

Spatial arrangement of nematodes around the banana plant in the Ivory Coast: related comments on the interaction among concomitant phytophagous nematodes

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ABSTRACT

Spatial arrangement of nematodes in soil and roots around the banana plant and its relation to interspecific interaction phenomena have been studied through the results of field experiments conducted in banana plantations in the Ivory Coast. The attractiveness of *Radopholus similis* towards the banana roots seems to be governed by the rhizogenic activity of some parts of the rhizome rather than by the strict origin of the roots on the rhizome. In the absence (or reduced densities) of one or more competitors, *R. similis* is able to colonize, with high population levels, the entire set of banana roots. In the presence of competitors, e.g. *Helicotylenchus multicinctus*, the arrangement and density of *R. similis*, in the soil as in the roots, is reduced and restricted to areas close to the rhizome. The higher the density of competitors, the more restricted the dispersion area of *R. similis* around the rhizome. Notions of ecological "niche" and "sub-niche" are discussed and applied to the nematodes-banana root system interaction, within the hypothesis of the succession of nematode species in a competitive hierarchy theory.

KEYWORDS: nematode, banana, interaction, niche, Ivory Coast, *Helicotylenchus multicinctus*, *Radopholus similis*.

RÉSUMÉ

La répartition spatiale des nématodes phytoparasites dans le sol et le système racinaire du bananier et sa relation avec des phénomènes d'interaction interspécifique ont été étudiées à travers les résultats de diverses expérimentations conduites en Côte d'Ivoire en bananeraies. L'attractivité de *Radopholus similis* vers les racines semble plus être fonction de l'activité rhizogénique des parties du rhizome que de la stricte origine des racines sur le rhizome. En l'absence (ou densités réduites) de compétiteurs, *R. similis* est capable d'infester, avec des taux de population élevés, la totalité du système racinaire du bananier. En présence de compétiteurs, dont *Helicotylenchus multicinctus*, la répartition et la densité de population de *R. similis*, aussi bien dans le sol que le système racinaire, est réduite et restreinte aux zones proches du rhizome, et cela d'autant plus que la densité des compétiteurs est élevée. Les notions de « niche » et de « sous-niche » écologiques sont discutées et appliquées à l'interaction nématodes-système racinaire du bananier, en prenant pour théorie la succession hiérarchique d'espèces compétitives.

INTRODUCTION

In the tropics, most of the time only polyspecific communities occur on crop plants (LUC & REVERSAT, 1985). This situation is especially true for banana plants and plantains which are, in the Ivory Coast, host plants for many concomitant



nematode species (ADIKO, 1988; FARGETTE & QUENEHERVE, 1988) and where interactions may occur.

By definition, interactions between two species of nematodes may be beneficial to one or both species, have no effect, or most commonly interfere with the well-being of one or both species. The antagonistic interaction (competition) can be caused by a spatial occupation or physical alteration or destruction of feeding sites, or by a physiological alteration of the host that decreases its suitability (NORTON, 1978; EISENBACK, 1985). As it is well known, the outcome of interspecific interactions may depend upon: i) initial population densities, ii) environmental conditions (edaphic factors, temperature, humidity, etc.) and iii) the genetic constitution of the strains of interactive species (PIANKA, 1981).

In nematology, the literature, as reviewed by EISENBACK (1985) is rather extensive on that subject but mainly deals with results of greenhouse experiments of the interaction between two nematode species. Furthermore, information is scarce about field studies (BIRD *et al.*, 1974; BOAG & ALPHEY, 1988), or involving tropical or sub-tropical crops (GUEROUT, 1965).

In this study, because there are not controlled conditions (greenhouse, sterile soil, inoculation), we must be very cautious in the interpretation of the results observed in the field which can be attributed to interaction with many biotic factors (soil microorganisms including insects, nematodes, fungi, bacteria, mycorrhizae, viruses, etc.).

The objectives of this study were: i) to confirm the equal attractiveness of the different roots and parts of the rhizome towards the different nematode species but especially *Radopholus similis*, ii) to demonstrate the evidence of competitors to *R. similis* among nematodes associated with the banana root system and iii) to discuss the related phenomena of the spatial arrangement of the nematode species on the unique root system of the banana plant. These informations being essential to the understanding of the disease at the root system scale should allow the emergence of new methods of nematode assessment and control.

MATERIALS AND METHODS

The data herein reported are parts of series of experimental field studies which examined the population fluctuations of nematodes associated with different banana plantations in the Ivory Coast. To investigate the attractiveness of the different roots and parts of the rhizome to *Radopholus similis* it was necessary to contrive a situation that initially was not complicated by interactions with other species. The field experiment was established at Blidah (Site 1) on a virgin land never cultivated before with bananas (formerly a *Raphia* spp forest) in the region of Azaguié and checked for the absence of *R. similis*. Then, it was possible to follow monthly the infestation of the entire root system by *R. similis*, introduced only by the planting material itself (QUENEHERVE & CADET, 1985*a*). The results on the interspecific interaction with *R. similis* comes from an experiment set on a peat soil at Yace (Site 2) in the Niecky valley. The fluctuations of nematode populations were monitored monthly over 2 years on control plots and on plots treated before plantation with methyl-bromide (100 g.a.i./m²). Methods, materials and horticultural results have already been published (QUENEHERVE *et al.*, 1991). The experiment on the spatial arrangement of nematodes in soil around the banana rhizome was conducted in October 1981. Two sites were selected: Agbo 102 (Site 3) on a clay-peat soil in the Niecky valley and Vidal 16 (Site 4), on a sandy-clay soil in the region of Azaguié. For each site, 10 trenches (1.0 × 0.5 × 1.0 m) were dug adjacent to the pseudostem of selected banana plants at flowering stage, in

the axis of the main sucker. Soil samples were taken with a trowel at 5-25 cm depth from adjacent to the pseudostem (A) and at 40-60 cm (B) and 90-110 cm (C) from the center of the pseudostem. Two other samples were taken from points A and C at 60-80 cm depth (fig. 1). Each sample was then analysed separately in order to estimate the level of nematode infestation. Standardized extraction techniques were used on soil (SEINHORST, 1962) and roots (SEINHORST, 1950). Statistical analysis was conducted on the nematode population levels at site 1 using a Wilcoxon signed-rank test. An analysis of variance, followed by a Duncan's new multiple range test was performed on $\log_{10}(x+1)$ transformed data at site 3 and 4.

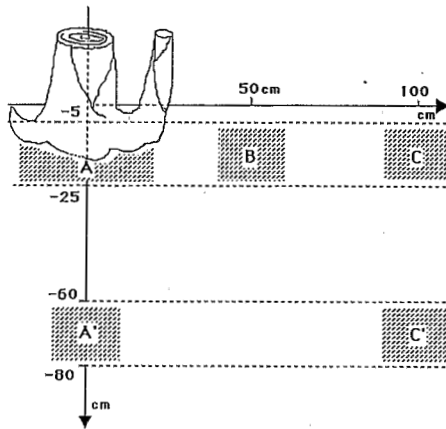


FIG. 1. — Localization of the soil sampling at site 3 (Agbo 102) and at site 4 (Vidal 2).

RESULTS

ATTRACTIVENESS OF THE ROOTS FROM DIFFERENT ORIGINS ON THE RHIZOME

From the analysis of the nematode fluctuations during this experiment (fig. 2) it appeared that, for a similar rhizogenic activity of the different parts of the rhizome, as observed in the early months after planting, the roots originating either from the mother plant (RMP) or from the main sucker (R1Y) had the same attractiveness for *R. similis* which was able to build comparable population infestation level (non-significant Wilcoxon signed-rank test). As soon as the rhizogenic activity differed, the infestation levels in *R. similis* were significantly higher ($p=0.04$, Wilcoxon signed-rank test) on the roots belonging to the part of the rhizome with the greatest rhizogenic activity, as observed on the roots originating from the pruned suckers (R1Y \emptyset) compared to those originating from the main sucker.

INFLUENCE OF A SOIL TREATMENT WITH METHYL-BROMIDE BEFORE PLANTING ON THE NEMATODE FLUCTUATIONS

On this peat soil, *Helicotylenchus multincinctus*, *R. similis*, *Hoplolaimus pararobustus*, respectively comprised 92%, 6%, and 2% of the endoparasitic nematode

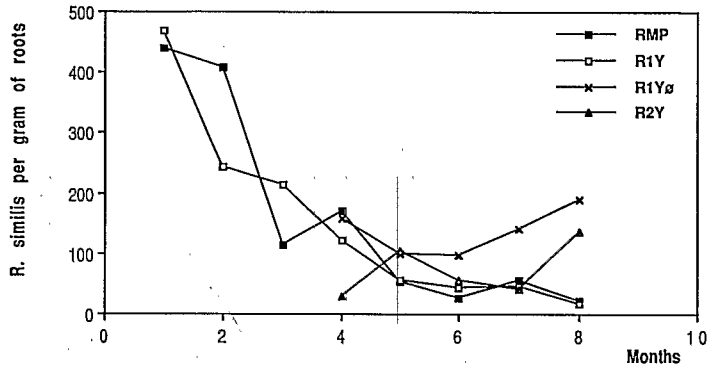


FIG. 2. — Fluctuation of *R. similis* in the banana root system during 8 months after planting. (RMP: roots of the mother plant; R1Y: roots of the sucker of first generation; R1YØ: roots of the pruned suckers of first generation; R2Y: roots of the sucker of second generation.)

population, while *Cephalenchus emarginatus* occurred as the only ectoparasitic species. At the time of planting the nematodes were undetectable with our sampling method on the plots previously treated with methyl bromide. The nematode fluctuations in the soil and in the roots (illustrated by the global root infestation which is the average of the partial infestations occurring in the roots belonging to the different parts of the rhizome, based on six replicates) are presented in figures 3 to 5.

During the first 12 months after treatment the soil population of *H. multicinctus* remained very low. It then began to increase and to follow the same fluctuation pattern that was observed on the control plots (fig. 3 A). The pattern of root infestation was fairly similar to that in the soil (fig. 3 B); it is noteworthy to observe the very high level of infestation on the control (average between 200 and 400 nematodes per gram of roots). In the months after methyl bromide treatment the population of *R. similis* became relatively greater in the soil as it declined in the roots (fig. 4 A-B).

During the first 5 months the numbers of *R. similis* in treated plots were higher than expected (average between 100 and 200 nematodes per gram of roots) for this soil type. Populations were similar in roots of the mother plant and in the main sucker. Later the population fluctuations followed the same pattern in both treated plots and controls.

The soil population of *H. pararobustus* was undetectable during the first 8 months after treatment with methyl bromide, while in the roots, a low infestation was observed from the first month (fig. 5 A-B). The population level of *H. pararobustus* remained lower than that observed on the control plots for more than 15 months; the fluctuation patterns on the treated plots as on the controls were similar.

C. emarginatus was undetectable during only the first 3 months after soil treatment and then the fluctuation patterns on the treated plots resembled those on the controls (fig. 6).

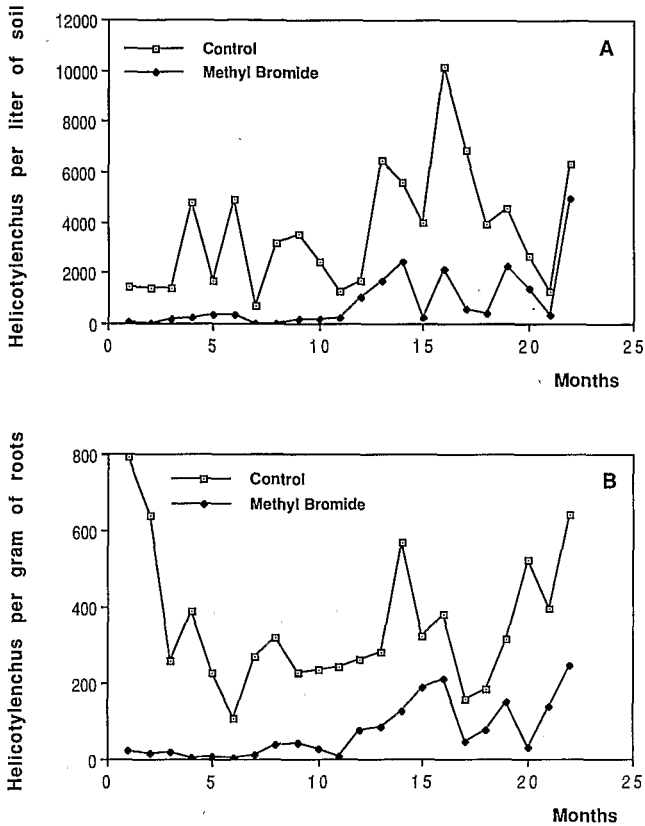


FIG. 3. — Fluctuation of *H. multincinctus* in the soil (A) and in the roots (B) on controls and after soil treatment at planting with methyl bromide (six replicates per sampling date).

NEMATODE ARRANGEMENT IN SOIL AROUND THE RHIZOME

The complete results of soil nematode infestations around the rhizome at the flowering stage over the two selected sites Agbo 102 and Vidal 2 are summarized in Table I. As a general trend all the nematode species were present in higher densities in the superior layer of soil (5 to 25 cm depth) than in the inferior (60 to 80 cm depth). At site 1, Agbo 102, the nematode species *H. multincinctus*, *H. pararobustus* and *C. emarginatus* had statistically the same uniform type of distribution within the two sampling depths. However, even if not significant, the trends in distribution were different between these nematode species. Densities of *H. multincinctus* were higher in the distal samplings while densities of *H. pararobustus* appeared higher near the rhizome. *R. similis* exhibited a significantly different soil arrangement with the highest densities near the rhizome and decreasing densities as the distance from the rhizome increased. At site 2, Vidal 2, populations of

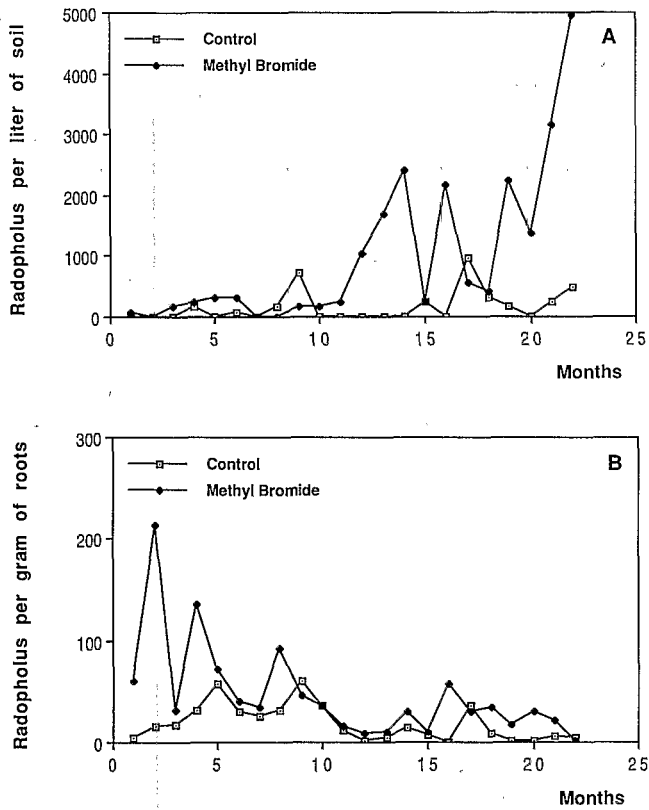


FIG. 4. — Fluctuation of *R. similis* in the soil (A) and in the roots (B) on controls and after soil treatment at planting with methyl bromide (six replicates per sampling date).

H. pararobustus and *R. similis* were significantly greater near the rhizome as observed with *R. similis* at the site 1, while *H. multicinctus* and *C. emarginatus* showed the reverse trend with the lowest densities near the rhizome.

DISCUSSION

Due to their mode of propagation, even when issued from infested materials, banana roots are produced free of nematodes (BLAKE, 1961; QUENEHERVE & CADET, 1985 *b*). Further infestations develop from nematodes in the soil in the vicinity of the roots. The purpose of the first experiment reported above was to know if these roots, originating from different parts of the rhizome (from the mother plant, from a young sucker, from a pruned sucker, etc.) showed the same attractiveness for the nematodes present in the soil, and particularly for *R. similis*. This aspect seems not to have been investigated previously. It appeared from this field study and from many other field observations (unpublished data) that there

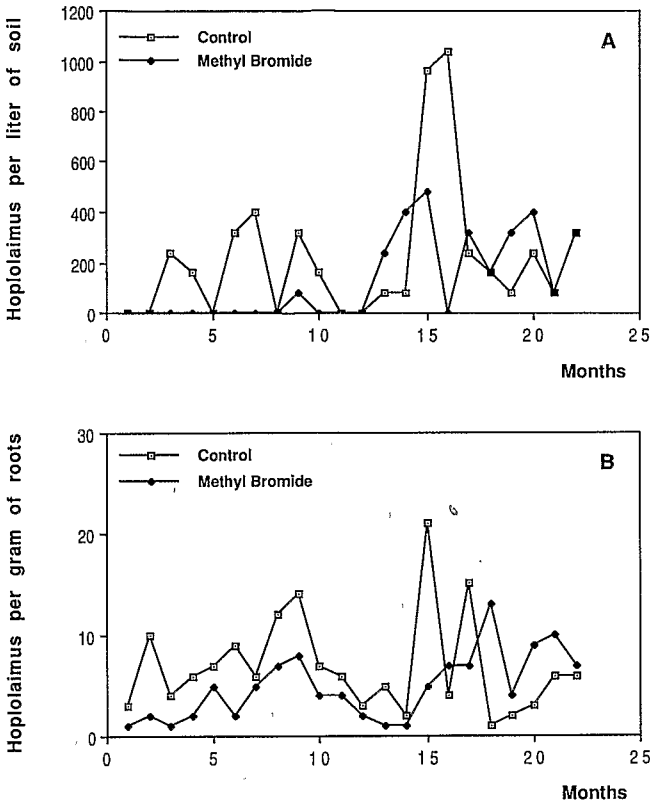


FIG. 5. — Fluctuation of *H. pararobustus* in the soil (A) and in the roots (B) on controls and after soil treatment at planting with methyl bromide (six replicates per sampling date).

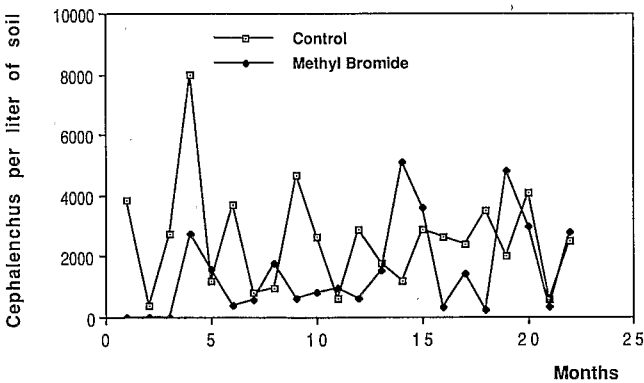


FIG. 6. — Fluctuation of *C. emarginatus* in the soil on controls and after soil treatment at planting with methyl bromide (six replicates per sampling date).

TABLE I. — *Nematode infestations per 250 cc of soil around the banana rhizome at the flowering stage at site 3, Agbo 102 and at site 4, Vidal 2. Means (10 replicates) followed by the same letters within a column are not significantly different ($p=0.05$) based on a Duncan's new multiple range test performed on $\log_{10}(x+1)$ transformed data.*

	<i>Helicotylenchus multicinctus</i>	<i>Radopholus similis</i>	<i>Hoplolaimus pararobustus</i>	<i>Cephalenchus emarginatus</i>
Agbo 102				
<i>Sampling points</i>				
A	585 a	666 a	332 a	1629 a
B	1586 a	178 b	118 a	1690 a
C	1272 a	129 b	88 a	1864 a
A'	22 b	46 b	12 b	176 b
C'	6 b	0 c	8 b	90 b
Vidal 2				
<i>Sampling points</i>				
A	215 ab	182 a	316 a	203 b
B	547 a	33 b	81 b	548 a
C	441 ab	31 b	97 b	700 a
A'	18 bc	3 c	14 bc	28 c
C'	11 c	1 c	1 c	31 c

was no difference between the roots whatever their origins on the rhizome. In that case, the attractiveness of *R. similis* towards the roots seemed governed by: i) the presence of roots in the soil area where *R. similis* was released from the outer cortical part of the rhizome and ii) the rhizogenic activity of the different parts of the rhizome. The center of dissemination of *R. similis* is also the center of origin of the roots. In the vicinity of the rhizome, during the active rhizogenic period, the proportion of new roots which are attractive to *R. similis* is greater than that of the older roots. With favourable environmental conditions this intense root growth enables *R. similis* populations to build rapidly (QUENEHERVE, 1989 a, 1989 b). As the ratio of young to old roots decreases, many phenomena may occur (interaction, reduction in the number of penetration sites, feeding sites, etc.) allowing a chronological decline in the infestation levels and an apparent shift of the multiplication sites towards others roots in a wave-like process. On bananas, after pruning, the suckers will usually remain alive and generate many roots in order to replace the foliar material lost. These new roots are very favorable for the multiplication of *R. similis* and only repetitive pruning can kill these suckers and stop the root emergence. It is clear that in these experiments in the absence of nematode interactions, either on virgin land or after a soil treatment with methyl bromide, *R. similis* was immediately able to colonize and to exploit the entire set of roots via the soil phase.

In fact, from a methodological point of view, field observations of interactions among nematode species are exceedingly difficult to estimate directly, except by population removal experiments and by allowing the resulting system to return to equilibrium. The observation of reduction in population density, in response to the presence of one or more competitors, may establish in that situation the direct evidence of interspecific competition.

After a previous soil treatment with methyl-bromide on a peat soil on a banana plantation, it was possible to follow the fluctuations of nematode populations over

two years. At the applied dosage (100 g. a.i./m²) methyl-bromide is known as a total biocide killing weeds, insects, nematodes, fungi and some bacteria (ANON., 1970). At the time of planting, the treatment was effective in suppressing nematodes from our soil samples (in the limit of our sampling method). After planting, it was obvious that soil re-infestation may arise not only from the infested planting material but also from deeper layers of soil still infested or from the irrigation system (unpublished data). This experiment demonstrated that in the absence (or under reduced density) of one or more competitors (which nature and densities were unknown, except for nematode species, due to the partially uncontrolled conditions of this field experiment), the nematode species *R. similis* was able to build higher population densities. Obviously in that case *H. multincinctus* could have been one of the associate competitors of *R. similis* but even if we made many concordant observations coming from other field experiments this assumption needs further studies in controlled conditions to evaluate the interaction in a two-species system. Furthermore, in natural conditions banana roots are always infested with numerous fungi which are early colonizers of the lesions caused by nematodes (BRUN & LAVILLE, 1965; STOVER, 1966); such associations and/or interactions should not be underestimated. The expression of *Fusarium* wilt was increased (etiological interaction) in the presence of *R. similis* (LOOS, 1959). PINOCHET and STOVER (1980) reported that both fungi *Cylindrocarpon musae* and *Fusarium moniliforme* significantly suppressed the multiplication of *R. similis* (ecological interaction). In Martinique, LORIDAT (1989) demonstrated the own pathogenicity of a fungus *Cylindrocladium* sp., often associated with *R. similis* in banana root necrosis. Therefore, additional studies are also needed to verify the complex relationships among other microorganisms and nematodes on bananas.

The study of the spatial arrangement of nematodes in the soil was very important in the definition of the area of influence of each nematode species. *R. similis* and *H. pararobustus* seemed to have the same behavior in confining their extension area to the close vicinity of the rhizome. On the contrary, the species *H. multincinctus* and *C. emarginatus* were found in higher densities at some distance from the rhizome. This corroborates the observations on the specific root lesions made by PINOCHET in 1977; the lesions caused by *R. similis* were observed closer to the rhizome and on the rhizome while the lesions caused by *H. multincinctus* were evenly distributed throughout the length of the roots. The vertical arrangement did not bring new information except that nematodes in the soil were present where the roots are distributed. In fact 50% of the banana roots are in the upper soil layer (0 to 20 cm depth) and 20 to 40% in the lower layer (20 to 40 cm depth), (BEUGNON & CHAMPION, 1966).

In conclusion, this study pointed out that, from an ecological interaction point of view, the nematode species *R. similis* is subject to competition and that interactions exist among nematodes and/or other microorganisms associated with banana roots. The arrangement of the nematodes in the soil around the root system is not regular but varies with the distance of sampling from the rhizome.

The hypothesis is that interaction (and more precisely the interspecific competition) may act as a major factor in the spatial arrangement of nematodes species around the banana root system. In the theoretical absence of competitors, the entire set of root used as food source could be referred to the "fundamental or pre-interactive niche (HUTCHINSON, 1957) for each phytophagous nematode species

taken individually. Due to interactions and overlapping pattern of resource utilisations, there are "post-interactive niches" which are subsets of the fundamental niche (HUTCHINSON, 1957; VANDERMEER, 1972).

At the root scale, first level of observation, the constant observation on each experiment (QUENEHERVE, 1989 *a*, 1989 *b*) of the successive multiplication of *R. similis* followed by *H. multicinctus* on the same type of roots could illustrate the hypothesis of a succession in a competitive hierarchy theory (HORN, 1981). The early successional species (*R. similis*) grow quickly to dominate early but, due to particular characteristics, they cannot survive interaction with other nematodes (e.g. *H. multicinctus*) or associated microorganisms. The latter species *H. multicinctus*, which is less strict in its requirements will then be able to dominate. This type of interaction is density-dependent and the more abundant (due to environmental conditions) the latter species, the faster the succession occurs within the root. This could explain the differences observed on different soil types between *R. similis* and *H. multicinctus* in our experiments. The situation is very similar for the nematode species *H. pararobustus*, which seems to share the same niche (vicinity of the rhizome) as *R. similis*. This may explain why *H. pararobustus* is able to build higher soil and root populations on bananas than usually observed in some cases where there is an absence or reduced density of competitors (e.g. *R. similis* and *H. multicinctus*): i) in respect to environmental factors (MATEILLE *et al.*, 1988) and ii) in respect to some chemical treatments (QUENEHERVE *et al.*, 1991).

This interaction theory leads to new interpretations at a second level of observation: the root system scale. *R. similis* is able not only to colonize but also to maintain high level of infestation and to proliferate in the outer part of the rhizome (QUENEHERVE & CADET, 1985 *a*). This interspecific competition speeds up the modification in the infestation levels of *R. similis* and the apparent shift of the multiplication sites towards new roots in a wave-like process (QUENEHERVE, 1989 *a*, 1989 *b*). From observations on the soil arrangement of *R. similis* in this study, and along the root length (PINOCHET, 1977), it seems that *R. similis* restricts its post-interactive niche to the cortical part of the rhizome and to the close vicinity in terms of soil and root length. The area of influence of this nematode species (but also *H. pararobustus*) being related with the degree of interaction and varying with environmental factors. On the contrary the post-interactive niche of *H. multicinctus* seems to be at a distance from the rhizome. This theory can also explain the observation of differences in the area of influence of *Meloidogyne* sp., as reported by PINOCHET (1977), or on the type of roots parasitized by the different nematode species (EDMUNDS, 1971) where for the sedentary endoparasitic species (*Meloidogyne* spp; *Rotylenchulus* sp), the post-interactive niche is situated at a distance from the rhizome.

These observations have a great importance from a practical point of view on the sampling methods and on the nematode control on bananas. It is a confirmation of the need: i) to consider every encountered nematode species, even if apparently it is not damaging, due to the interspecific interactions and their possible etiological consequences (QUENEHERVE *et al.*, 1991) and ii) to have a sampling method adapted to this particular arrangement of the nematode infestations in respect to the banana root system.

The investigation on the interactions among concomitant phytophagous nematodes on bananas needs a dynamic approach due to the great spatial and temporal

variability characteristics not only of the nematode communities associated with bananas but also with the banana plant itself and the other microorganisms of its rhizosphere.

The soil is a highly complex set of multiple interactions and the joint effect of two species upon a third in a 3-species system cannot always be predicted from the separate interactions in three component 2-species systems. Furthermore, interactions vary with environmental factors. Therefore, further studies should be done in greenhouse-type experiments on the interaction at the root scale in a two-species system. These informations should be useful in the understanding of the disease at the root system scale and allow the emergence of new methods of nematode assessment and control on bananas.

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