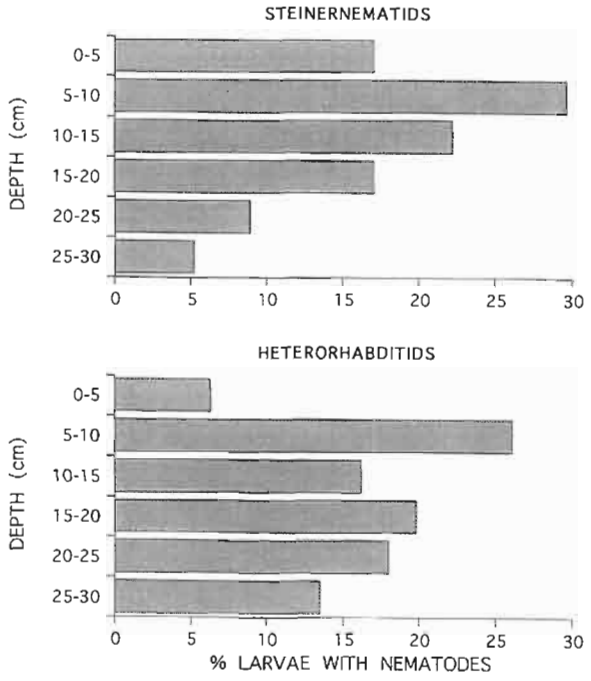

Fig. 4. *Presence of steinernematid and heterorhabditid nematodes at six soil depths in all the samples taken during the whole study.*

presence of a crop in the field can affect the presence of entomopathogenic nematodes in the soil, either directly by the action of the roots, that play an important role in the formation of the soil structure by giving it greater humidity, porosity and aeration, or indirectly because of regular watering that prevents excessive desiccation of the soil, regular supply of insects that can become hosts, etc. Several authors (Blackshaw, 1988; Vänninem *et al.*, 1989) have suggested that these agricultural practices can have an effect on the presence of entomopathogenic nematodes. However, Sturhan (1996) and our results do not seem to support this theory. The analysis of our results (*e.g.*, P3, Fig. 3) leads us to conclude that agricultural practices apparently have no effect on the presence of entomopathogenic nematodes, as these nematodes have been regularly observed both in sites under permanent cultivation and in sites without crops for a long period. This suggests the existence of an adaptability that allows these natural populations of entomopathogenic nematodes to survive under the fluctuating and adverse conditions generated by agricultural practices. Such phenomena as diapause and quiescence (Ishibashi & Kondo, 1986) and anhydrobiosis (Womersley, 1990, 1993) can explain the persistence of the entomopathogenic nematodes in these agricultural soils, as well as their reappearance after the summer period.

Moyle and Kaya (1981) have shown that certain species of *Steinernema* prefer to search for hosts close to the surface, and Georgis and Poinar (1983) and later Choo *et al.* (1989) have established that species of *Heterorhabditis* are more suited to searching for hosts at a greater depth. The present data confirms these observations in that *S. feltiae* is generally present in greater numbers in the upper layers (0-20 cm) of the section of soil analysed, while *H. bacteriophora* is more abundant in the lower layers (as deep as 30 cm). Villani and Wright (1990) observed that many soil-inhabiting animals undergo vertical migrations to avoid the damaging effects of temperature or lack of humidity. Although there are many laboratory studies of vertical distribution of entomopathogenic nematodes and of their ability to find a host at different depths (Schroder & Beavers, 1987; Gaugler *et al.*, 1989 *a,b*; Choo *et al.*, 1989; Westerman & Godthelp, 1990; Nguyen & Smart, 1990; Shapiro *et al.*, 1993), the importance of this avoidance behaviour for the survival of entomopathogenic nematodes has not yet been studied. Our results do not show any clear trend, perhaps because of the interference of the agricultural practices carried out in these soils. However, it can be observed that in autumn, *i.e.*, after the nematode populations had been subjected to the harmful effects of high summer temperatures at the soil surface, a greater number of nematodes (with steinernematid and heterorhabditid nematodes in equal numbers) were present in the deepest layers of the ground. In winter, when the surface temperature presented no danger to their survival, there was a greater number of nematodes in the surface layers of the soil, as Glazer *et al.* (1996) have also observed. These results could indicate that entomopathogenic nematodes display an avoidance behaviour from adverse conditions through migration to greater depths.

To conclude, the present results confirm that natural populations of entomopathogenic nematodes are capable of persisting and surviving for a long period in the soil. These nematodes are better adapted to the fluctuating and adverse conditions characteristic of their environment, and they survive in greater numbers, than populations of entomopathogenic nematodes artificially introduced. This issue should be considered when selecting the entomopathogenic nematodes the most suitable for use in biological pest control programmes.

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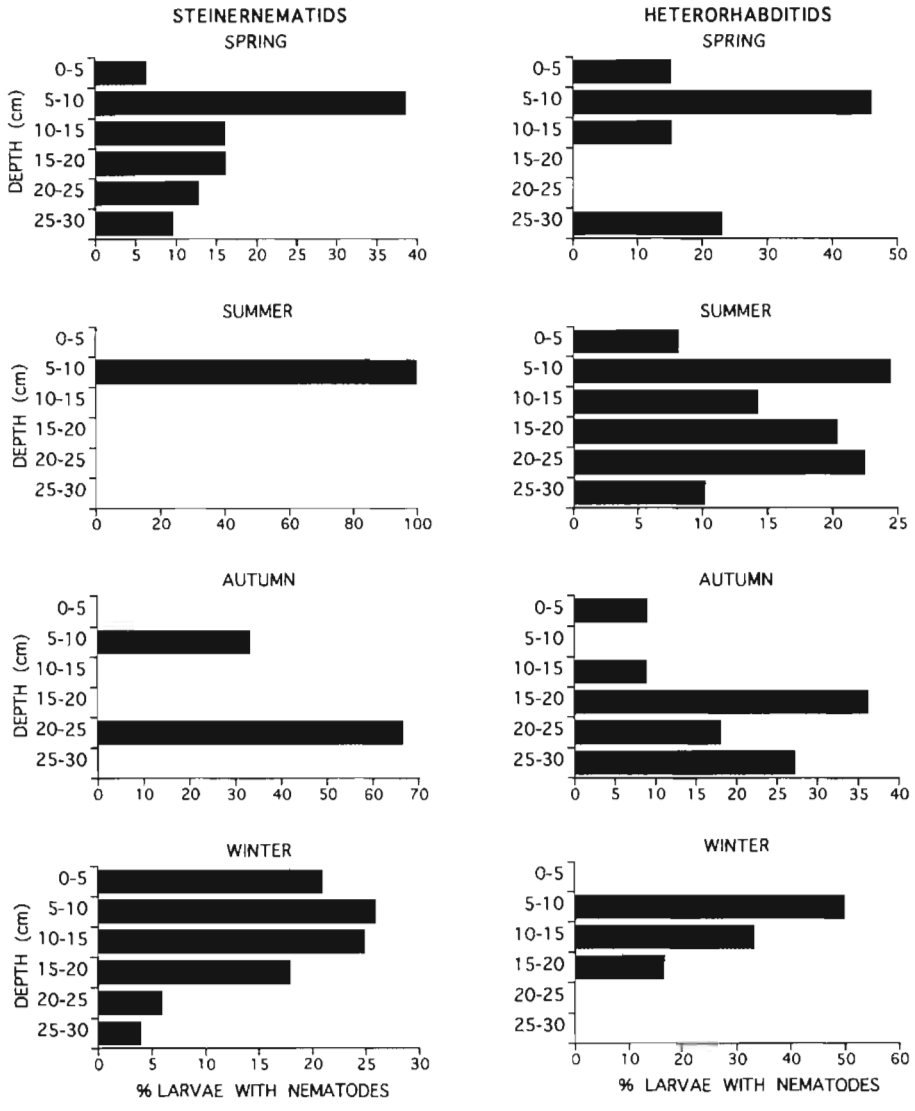

Fig. 5. *Presence of steinernematid and heterorhabditid nematodes at six soil depths during the various seasons studied. (ten samples per season).*

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