Parasitic nematodes on *Musa* AAA (Cavendish subgroup cvs 'Grande naine', 'Valery' and 'Williams')

M. Araya[1] and T. Moens[2]

Abstract

Among the biotic factors affecting yield, banana-root nematodes are second only to black Sigatoka (*Mycosphaerella fijiensis*). The three commercial cultivars, 'Grande naine', 'Valery' and 'Williams' are equally susceptible, and in plantations in Costa Rica usually only polyspecific communities occur, consisting of a mixture of the migratory endoparasitic *Radopholus similis* and *Pratylenchus coffeae*, the ecto-endoparasitic *Helicotylenchus multicinctus*, and the sedentary endoparasitic *Meloidogyne incognita*, or rarely *M. javanica*. Based on their frequencies and population densities the relative importance of nematode genera in Costa Rica was established in decreasing order as follows: *R. similis* > *Helicotylenchus* spp. > *Meloidogyne* spp. > *Pratylenchus* spp. *R. similis* is the most abundant nematode, accounting for 82 to 97% of the overall root population. High populations of *R. similis* are found throughout the year and in all counties producing bananas. The nematodes damage the root and corm tissue. *R. similis* enters the root mainly by the root tip, but any portion of the entire root length may be invaded. Adults and juveniles occupy an intercellular position in the cortical parenchyma, in which they move actively, causing damage as they feed on the cytoplasm of the surrounding cells. The four nematode genera develop and complete their life cycle inside the banana roots. In highly infected roots, *R. similis* sometimes crosses the endodermis and invades the stele. Reddish brown lesions appear throughout the cortex. In some Costa Rican banana growing areas, crop losses on nematode infected plantations can be high, up to 30-50%. Infected plants have poor root anchorage and the ability of the root system to take up water and nutrients is reduced, which results in losses in bunch weight and crop longevity, and a lengthening in the plant production cycle. Pathogenicity studies have shown that *R. similis* restricts banana root system growth and reduces the concentration of K in the root dry matter. All the phenological stages can be infected by any of the four genera, but again, *R. similis* is the most frequent and the most abundant at any stage. Even the roots of very small peepers (suckers 10 cm high) can be infected, and in the case of *R. similis,* it is common to find nematodes in the corm tissue also. This suggests that root infection of these young suckers in infected plants is caused by either *R. similis* coming from the corm or from the soil.

Resumen - Nematodos parásitos de *Musa* AAA (subgrupo Cavendish cvs 'Grande naine', 'Valery' y 'Williams')

Entre los factores bióticos que afectan el rendimiento en banano, los nematodos son el segundo en importancia después de la Sigatoka negra (*Mycosphaerella fijiensis*). Los tres cultivares comerciales 'Grande naine', 'Valery' y 'Williams', son igualmente susceptibles y en las plantaciones locales, usualmente solo comunidades poliespecíficas ocurren, consistiendo de una mezcla de los endoparásitos migratorios *Radopholus similis* y *Pratylenchus coffeae*, el ecto-endoparásito *Helicotylenchus multicinctus* y el endoparásito sedentario *Meloidogyne incognita* o raramente *M. javanica*. Basado en las frecuencias y densidades poblacionales, la importancia relativa de los géneros de nematodos en Costa Rica se estableció en orden decreciente como sigue: *R. similis* > *Helicotylenchus* spp. > *Meloidogyne* spp. > *Pratylenchus* spp. *R. similis* es el nematodo más abundante y representa de un 82-97% de la población total en las raíces. Altas poblaciones de *R. similis* se encuentran durante todo el año en todos los cantones productores de banano. El daño

[1] Corporación Bananera Nacional (CORBANA S.A.) Apdo 390, 7210 Guápiles, Costa Rica.
e-mail: maaraya@corbana.co.cr. [2]INIBAP, CATIE 7170 Turrialba, Costa Rica. e-mail: tmoens@catie.ac.cr.

se localiza en las raíces y cormo. *R. similis* penetra las raíces principalmente por la parte terminal (caliptra), pero cualquier parte de la raíz puede ser invadida. Adultos y juveniles ocupan una posición intercelular en el parénquima cortical donde ellos se mueven activamente causando daño conforme se alimentan del citoplasma de las células vecinas. Los cuatro géneros de nematodos se desarrollan y completan su ciclo de vida dentro de las raíces de banano. En raíces altamente infectadas, *R. similis* algunas veces pasa la endodermis e invade el cilindro vascular. Coloraciones café rojizas aparecen a través de toda la corteza. En algunas plantaciones locales infectadas las pérdidas en rendimiento alcanzan hasta un 30-50%. Plantas infectadas carecen de buen anclaje y la habilidad de las raíces para absorber agua y nutrientes se reduce, lo que resulta en pérdida de peso del racimo y longevidad de la planta y se alarga los intervalos entre ciclos de producción. Estudios de patogenicidad muestran que *R. similis* restringe el crecimiento del sistema radical y reduce la concentración de K en las raíces. Todos los estados fenológicos de la planta de banano pueden ser infectados por cualquiera de los cuatro géneros, pero nuevamente *R. similis* es el más frecuente y abundante en cualquier estado de desarrollo de la planta. Aún raíces de hijos muy pequeños (10 cm de altura) pueden ser infectadas y en el caso de *R. similis* es común también encontrarlo en el cormo. Esto sugiere que la infección de las raíces en hijos nuevos de plantas infectadas, ocurre igualmente de *R. similis* procedente del cormo o del suelo.

Introduction

Banana is an important crop in Costa Rica accounting for almost 17% of the agricultural gross national product. In 2003, 1.85 million tonnes were exported, produced on 42,000 ha, generating a total income of US $541 million FOB (Sánchez and Zuñiga 2004). Besides the constraints of banana market requirements and demands, there are other limiting factors. Among the biotic factors affecting yield, banana-root nematodes are second only to black Sigatoka (*Mycosphaerella fijiensis*). Nematodes reduce bunch weight and plant longevity, and increase the crop cycle duration (Quénéhervé 1991).

In Costa Rican plantations (Araya *et al*. 1995, 2002) usually only polyspecific communities occur, consisting of a mixture of *Radopholus similis*, *Helicotylenchus multicinctus*, *Meloidogyne incognita*, *M. javanica*, and *Pratylenchus* spp. Here we report some research results related to the parasitic behaviour and nematode damage under controlled conditions on commercial banana plantations in Costa Rica.

Host suitability

The commercial cultivars planted are ‘ Grande naine’, ‘Valery’ and ‘Williams’, which are part of the *Musa* AAA Cavendish subgroup. All these cultivars are equally susceptible to *R. similis* (Figure 1) and their reaction to each of the other three most important

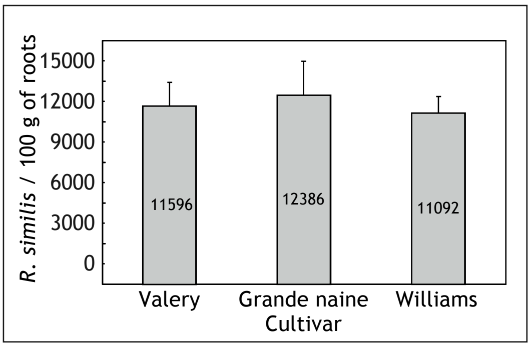

Figure 1. *Radopholus similis* numbers in banana (*Musa* AAA subgroup Cavendish cvs ‘Valery’, ‘ Grande naine’ and ‘Williams’). Each bar is the mean ± standard error of 250 root samples. Each sample contains roots of 5 plants.

Musa parasitic nematodes is similar. This reaction agrees with pot experiments, carried out under our conditions with *R. similis* (Moens *et al*. 2003) and with the other nematodes (Araya *et al*. 2003). Also, other researchers found similar results, inoculating Cavendish subgroup cultivars with *R. similis* (Stoffelen *et al*. 2000, Viaene *et al*. 2000 and 2003), *M. incognita* (Pinochet *et al*. 1998, Van den Bergh *et al*. 2002a, b), *P. coffeae* (Viaene *et al*. 1998, Stoffelen *et al*. 1999a, 2000, Viaene *et al*. 2000, Van den Bergh *et al*. 2002a) and *H. multicintus* (Barekye *et al*. 2000).

Nematode frequencies and populations

In surveys in Costa Rica from 1994 to 1999, looking at root samples extracted from five plants on each occasion, *R. similis* was the most abundant nematode, ranging from 82 to 86%, while *Helicotylenchus* spp., *Meloidogyne* spp. and *Pratylenchus* spp. varied respectively from 8 to 10%; 5 to 9% and < 1% of the root population (Araya *et al*. 1995, 2002). The four nematode genera detected are well known pathogens in banana roots (McSorley and Parrado 1986, Sarah 1989, Gowen 1995, Sarah *et al*. 1996, Bridge *et al*. 1997, De Waele and Davide 1998, Marin *et al*. 1998).

Nematode frequency was very stable in the different years (Table 1). The highest frequency, above 95%, was always found for *R. similis*, followed by *Helicotylenchus* spp., ranging from 52 to 60%. The four nematode genera counted were detected in all counties and all months of the year. The favorable climatic conditions (Figure 2), without a dry season and only small variations in temperature, promote adequate plant growth throughout the year. This may explain the low variation observed in nematode population densities and frequencies.

Table 1. Absolute frequency by year (1994-1999) of the banana (*Musa* AAA) root parasitic nematodes in Costa Rica as a percentage of the total number of samples.

	Year						
	94	95	96	97	98	99	Total
No. of samples	11 688	10 618	11 253	10 929	12 707	14 525	71 720
	Percentage of samples with nematode species						Mean
R. similis	95	96	96	99	98	97	97
Helicotylenchus	56	56	52	54	56	60	56
Meloidogyne	68	59	51	57	48	47	56
Pratylenchus	15	13	11	13	13	14	13

The distribution of the root samples per nematode population density interval clearly indicated that *R. similis* accounted for the highest population (Figure 3). From the 71 720 recorded root samples, only 2324 (3%) were free of the nematode and 37 489 (52%) contained more than 10 000 individuals per 100 g of roots. These high populations and frequencies were probably encouraged by the long-term banana monoculture and the affinity between this nematode and the type of commercial banana planted (*Musa* AAA) (Orton and Siddiqi 1973). The high populations of *R. similis* agree with its high reproductive fitness *in vitro* on carrot discs (Fallas and Sarah 1995, Stoffelen *et*

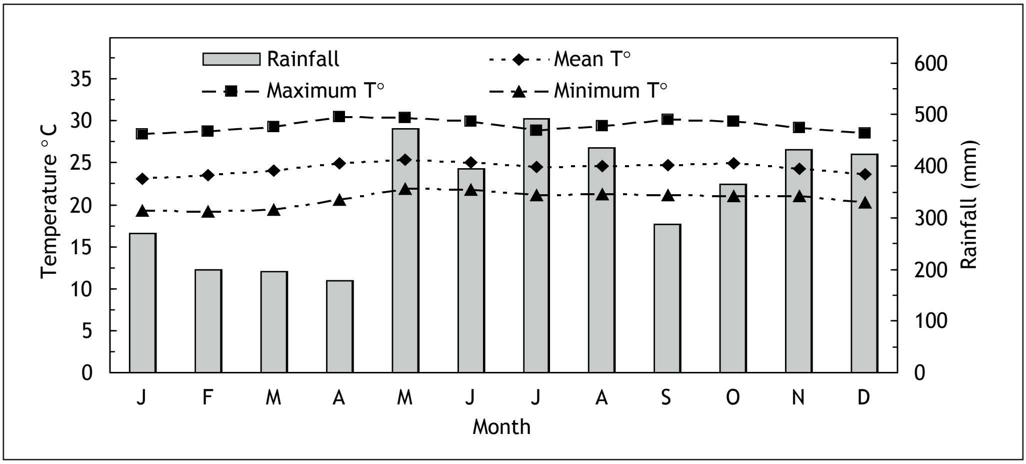

Figure 2. Average of 15 years (1989-2003) of the monthly mean, maximum and minimum temperature (°C) and rainfall (mm) in a Costa Rican export banana-growing area.

al. 1999b) and on banana plants under controlled conditions (Fallas *et al*. 1995, Binks and Gowen 1997, Stoffelen *et al*. 1999c).

The high *R. similis* populations and frequencies are consistent with other local studies (Jiménez 1972, López 1980, Figueroa 1989) and with observations from the Philippines (Boncato and Davide 1992), Colombia (Gómez 1980), and Ecuador (Gómez 1997). The behavior of *R. similis* as a main banana root nematode agrees with the results of Fargette and Quénéhervé (1988), Speijer and Fogain (1999), and Kashaija *et al*. (1999) in African countries, Stanton (1994) in Australia, Davide (1994) in the Philippines, Pone (1994) in the Pacific Islands, Jiménez *et al*. (1998) in Ecuador and Gómez (1980) in Colombia.

Helicotylenchus spp. was absent in 31,608 (44%) of the samples and in only 1,779 (2%) reached levels above 10 000 nematodes per 100 g of roots (Figure 3). *Helicotylenchus* spp. populations were lower than *R. similis*, in agreement with other results (Gómez 1980). More likely, this is because this nematode does not reproduce as fast as *R. similis* and the life cycles of the nematodes differ. *H. multicinctus* was found to have a life cycle of 42 days at 28°C on *Arabidopsis thaliana* and the adult females laid 4 eggs per day for a period of 10-12 days (Orion and Bar-Eyal 1995). In contrast, the *R. similis* life cycle was completed in 20-25 days at 24-32°C on banana roots and the adult females laid 4-5 eggs per day for 15 days (Loos 1962). This means that *R. similis* could be expected to have more generations and more individuals per generation in the same period of time.

More than 33,564 (46%) samples were free of *Meloidogyne* spp. and only 1113 (2%) showed densities higher than 10,000 nematodes per 100 g of roots (Figure 3). This low population density and frequency could be related to the feeding behavior of *R. similis*. Pinochet (1977) and Santor and Davide (1992) found that the presence of *R. similis* on the galls, induced by *M. incognita,* caused deterioration and disintegration of the giant cells, which, in turn, affected the development and reproduction of *M. incognita*.

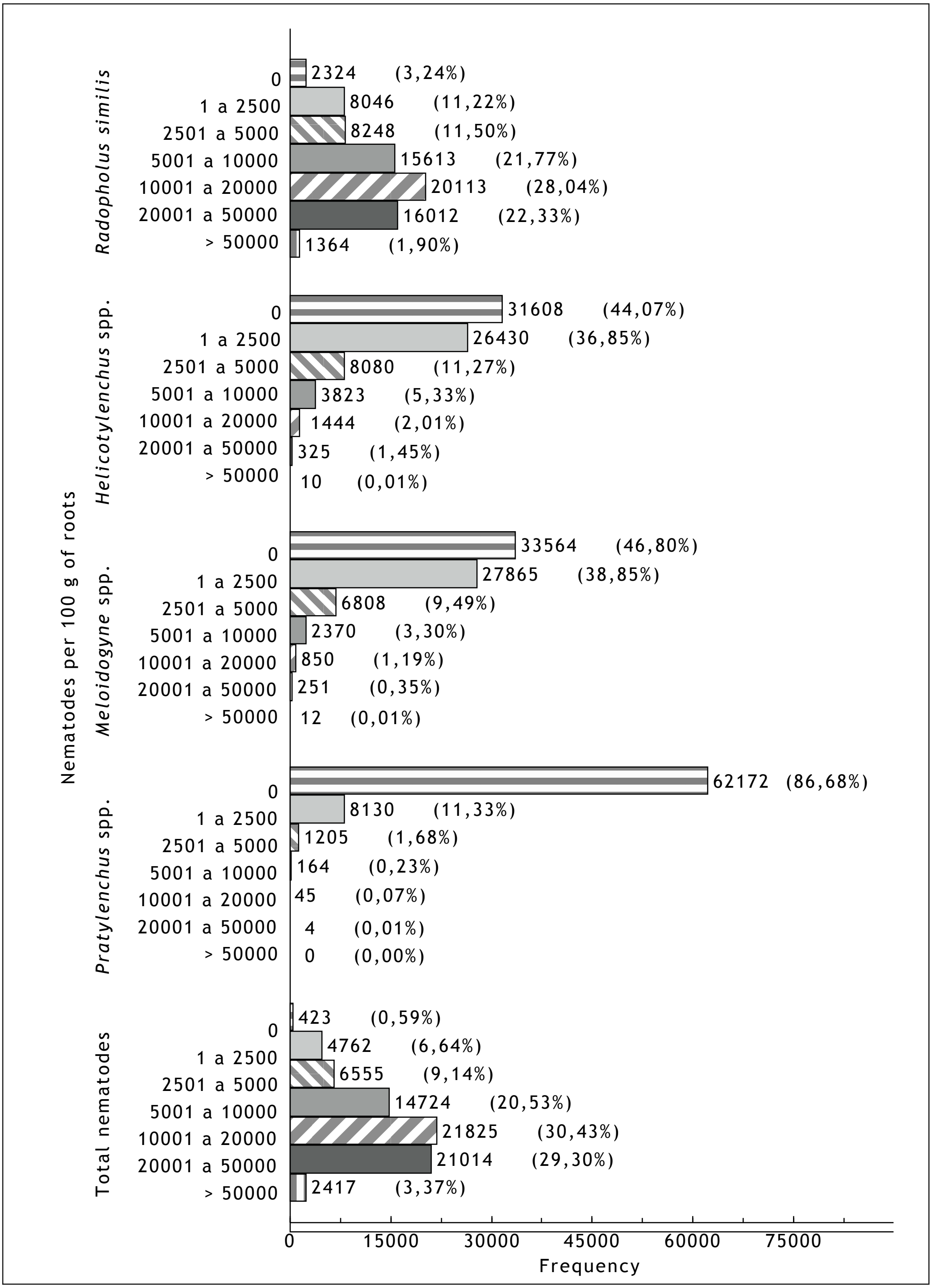

Figure 3. Frequency of nematodes according to the specific ratios per 100 g of fresh roots in 71 720 banana (*Musa* AAA) root samples recorded from 1994 to 1999. Total nematodes = *R. similis* + *Helicotylenchus* spp. + *Meloidogyne* spp. + *Pratylenchus* spp.

Pratylenchus spp. were only present in 9548 (13%) samples, with just 49 (0.08%) above 10,000 nematodes per 100 g of roots (Figure 3). This is reasonable, because *Pratylenchus* spp. has the same habitat as *R. similis* and a longer life cycle (Siddiqi 1972). This means that while they compete for the same feeding site, *R. similis,* with its higher reproduction rate, suppresses the growth of *Pratylenchus* spp.

When all nematodes were pooled (total nematodes), only 423 samples (1%) were nematode free and 45,256 (63%) samples contained more than 10,000 nematodes per 100 g of roots (Figure 3). Similar frequency, abundances and distributions were observed when sampling was done at flowering and harvest of individual plants on three experiments (Figures 4, 5 and 6). Only in the experiment carried out on the newest farm (Figure 6), which was planted about nine years ago, produced samples free (4%) of any parasitic nematode (Araya *et al*. 2003).

Nematode populations according to sucker height and phenological stage of the plant

The suitability of different phenological stages of the plant for parasitic nematodes was evaluated in five experiments by sampling roots of suckers of different heights and by sampling plants at flowering, harvest and 30, 60 and 90 days after harvest (Araya *et al*. 2003). On three farms, Anabel, Calinda, and Esmeralda, no difference in the *R. similis* population was found among suckers from 10 to 350 cm height or even with recently flowered or harvested plants (Figure 7). The lowest *R. similis* population found on any of the farms and at any sucker height or plant stage, was higher than 14,000 nematodes per 100 g of roots.

Helicotylenchus spp. populations were low with the exceptions of those found on the Anabel and Nueva Esperanza farms. On Anabel, the highest populations were observed in suckers of 340-350 cm height, while on Nueva Esperanza, populations increased up to the flowering stage (Figure 8). When individual plants were sampled five times progressively (at flowering, at harvest, and 30, 60 and 90 days after harvesting), the *R. similis* population decreased as plants aged on the three farms. The lowest population was consistently found to be at 90 days after harvest (Figure 9). Nevertheless, the nematodes that remain in the harvested plants act as a reservoir and can become a source of inoculum for the other members of the plant production unit.

Pathogenicity and symptoms of *Radopholus similis*

Moens *et al*. (2003) found a linear reduction of root weight when *R. similis* was inoculated at densities increasing from 0.14 to 2.24 nematodes per mL of substrate, corresponding to 254 to 2128 *R. similis* per pot, respectively. Root weight decreased by 3.9 g (16%) with each successive inoculation of 1000 nematodes (Figure 10A). Sarah *et al*. (1993) found that after exposing ‘Valery’ plants in 1.8 L pots to *R. similis* populations from different places around the world, root weights decreased from 19 to 80%, 8 weeks after inoculation with 300 individuals. Also, Marin *et al*. (1999), using ‘Grande naine’ plants in 1.4 L pots inoculated with 200 *R. similis* from different countries, observed root weight reductions of up to 21% after 8 weeks. Hahn *et al*. (1996) found decreases in root weight ranging from 8 to 26% in ‘Valery’ plants in 0.8 L pots 8 weeks after inoculation with 100 *R. similis*, and up to 30% 12 weeks after inoculation

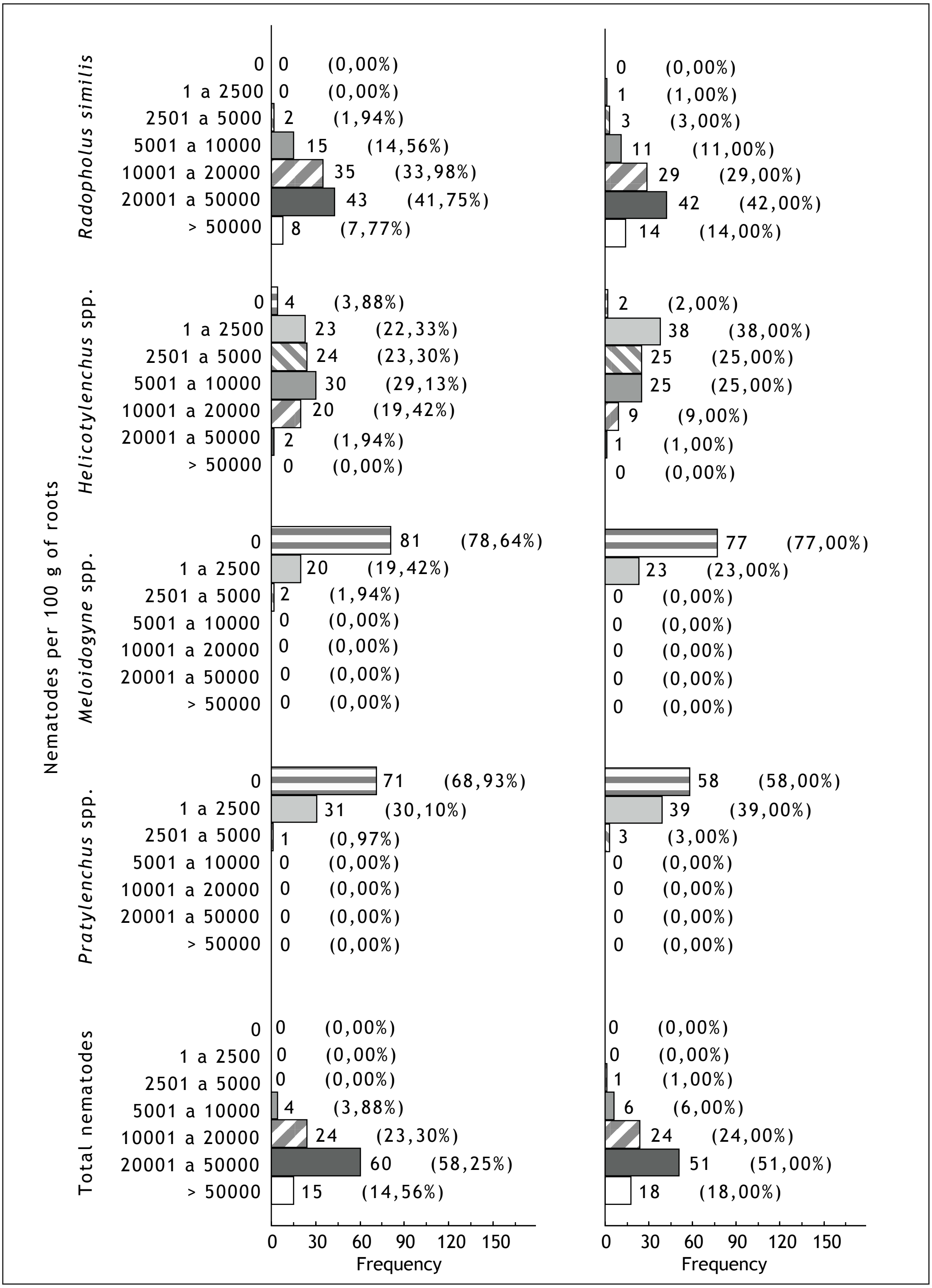

Figure 4. Frequency of nematodes according to the specific ratios in 103 individual banana (*Musa* AAA) root samples recorded on the Productora Tropical farm. Total nematodes = *R. similis* + *Helicotylenchus* spp. + *Meloidogyne* spp.+ *Pratylenchus* spp.

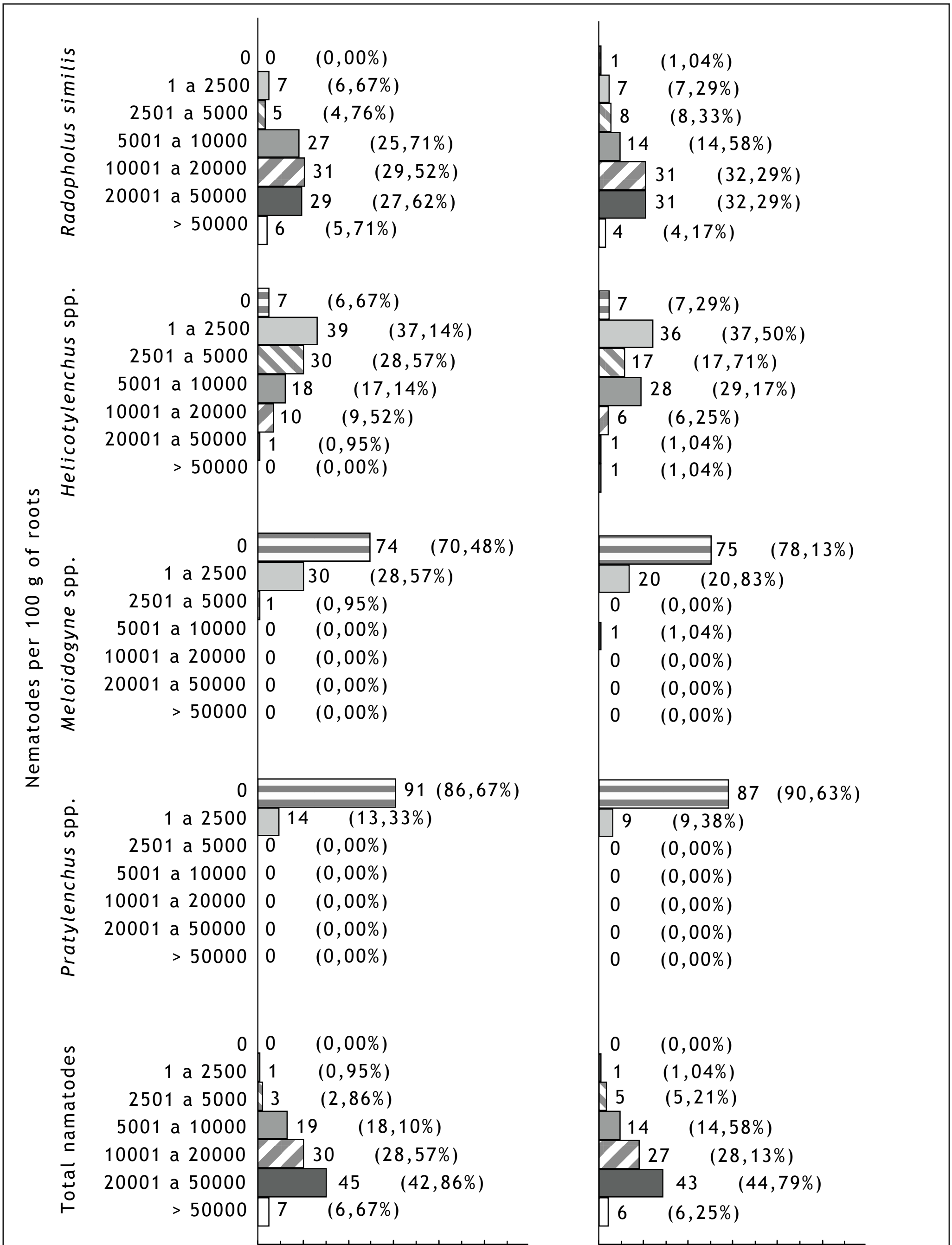

Figure 5. Frequency of nematodes according to the specific ratios in 105 individual banana (*Musa* AAA) root samples recorded on the San Pablo farm. Total nematodes = *R. similis* + *Helicotylenchus* spp. + *Meloidogyne* spp. + *Pratylenchus* spp.

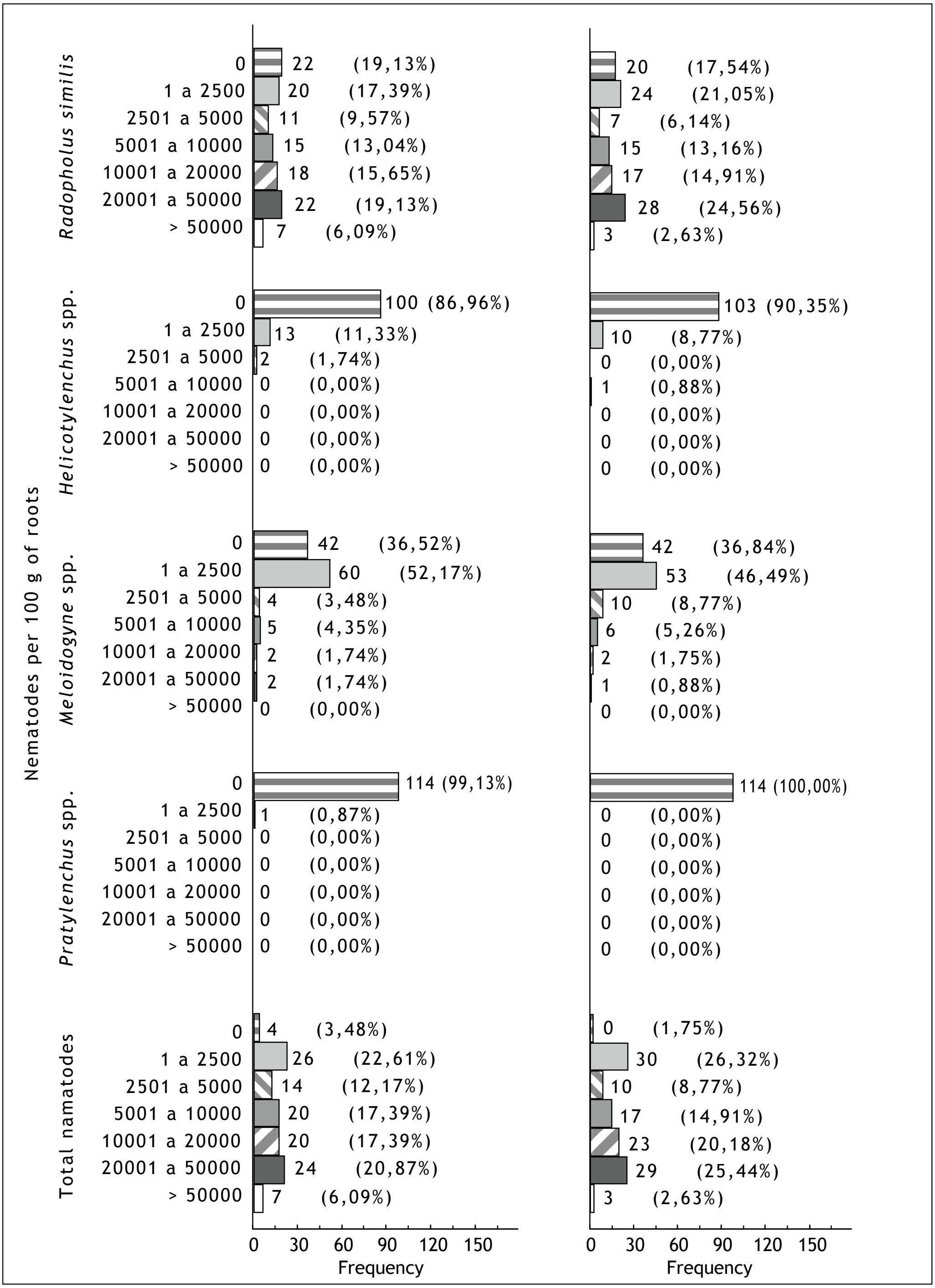

Figure 6. Frequency of nematodes according to the specific ratios in 115 individual banana (*Musa* AAA) root samples recorded on the La Rebusca farm. Total nematodes = *R. similis* + *Helicotylenchus* spp. + *Meloidogyne* spp. + *Pratylenchus* spp.

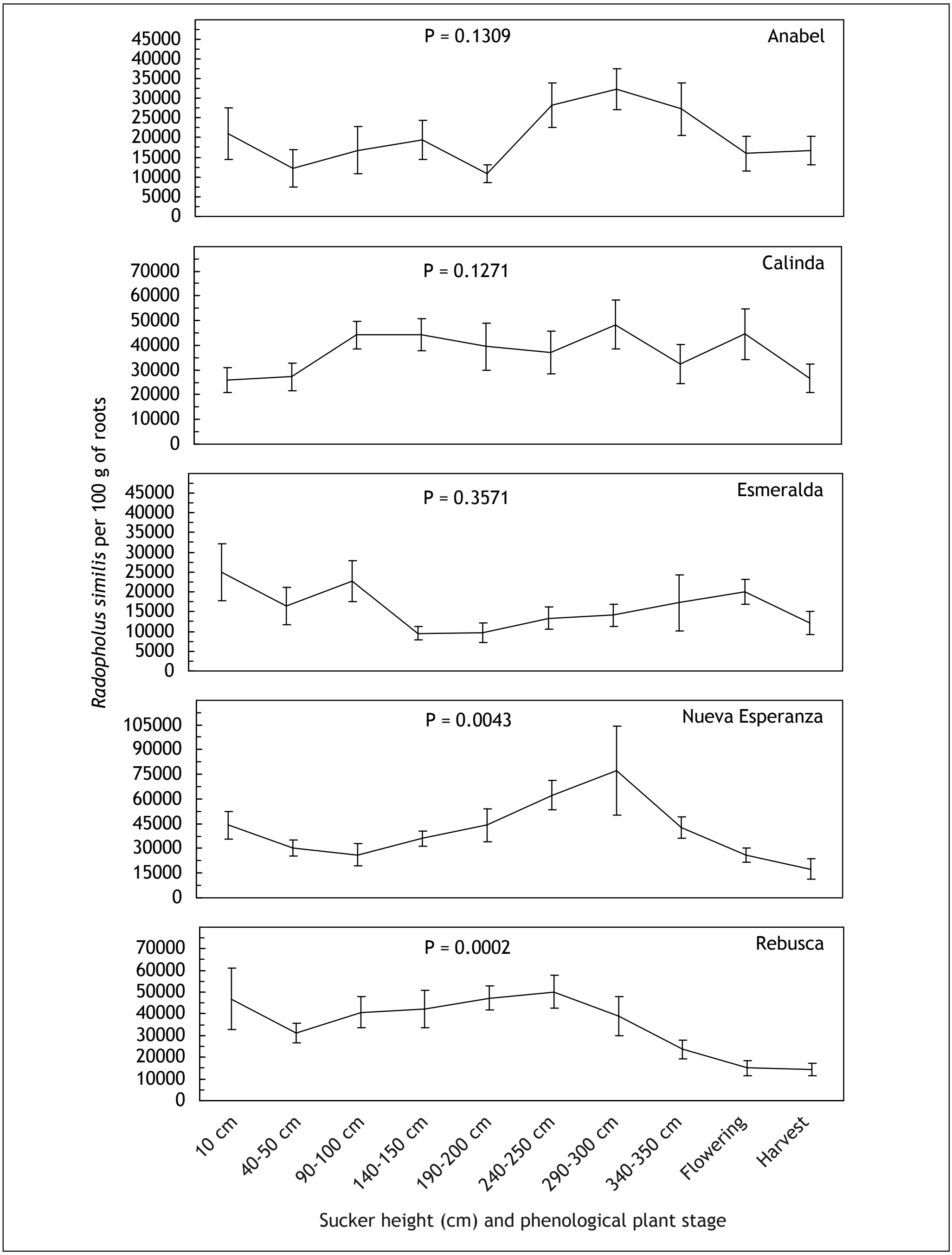

Figure 7. *Radopholus similis* according to sucker height (cm) or phenological banana (*Musa* AAA cv. 'Grande naine') plant stage.

Each point is the mean ± standard error of 15 samples. All the samples were taken in a maximum of 3 days. Each sample was composed of the roots of 5 plants. The p values correspond to the comparison among the means of the different sucker heights or plant stages. The names in the upper right corner are the farms where the experiment was done.

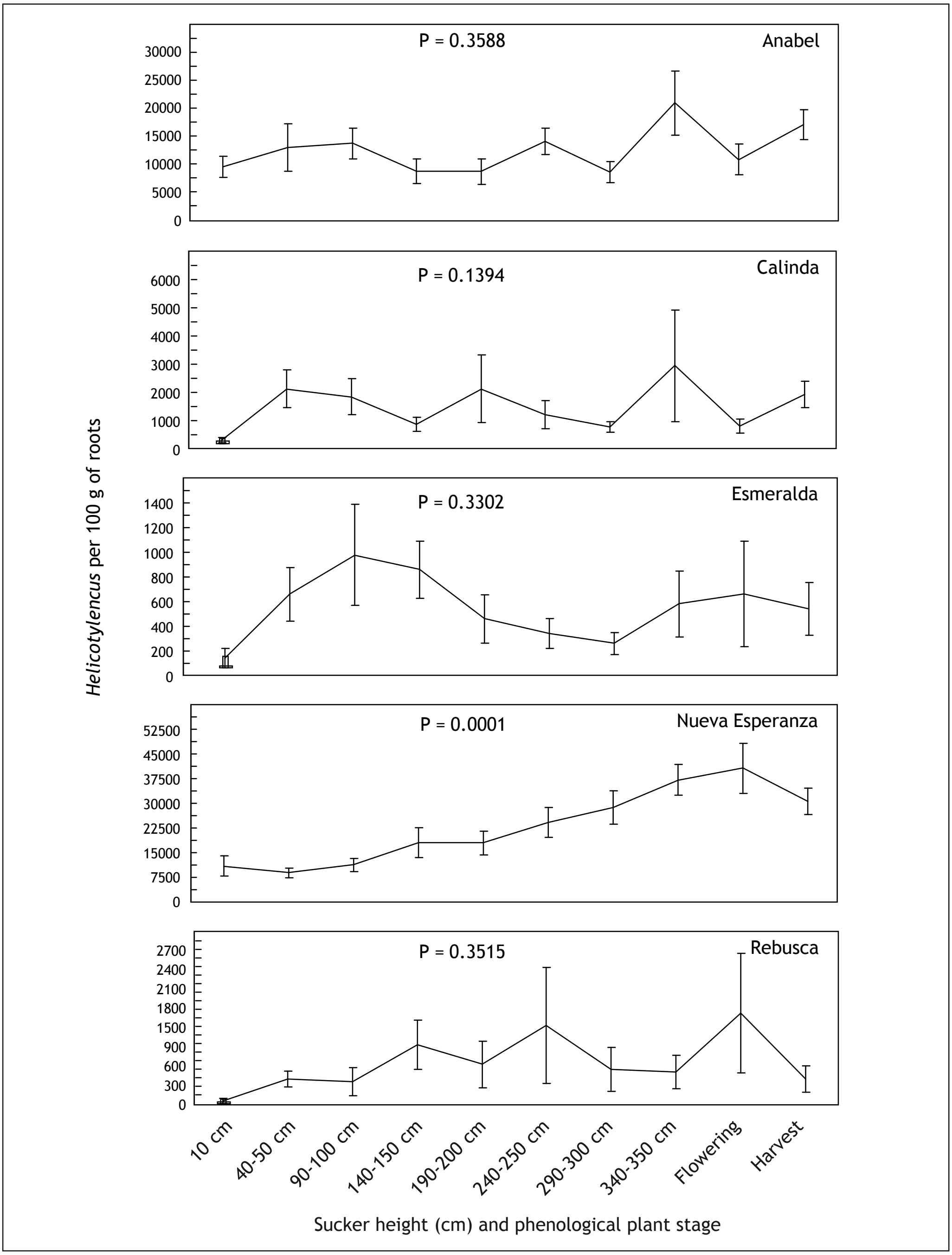

Figure 8. *Helicotylenchus* spp. according to sucker height (cm) or phenological banana (*Musa* AAA cv. 'Grande naine') plant stage.

Each point is the mean ± standard error of 15 samples. All the samples were taken in a maximum of 3 days. Each sample was composed of the roots of 5 plants.

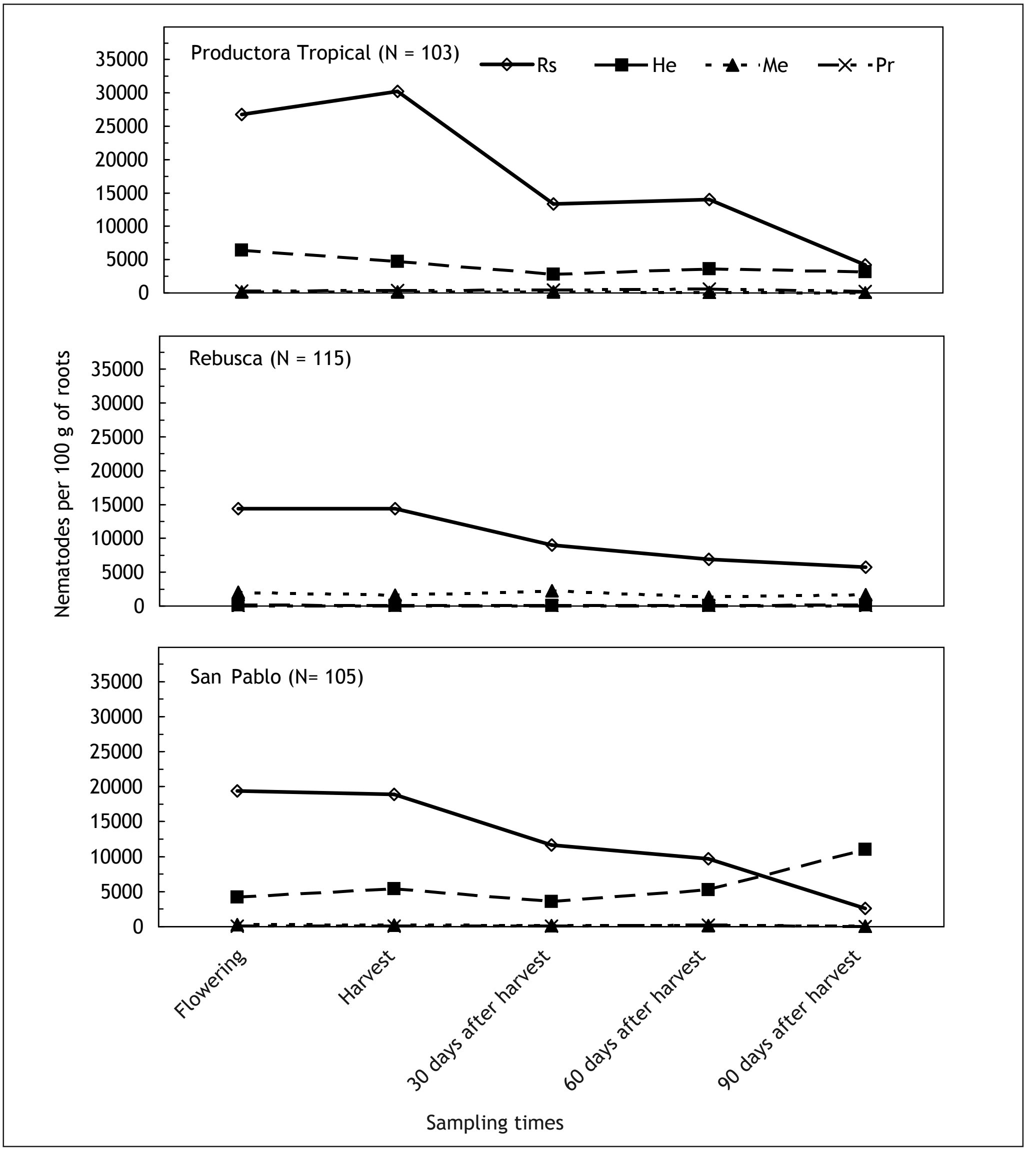

Figure 9. Nematode numbers in individual plants sampled 5 times progressively (at flowering, at harvest, and 30, 60 and 90 days after harvest). Rs = *Radopholus similis*, He= *Helicotylenchus* spp., Me = *Meloidogyne* spp. and Pr = *Pratylenchus* spp.

with 300 *R. similis*. Fallas *et al*. (1995), evaluating 'Valery' plants in 0.8 L pots inoculated with 100 *R. similis*, found decreases in root weight of 11 to 53% after 12 weeks. A reduction in the K concentration in the root dry matter was observed when 'Grande naine' plants were inoculated with different initial *R. similis* populations (Figure 10B). Other nutrients that varied significantly were N, S, Ca and Cu.

Fogain and Gowen (1995) found root necrosis of 3 to 12%, 6 weeks after inoculating ' Grande naine' plants in 1 L pots with 300 *R. similis*. Fogain *et al*. (1996) observed

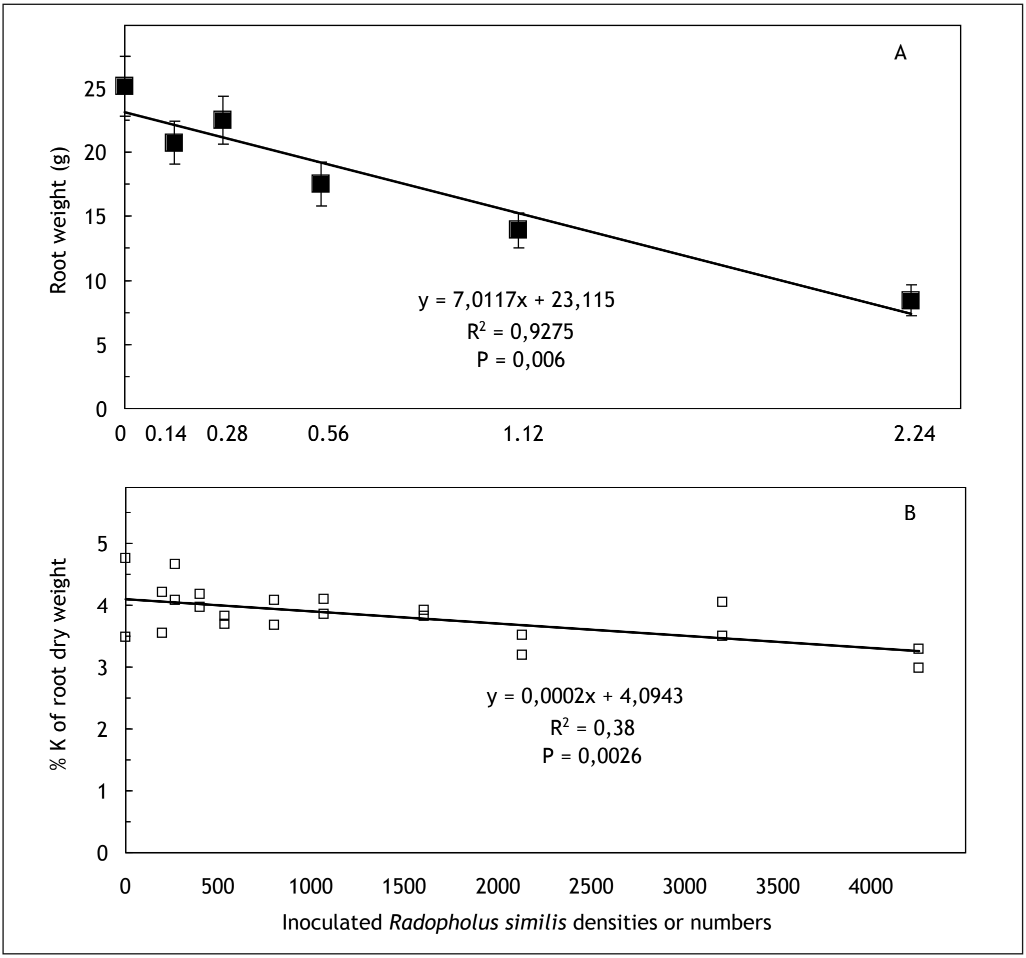

Figure 10. Effect of initial *Radopholus similis* inoculation densities per ml of substrate or numbers per 1.8 L pots on *Musa* AAA cv. Grande naine. A) root weight.
Each point is the mean ± standard error of 12 repetitions over 8 weeks of exposure. B) % K of the dry root weight. Each point is the mean ± standard error of 12 repetitions, with an exposure time of 12 weeks.

a high root lesion index in follower suckers of plantain cultivars in 10 L pots inoculated with 1000 *R. similis*. Moens *et al*. (2001) found a significant correlation between *R. similis* and root necrosis or damage, ranging from 0.62 to 0.75, in root samples from commercial banana plantations.

'Giant Cavendish' bananas inoculated with 1000, 2000, 3000 or 4000 *R. similis* suffered bunch weight reductions of 17, 42, 51, and 61% respectively (Davide and Marasigan, 1985). In a local study, ' Grande naine' plants, initially grown in 1.8 L pots, were inoculated with 1000 *R. similis* or *M. incognita* or *P. coffeae* or *H. multicinctus*. The *R. similis* and *P. coffeae* were cultured on carrot disks and *M. incognita* and *H. multicinctus* on potted banana plants. Three weeks later, plants were transferred to 200 L drums containing sterilized soil and allowed to develop until harvest, when root content, damage and bunch weight were recorded. Plants inoculated with *R. similis* had 3.6 kg (66%) less root weight, 6.4 kg (27%) less bunch weight and 262% more root damage than non-inoculated plants (Figure 11A-B).

The root and corm symptoms (Figure 12A-D) agree with those reported in the literature (Tarté and Pinochet 1981, Gowen and Quénéhervé 1990, Gowen 1995, Sarah 2000). Black and brown discoloration was observed in roots and corm after washing the surface free of soil. However, in early infections pre-symptomatic roots (Figure 12C) hold a lot of nematodes and when there is excess soil water, symptoms are easily confused with those caused by waterlogging. When the corm was lightly peeled, a purple, reddish-brown discoloration was easily seen, similar to that found in longitudinally split roots, where lesions extended from the epidermis towards the vascular cylinder.

Pathogenicity and symptoms of *Meloidogyne incognita*

In pot experiments with 22 Vietnamese banana genotypes, fresh root weight increased significantly in 2 of the 3 experiments in plants inoculated with 500 to 4000 *Meloidogyne*

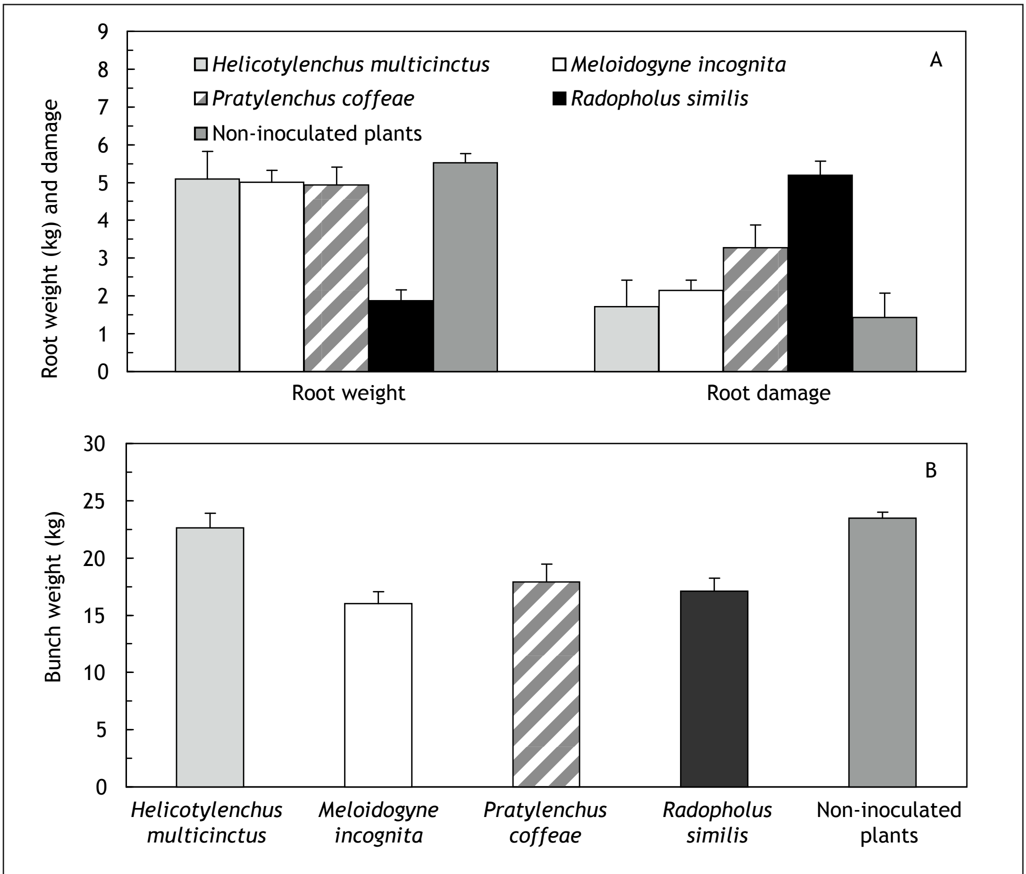

Figure 11. Root fresh weight, root damage and bunch weight at harvest of *Musa* AAA cv. 'Grande naine' plants inoculated with 1000 nematodes compared with plants without nematode inoculation.

Each bar is the mean ± standard error of 10 observations. The scale used for root damage was from 0 to 10.

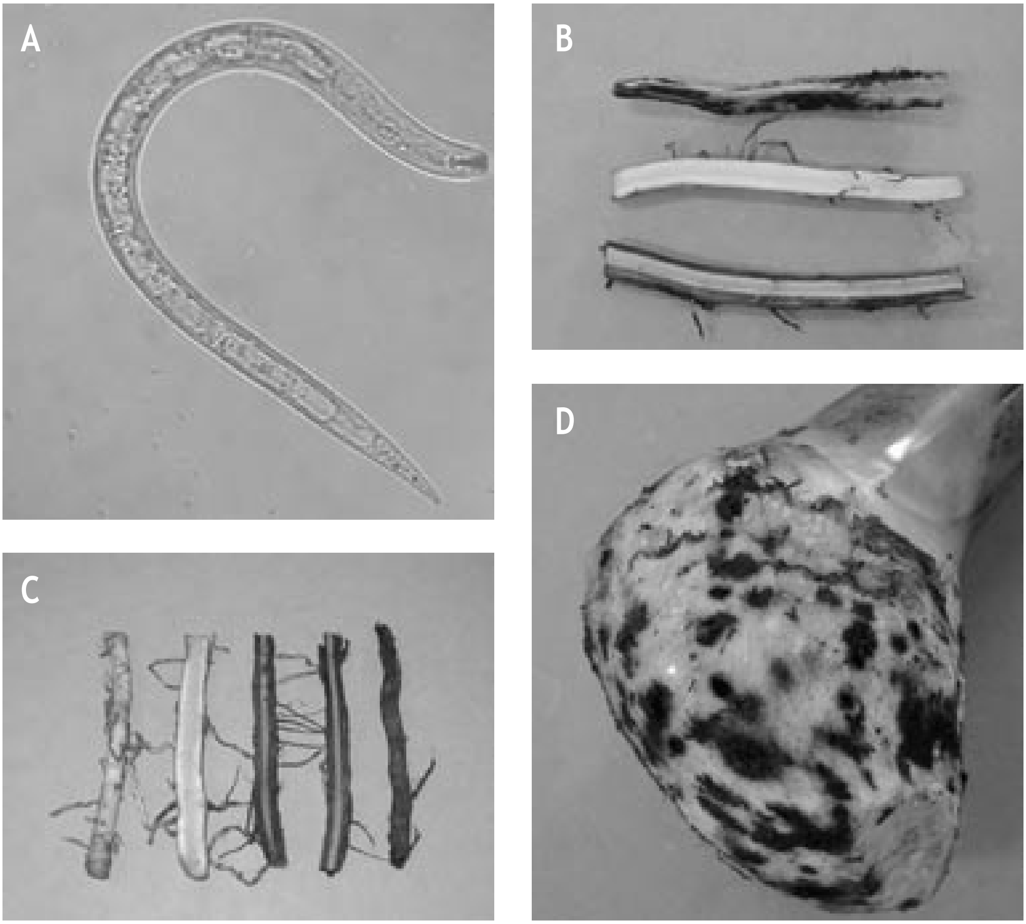

Figure 12. *Radopholus similis* and infection-induced symptoms in banana roots and corm. A) Adult female of *R. similis* at 20x magnification. B) In the center a healthy root (cream-white color) and on either side, roots with purple, reddish-brown discoloration extending from the epidermis to the vascular cylinder, C) On the right, two apparently healthy, asymptomatic roots containing 19 240 *R. similis* per 100 g of roots. On the right, three roots completely damaged first by *R. similis* (88 560 / 100 g of roots) and later by waterlogging, and D) Reddish-brown discoloration on the corm tissue.

spp. (Van den Bergh *et al*. 2002a). Also, in very young banana roots under *in vitro* conditions, *M. incognita* can penetrate the roots and cause damage (Coosemans *et al*. 1994). Jonathan and Rajendran (2000a) found a significant reduction in root weight for the higher initial inoculations in their study working with increasing inoculations from 0 to 10 000 individuals in pots of 105 kg soil capacity. In contrast, no negative effect on growth was observed in *Musa* AAB plants, inoculated with *M. incognita* and cultivated in 10 L pots in Ivory Coast (Adiko 1989).

In Malaysia, Razak (1994) reported stunted growth and small bunches due to the infection of *M. incognita* in 'Pisang nangka' and 'Pisang mas'. Similar effects on plant growth have been reported in India (Patel *et al*. 1996) where a delay in flowering was also observed. Van den Bergh *et al*. (2000) reported that *Meloidogyne* spp. had the most negative effect on the bunch characteristics of banana plants in Vietnam. High

Meloidogyne spp. populations, up to 66,000 per 100 g of roots, have been reported in ' Grande naine' vitroplants in field conditions in Cameroon (Fogain 1994).

'Giant Cavendish' bananas, inoculated with 1000, 10 000 or 20 000 *M. incognita,* suffered bunch weight reductions of 26, 45 and 57% respectively (Davide and Marasigan 1985). In our experiment, carried out in 200 L drums, *M. incognita* (Figure 13A-C) did not significantly reduce root weight, 0.5 kg (9%), and did not significantly increase root damage, but it did significantly suppress bunch weight by 7.5 kg (32%) (Figure 11A-B). This reduction in yield coincides with Jonathan and Rajendran's results (2000b), which found bunch weight increases of 31% when controlling this nematode with nematicide. The observed root symptoms (Figure 13D) are close to those reported by Sikora and Schlösser (1973), Pinochet (1977), Tarté and Pinochet (1981), De Waele and Davide (1998) and De Waele (2000). Deformation, bifurcation, swellings and stunting on primary and secondary roots are the most common symptoms where fine roots are rare. Sometimes gall formation is observed close to the root tip.

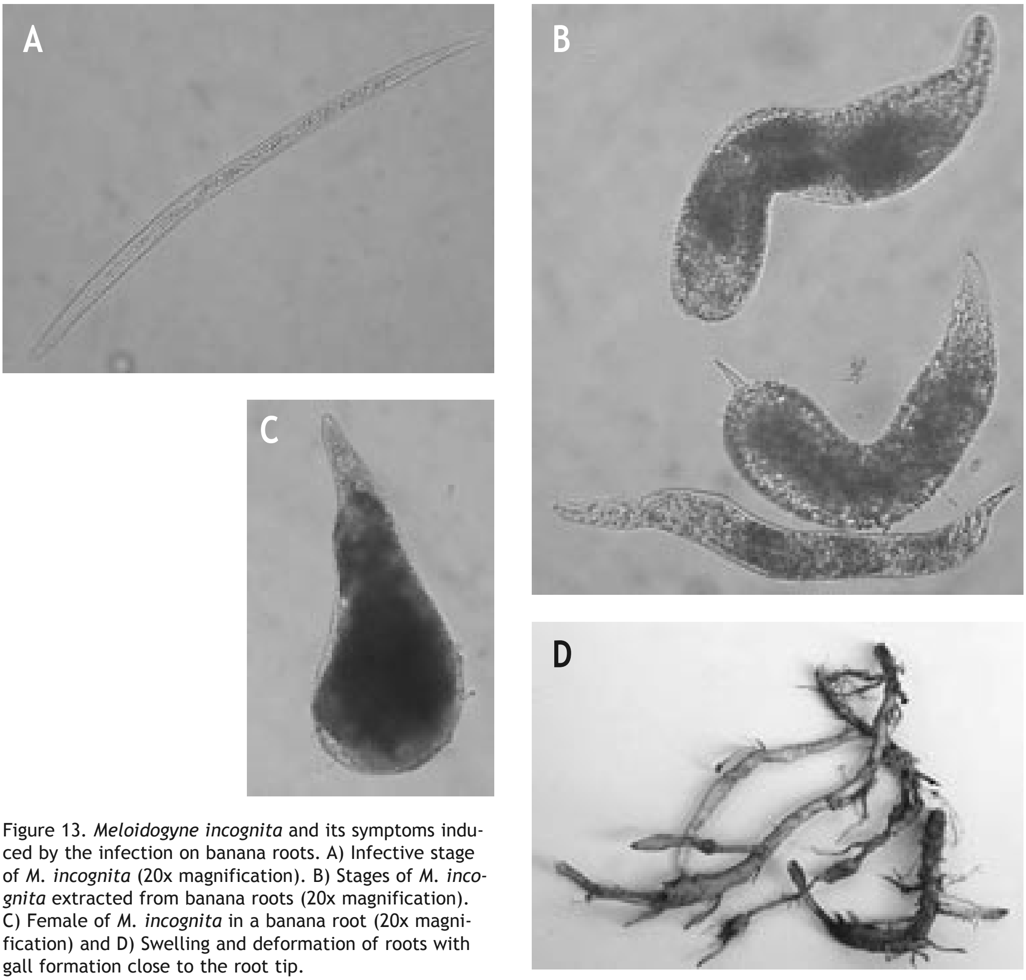

Figure 13. *Meloidogyne incognita* and its symptoms induced by the infection on banana roots. A) Infective stage of *M. incognita* (20x magnification). B) Stages of *M. incognita* extracted from banana roots (20x magnification). C) Female of *M. incognita* in a banana root (20x magnification) and D) Swelling and deformation of roots with gall formation close to the root tip.

Pathogenicity and symptoms of *Pratylenchus coffeae*

Van den Bergh *et al.* (2002a) observed a reduction in fresh root weight in 3 experiments with 24 Vietnamese genotypes of banana inoculated with 1,000 *P. coffeae*. Pinochet (1978), Tarté (1980), Rodríguez (1990), Bridge *et al*. (1997) also found that *Pratylenchus* spp. damaged banana roots and reduced yield. In our experiment, carried out in 200 L drums, *P. coffeae* (Figure 14A) did not significantly reduce root weight - 0.58 kg (11%), but it did significantly increase root damage by 129%, and significantly suppressed bunch weight by 5.6 kg (24%) (Figure 11A-B). Symptoms (Figure 14B) induced by *P. coffeae* infection were very similar to those caused by *R. similis* and coincided with those described by Pinochet (1978), Bridge *et al*. (1997) and Gowen (2000a). Purple or black necrosis of the epidermis and cortical root parenchyma with surface cracks occurred.

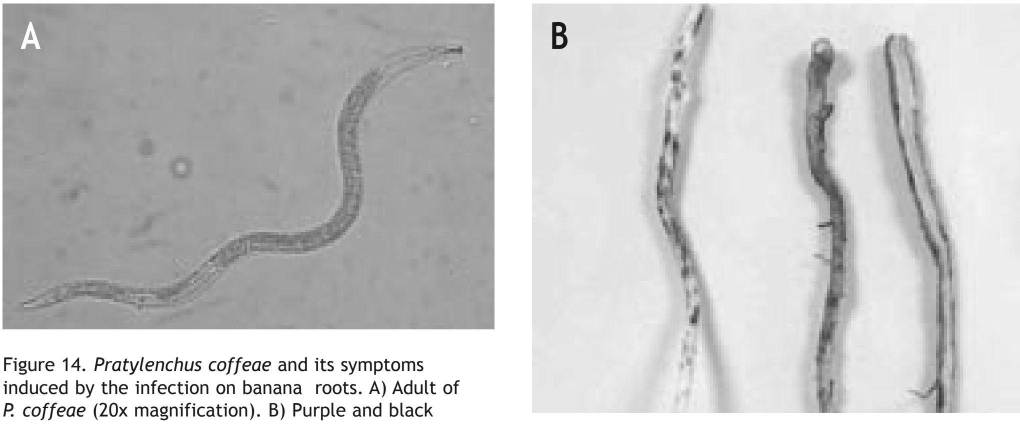

Figure 14. *Pratylenchus coffeae* and its symptoms induced by the infection on banana roots. A) Adult of *P. coffeae* (20x magnification). B) Purple and black necrosis extending from the root epidermis to the vascular cylinder.

Pathogenicity and symptoms of *Helicotylenchus multicinctus*

Helicotylenchus multicinctus and *H. dihystera* (McSorley and Parrado 1986, Davide 1996, Mani and Al Hinai 1996, Chau *et al*. 1997) damage the banana root system and reduce yield by 19% (Speijer and Fogain 1999) to 34% (Reddy 1994). There are mixed reports on the effect of *H. multicinctus* in potted plants. Barekye *et al*. (1999) found a root weight reduction in some *H. multinctus* inoculated plants compared with plants without nematodes. In Uganda, a non-significant reduction in root weight was observed in *Musa* AAA-East Africa cultivar 'Kisansa' plants inoculated with 1000 *H. multicintus* (Barekye *et al*. 2000). In greenhouse experiments, we observed fresh root weight reductions in *Musa* AAA 'Grande naine' plants inoculated with 515 *H. multicinctus*.

In Florida, *H. multicinctus* can cause severe root damage resulting in the toppling of mature plants (McSorley 1986, Gowen 1995). According to McSorley and Parrado (1986), this nematode is more important in subtropical banana production areas. In Lebanon, *H. multicinctus* is considered the most important banana root parasitic nematode (Sikora and Schlösser 1973). The same authors felt that this nematode, together with *M. incognita,* was associated with the general decay of the banana root system observed.

In our experiment carried out in 200 L drums, *H. multicinctus* (Figure 15A) did not significantly reduce either root weight, 0.42 kg (8%), or increase root damage, 19%, or suppress bunch weight, 0.9 kg (4%) (Figure 11A-B). However, in Israel, bunch weight increased by 18% when controlling this nematode with nematicide (Minz *et al*. 1960). The symptoms (Figure 15B) in the plants infected with *H. multicinctus* in drums coincide with those observed by McSorley (1986) and Gowen (2000b). Tertiary roots appeared necrotic and fell off when the roots were handled. Thicker and larger roots showed small black-brown surface lesions and larger necrotic areas.

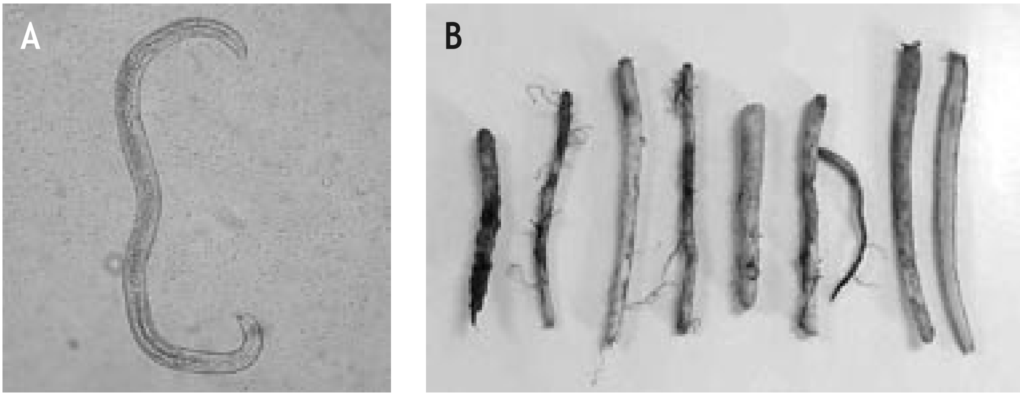

Figure 15. *Helicotylenchus multicinctus* and its symptoms induced by the infection on banana roots. A) Adult of *H. multicinctus* (20x magnification). B) Small black-brown root surface lesions and larger necrotic areas.

Practical implications of mixed nematode populations

The different parasitic habits of the nematode genera present - migratory endoparasites (*R. similis* and *Pratylenchus* spp.), sedentary endoparasites (*Meloidogyne* spp.) and ecto-endoparasites, feeding on subsurface tissue (*H. multicinctus*) - are likely to exacerbate root damage, because of lesions at feeding sites in the root cortex and throughout the root tissue. Usually control is recommended when *R. similis* population density exceeds a specific number per 100 g of roots, but the other nematodes also reduce the root system and yield. Therefore, development of nematode management tactics requires consideration of the damage caused by the total phytonematode population.

In current breeding programmes, resistance to black Sigatoka is, together with a high yield and good postharvest qualities, the most important factor in the screening process. Nevertheless, some programs could also incorporate resistance to *R. similis*. This is the case in different FHIA hybrids. Part of the 'Pisang jari buaya' group (*Musa* AA) demonstrated resistance (Wehunt *et al*. 1978, Viaene *et al*. 2000 and 2003), and this trait was, through the SH-3142 improved diploid (Pinochet and Rowe 1979), successfully incorporated into a series of FHIA hybrids. Other potential sources of resistance to *R. similis* are 'Kunnan' and 'Paka' (*Musa* AA section Eumusa) (Collingborn and Gowen 1997), and the Fe'i varieties 'Menei' and 'Rimina' (section Australimusa) (Stoffelen *et al*. 1999a). Even if this resistance was identified, isolated and incorporated into commercial cultivars, this would not resolve the problem, because of the existence of polyspecific nematode communities. Changes in the nematode composition will occur, favouring root parasitic nematodes to which these hybrids are not resistant. Also, differences in the aggressiveness of *R. similis* have been reported (Sarah *et al*. 1993, Fallas *et al* 1995, Marin *et al*. 1999) when comparing populations. Therefore, broad-spectrum resistance should be sought, conferring resistance to a wide range of known *R. similis* biotypes, and to the other important parasitic nematodes. Up to now, 'Yangambi km5' shows resistance to *R. similis* (Sarah *et al*. 1992, Price 1994) and *P. coffeae* (Viaene *et al*. 1998), but its progeny produce abnormal leaves and/or erect and semi-erect bunches (Stoffelen *et al*. 1999a). Another source of resistance to these two nematodes is *Musa acuminata* spp. *burmannicoides* 'Calcutta 4' (Viaene *et al.* 2000). This variety has already been used in the IITA breeding programme (Swennen and Vuylsteke 1993, Tenkouano *et al*. 2003), and experiments are on-going.

References

Adiko A. 1989 Effect of *Meloidogyne incognita* on plantain, *Musa* AAB. International Nematology Network Newsletter 6:27-30.

Araya M., M. Centeno & W. Carrillo. 1995 Densidades poblacionales y frecuencia de los nematodos parásitos del banano (*Musa* AAA) en nueve cantones de Costa Rica. Corbana 20:6-11.

Araya M., D. De Waele, & R. Vargas. 2002 Occurrence and population densities of nematode parasites of banana (*Musa* AAA) roots in Costa Rica. Nematropica 32:21-33.

Araya M., T. Moens & C. Calvo. 2003 Sección de nematología. Pp. 66-111 *in* Informe anual 2002. Corporación Bananera Nacional, Dirección de Investigaciones.

Barekye A., I.N. Kashaija, E. Adipala & W.K. Tushemereirwe. 1999. Pathogenicity of *Radopholus similis and Helicotylenchus multicinctus* on bananas in Uganda. Pp. 319-326 *in* Mobilizing IPM for sustainable banana production in Africa. (E.A. Frison, C.S. Gold, E.B. Karamura and R.A. Sikora, eds). IPGRI-INIBAP, Montpellier, France.

Barekye A., I.N. Kashaija, W.K. Tushemereirwe & E. Adipala. 2000. Comparison of damage levels caused by *Radopholus similis* and *Helicotylenchus multicinctus* on bananas in Uganda. Annals of Applied Biology 137: 273-278.

Binks R.H. & S.R. Gowen. 1997. Early screening of banana and plantain varieties for resistance to *Radopholus similis*. International Journal of Nematology 7:57-61.

Boncato A.A. & R.G. Davide. 1992. *Radopholus similis* on Giant Cavendish banana in Davao del Norte: host range, relative distribution, and density. Pp. 45-52 *in* Studies on nematodes affecting bananas in the Philippines (R.G. Davide, ed.). Philippine Agriculture and Resources Research Foundation, Inc., Los Baños, Philippines.

Bridge J., R. Fogain & P. Speijer 1997 The root lesion nematodes of banana. *Pratylenchus coffeae* (Zimmermann, 1898) Filip. & Schu. Stek., 1941. *Pratylenchus goodeyi* Sher & Allen, 1953. *Musa* Pest Fact Sheet No. 2. INIBAP, Montpellier, France.

Chau N.N., N.V. Thanh, D. De Waele & E. Geraert. 1997. Plant-parasitic nematodes associated with banana in Vietnam. International Journal of Nematology 7:122-126.

Collingborn F.M.B. & S.R. Gowen. 1997. Screening of banana cultivars for resistance to *Radopholus similis* and *Pratylenchus coffeae*. Info*Musa* 6(2):3.

Coosemans J., K. Duchateau & R. Swennen. 1994. Root-knot nematode (*Meloidogyne* spp.) infection on banana (*Musa* spp.) *in vitro*. Arch. Phytopath. Pflanz. 29:165-169.

Davide R. 1996. Overview of nematodes as a limiting factor in *Musa* production. Pp. 27-31 *in* New Frontiers in Resistance Breeding for Nematode, *Fusarium* and Sigatoka (E.A. Frison, J.P. Horry and D. De Waele, eds). INIBAP, Montpellier, France.

Davide R.G. 1994. Status of nematode and weevil borer problems affecting banana in the Philippines. Pp. 79-88 *in* Banana nematodes and weevil borers in Asia and the Pacific. (R.V. Valmayor, R.G. Davide, J.M. Stanton, N.L. Treverrow, and V.N. Roa, eds). INIBAP/ASPNET, Los Baños, La Laguna, Philippines.

Davide R.G. & L.Q. Marasigan. 1985. Yield loss assessment and evaluation of resistance of banana cultivars to the nematode *Radopholus similis* Thorne and *Meloidogyne incognita* Chitwood. Philippine Agriculturist 68: 335-349.

De Waele D. 2000. Root-knot nematodes. Pp. 307-314 *in* Diseases of banana, Abacá and Enset (D.R. Jones, ed.). CABI Publishing, Wallingford, UK.

De Waele D. & R.G. Davide. 1998. The root-knot nematodes of banana *Meloidogyne incognita* (Kofoid & White, 1919) Chitwood, 1949. *Meloidogyne javanica* (Treub, 1885) Chitwood, 1949. *Musa* Pest Factsheet No. 2. INIBAP, Montpellier, France.

Fallas G.A., J.L. Sarah & M. Fargette. 1995. Reproductive fitness and pathogenicity of eight *Radopholus similis* isolates on banana plants (*Musa* AAA cv. Poyo). Nematropica 25:135-141.

Fallas G.A. & J.L. Sarah. 1995. Effect of temperature on the *in vitro* multiplication of seven *Radopholus similis* isolates from different banana producing zones of the world. Fundamental and Applied Nematology 18:445-449.

Fargette M. & P. Quénéhervé. 1988. Populations of nematodes in soil under banana, cv. Poyo, in the Ivory Coast. 1. The nematofauna occurring in the banana producing areas. Revue Nématologie. 11:239-244.

Figueroa A. 1989. Dinamicas poblacionales de cuatro géneros de nematodos parásitos en plátano (*Musa* AAB, subgrupo plátano cv. Curraré). Asbana 13(32):5-7.

Fogain R., S. Gowen & F. Mekemda. 1996. Screening for susceptibility to *Radopholus similis*: evaluation of plantains AAB and diploid AA, AB, and BB. Tropical Agriculture (Trinidad) 73:281-285.

Fogain R. & S. Gowen. 1995. Pathogenicity on maize and banana among isolates of *Radopholus similis* from four producing countries of Africa and Asia. Fruits 50:5-9.

Fogain R. 1994. Root knot nematodes: a serious threat to banana productions in Cameroon? *MusA*frica 4(3): 3.

Gómez J.T. 1997. Dispersión y niveles de infestación de *Radopholus similis* Cobb en algunas plantaciones bananeras del Ecuador. Nematropica 27:111 (abstract).

Gómez J.T. 1980. Determinación de la infestación de fitonematodos en plantaciones bananeras de Urabá, Colombia. Fitopatología Colombiana 9(1):19-32.

Gowen S.R. 2000a. Root-lesion nematodes. Pp. 303-306 *in* Diseases of Banana, Abacá and Enset (D.R. Jones, ed.). CABI Publishing. Wallingford, UK.

Gowen S.R. 2000b. Spiral nematode. Pp. 306-307 *in* Diseases of Banana, Abacá and Enset (D.R. Jones, ed.). CABI Publishing. Wallingford, UK.

Gowen S. 1995. Pests. Pp. 382-402 *in* Bananas and Plantains (S. Gowen, ed.). Chapman & Hall, London, UK.

Gowen S. & P. Quénéhervé. 1990. Nematode parasites of bananas, plantains and abaca. Pp. 431-460 *in* Plant Parasitic Nematodes in Subtropical and Tropical Agriculture (M. Luc, R.A. Sikora and J. Bridge, eds). CAB International, Wallingford, UK.

Hahn M.L., J.L. Sarah, M. Boisseau, N.J. Vines, D.J. Wright & P.R. Burrows. 1996. Reproductive fitness and pathogenicity of selected *Radopholus similis* populations on two banana cultivars. Plant Pathology 45:223-231.

Jonathan E.I. & G. Rajendran. 2000a. Pathogenic effect of root-knot nematode *Meloidogyne incognita* on banana *Musa* sp. Indian Journal of Nematology 30:13-15.

Jonathan E.I. & G. Rajendran. 2000b. Assessment of avoidable yield loss in banana due to root-knot nematode *Meloidogyne incognita*. Indian Journal of Nematology 30:162-164.

Jiménez M.F. 1972. Fluctuaciones anuales de la población de *Radopholus similis* en la zona bananera de Pococí, Costa Rica. Nematropica 2:33-38.

Jiménez F., I. Ma, C. Triviño & L. Velasco. 1998. Influencia de la temperatura y la precipitación en la fluctuación poblacional de *Radopholus similis* en las zonas Oriental y Central del Ecuador. Pp. 547-555 *in* Memorias XIII Reunión ACORBAT 1998. (L. Hidalgo Arizaga, ed.). CONABAN, Guayaquil, Ecuador.

Kashaija I.N., R. Fogain & P.R. Speijer. 1999. Habitat management for control of banana nematodes. Pp. 109-118 *in* Mobilizing IPM for Sustainable Banana Production in Africa. (E.A. Frison, C.S. Gold, E.B. Karamura & R.A. Sikora, eds). INIBAP, Montpellier, France.

Loos C.A. 1962. Studies on the life-history and habits of the burrowing nematode, *Radopholus similis*, the cause of black-head disease of banana. Proceedings of the Helminthological Society 29:43-52.

López Ch.R. 1980. Determinación de los nematodos fitoparásitos asociados al plátano (*Musa acuminata* x *Musa balbisiana*, AAB) en Río Frío. Agronom. Costarr. 4:143-147.

Mani A. & M.S. Al Hinai. 1996. Population dynamics and control of plant parasitic nematodes on banana in the Sultanate of Oman. Nematologia Mediterranae 24:295-299.

Marin D.H., K.R. Barker, D.T. Kaplan, T.B. Sutton & C.H. Opperman. 1999. Aggressiveness and damage potential of Central American and Caribbean populations of *Radopholus* spp. in banana. Journal of Nematology 31: 377-385.

Marin D.H., T.B. Sutton & K.R. Barker. 1998. Dissemination of bananas in Latin America and the Caribbean and its relationship to the occurrence of *Radopholus similis*. Plant Disease 82:964-974.

McSorley R. 1986. Nematode problems on bananas and plantains in Florida. Nematology Circular No 133. Florida Department Agriculture & Consumer Services, Division of Plant Industry.

McSorley R. & J. L. Parrado. 1986. *Helicotylenchus multicinctus* on bananas: an international problem. Nematropica 16:73-91.

Minz G., D. Ziv & D. Strich-Harari. 1960. Decline of banana plantations caused by spiral nematodes, in the Jordan Valley, and its control by DBCP. Ktavim 10:147-157.

Moens T., M. Araya, R. Swennen, D. De Waele & J. Sandoval. 2003. Growing medium, inoculum density, exposure time and pot volume: factors affecting the resistance screening for *Radopholus similis* in banana (*Musa* spp.). Nematropica 33:9-26.

Moens T., M. Araya & D. De Waele. 2001. Correlations between nematode numbers and damage to banana (*Musa* AAA) roots under commercial conditions. Nematropica 31:55-65.

Orion D. & M. Bar-Eyal. 1995. Observations on the life cycle and behavior of *Helicotylenchus multicinctus* in monoxenic culture of *Arabidopsis thaliana*. Nematropica 25: 67-70.

Orton W.K.J. & M.R. Siddiqi. 1973. *Radopholus similis*. C.I.H. Description of plant-parasitic nematodes. No. 27. Commonwealth Institute of Helminthology, UK. 4pp.

Patel B.A., R.V. Byas, D.J. Patel & R.S. Patel. 1996. Susceptibility of banana cultivars to root-knot nematodes (*Meloidogyne* spp.). Info*Musa* 5(2):26-27.

Pinochet J., M.C. Jaizme, C. Fernandez, M. Jaumot & D. De Waele. 1998. Screening bananas for root-knot (*Meloidogyne* spp.) and lesion nematode (*Pratylenchus goodeyi*) resistance for the Canary Islands. Fundamental and Applied Nematology 21:17-23.

Pinochet J. & P. Rowe. 1979. Progress in breeding for resistance to *Radopholus similis* on bananas. Nematropica 9:40-43.

Pinochet J. 1978. Histopathology of the root lesion nematode, *Pratylenchus coffeae* on plantains, *Musa* AAB. Nematologica 24: 337-340.

Pinochet J. 1977. Occurrence and spatial distribution of root-knot nematodes of bananas and plantains in Honduras. Plant Disease Reporter 61:518-520.

Pone S. 1994. Status of nematode and weevil borer problems affecting banana in some of the Pacific Islands. Pp. 90-105 *in* Banana Nematodes and Weevil Borers in Asia and the Pacific. (R.V. Valmayor, R.G. Davide, J.M. Stanton, N.L. Treverrow & V.N. Roa, eds). INIBAP/ASPNET, Los Baños, Philippines.

Price N.S. 1994. Field trial evaluation of nematode susceptibility within *Musa*. Fundamental and Applied Nematology 17:391-396.

Quénéhervé P., P. Cadet, T. Mateille & P. Topart. 1991. Population of nematodes in soils under banana cv. Poyo, in the Ivory Coast. 5. Screening of nematicides and horticultural results. Revue Nématologie 14:231-249.

Razak A.R. 1994. Plant parasitic nematodes, a potential threat to commercial cultivation of banana in Malaysia. Pp. 34-45 *in* Banana Nematodes and Weevil Borers in Asia and the Pacific. (R.V. Valmayor, R.G. Davide, J.M. Stanton, N.L. Treverrow and V.N. Roa, eds). INIBAP/ASPNET, Los Baños, Philippines.

Reddy P.P. 1994. Status of banana nematodes in India. Pp, 247-254 *in* Banana Nematodes and Weevil Borers in Asia and the Pacific. (R.V. Valmayor, R.G. Davide, J.M. Stanton, N.L. Treverrow and V.N. Roa, eds). INIBAP/ASPNET, Los Baños, Philippines.

Rodríguez R.R. 1990. Los nematodos de la platanera (*Musa acuminata* AAA, subgrupo Cavendish Enana) en Canarias (1963-1984). Las Palmas de Gran Canarias, Caja Insular de Ahorros de Canarias. 58pp.

Sánchez R.O. & M. Zuñiga. 2004. Costa Rica, estadísticas de exportación bananera 2003. Corporación Bananera Nacional S.A. (CORBANA). 60pp.

Santor W. & R.G. Davide. 1992. Interrelationship of *Radopholus similis* and *Meloidogyne incognita* in banana. Pp. 71-77 *in* Studies on Nematodes Affecting Bananas in the Philippines (R.G. Davide, ed.). Philippine Agriculture and Resources Research Foundation Inc. Los Baños, Philippines.

Sarah J.L. 2000. Burrowing nematode. Pp. 295-303 *in* Diseases of Banana, Abacá and Enset (D.R. Jones, ed.). CABI Publishing. Wallingford, UK.

Sarah J.L., J. Pinochet & J. Stanton. 1996. El nematodo barrenador del banano *Radopholus similis* Cobb. Plagas de *Musa* – Hoja divulgativa No. 1. INIBAP, Montpellier, France.

Sarah J.L., C. Sabatini & M. Boisseau. 1993. Differences in pathogenicity to banana (*Musa* sp. cv. Poyo) among isolates of *Radopholus similis* from different production areas of the world. Nematropica 23:73-79.

Sarah J.L., F. Blavignac, C. Sabatini & M. Boisseau. 1992. Une méthode de laboratoire pour le criblage variétal des bananiers vis-à-vis de la résistance aux nématodes. Fruits 47:559-564.

Sarah J. L. 1989. Banana nematodes and their control in Africa. Nematropica 19:199-216.

Siddiqi M.R. 1972. *Pratylenchus coffeae*. C.I.H. Description of Plant-Parasitic nematodes. Set 1, No. 6. Commonwealth Institute of Helminthology, UK. 3pp.

Sikora R.A. & E. Schlösser. 1973. Nematodes and fungi associated with root systems of bananas in a state of decline in Lebanon. Plant Disease Reporter 57:615-618.

Speijer P.R. & R. Fogain. 1999. *Musa* and Ensete nematode pest status in selected African countries. Pp. 99-108 *in* Mobilizing IPM for Sustainable Banana Production in Africa. (E.A. Frison, C.S. Gold, E.B. Karamura, & R.A. Sikora, eds). INIBAP, Montpellier, France.

Stanton J.M. 1994. Status of nematode and weevil borer problems affecting banana in Australia. Pp. 48-56 *in* Banana Nematodes and Weevil Borers in Asia and the Pacific. (R.V. Valmayor, R.G. Davide, J.M. Stanton, N.L. Treverrow & V.N. Roa, eds). INIBAP/ASPNET, Los Baños, Philippines.

Stoffelen R., R. Verlinden, J. Pinochet, R.L. Swennen & D. De Waele. 2000. Host plant response of *Fusarium* wilt resistant *Musa* genotypes to *Radopholus similes* and *Pratylenchus coffeae*. International Journal of Pest Management 46:289-293.

Stoffelen R., R. Verlinden, N.T. Xuyen, R. Swennen & D. De Waele. 1999a. Screening of Papua New Guinea bananas to root-lesion and root-knot nematodes. Info*Musa* 8(1):12-15.

Stoffelen R., M.I. Jiménez, C. Dierckxsens, V.T.T. Tam, R. Swennen & D. De Waele. 1999b. Effect of time and inoculum density on the reproductive fitness of *Pratylenchus coffeae* and *Radopholus similis* populations on carrot disks. Nematology 1:243-250.

Stoffelen R., V.T.T. Tam, R.L. Swennen & D. De Waele. 1999c. Host plant response of banana (*Musa* spp.) cultivars from Southeast Asia to nematodes. International Journal of Nematology 9:130-136.

Swennen R. & D. Vuylsteke. 1993. Breeding black Sigatoka resistant plantains with a wild banana. Tropical Agriculture (Trinidad) 70:74-77.

Tarté R. & J. Pinochet. 1981. Problemas nematológicos del banano, contribuciones recientes a su conocimiento y combate. UPEB, Panamá. 32pp.

Tarté R. 1980. La importancia del conocimiento de la biología y comportamiento de los nematodos parásitos del banano en el desarrollo de métodos eficientes de control. Augura 6:13-21.

Tenkouano A., D. Vuylsteke, J. Okoro, D. Makumbi, R. Swennen & R. Ortiz. 2003. Diploid banana hybrids TMBx5105-1 and TMB2x9128-3 with good combining ability, resistance to black sigatoka and nematodes. HortScience 38:468-472.

Van den Bergh I., D.T.M. Nguyet, N.T. Tuyet, H.H. Nhi & D. De Waele. 2002a. Screening of Vietnamese *Musa* germplasm for resistance to root knot and root lesion nematodes in the greenhouse. Australasian Plant Pathology 31:363-371.

Van den Bergh I., D.T.M. Nguyet, N.T. Tuyet, H.H. Nhi & D. De Waele. 2002b. Responses of Vietnamese *Musa* genotypes to *Meloidogyne* spp. under field conditions. Nematology 4:917-923.

Van den Bergh I., V.T. Tam & N.N. Chau. 2000. Assessment of the occurrence and damage potential of nematodes on bananas in North and Central Vietnam. Pp. 134-149 *in* Highlights of *Musa* research and Development in Vietnam. (H.H. Nhi, A. Molina, I. Van den Bergh & P.T. Sen, eds). VASI, Hanoi, Vietnam.

Viaene N., L.F. Durán, J.M. Rivera, J. Dueñas, P. Rowe & D. De Waele. 2003. Responses of banana and plantain cultivars, lines and hybrids to the burrowing nematode *Radopholus similis*. Nematology 5:85-98.

Viaene N., L.F. Durán, J. Dueñas, J.M. Rivera, D. De Waele & P. Rowe. 2000. Reacción de híbridos y genotipos naturales de *Musa* al ataque de los nematodos *Radopholus similis* y *Pratylenchus coffeae* en ambiente de casa de sombra. P;9 *in* XIV Reunión de ACORBAT, San Juán, Puerto Rico.

Viaene N., J. Dueñas, J.M. Rivera, P. Rowe & D. De Waele. 1998. Determinación experimental de la reacción a los nematodos *Radopholus similis* y *Pratylenchus coffeae* de germoplasma selecto de *Musa* en casa de sombra. Pp. 43-67 *in* Informe técnico 1997. Fundación Hondureña de Investigación Agrícola, Programa de Banano y Plátano, La Lima, Honduras.

Wehunt E.J., D.J. Hutchinson & D.I. Edwards. 1978. Reactions of banana cultivars to the burrowing nematode. Journal of Nematology 10:368-370.