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GENOTYPIC DIFFERENCES IN THE GROWTH OF BANANAS (*MUSA* SPP.) INFECTED WITH MIGRATORY ENDOPARASITIC NEMATODES. 1. ROOTS

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SUMMARY

The effects of nematodes on root morphology and the association of root characteristics with resistance to nematodes of seven banana varieties were investigated in two experiments. Banana plants were grown in controlled conditions within polytunnels and harvested on three occasions for the measurement of root morphology and biomass. Varieties differed in their resistance to nematodes, from resistant (Yg Km5, FHIA 17, FHIA 03) and partly resistant (FHIA 01, FHIA 25) to not resistant ((FHIA 23, Williams). Nematodes reduced the root dry weight of FHIA 01, FHIA 17 and FHIA 23 at some harvests. Primary root number was on average 9.5 % lower in nematode-infected plants than controls, with no differences among the varieties. Thus, there was no simple association between the resistance of these varieties and their tolerance to nematodes. Varieties differed in root morphology. Root dry weight was greatest for resistant varieties Yg Km5 and FHIA 03, and least for non-resistant varieties FHIA 23 and Williams. Thus, resistance to nematodes was associated with varieties with greater root mass and more and larger primary roots.

INTRODUCTION

Nematodes are a major constraint to banana crop production. Crop losses of more than 75 % due to nematodes have been reported in Côte d'Ivoire and South Africa (Sarah, 2000). In Central and South America, crop losses tend to be 5–30 % (Sarah, 2000). Nematodes cause severe damage to primary roots. The destruction of root and corm tissues reduces water and mineral uptake, which then restricts plant growth and development (Sarah *et al.*, 1996). Damage to the root system by nematodes also causes plants to topple over (Orton Williams and Siddiqi, 1973).

Root systems are responsible for the absorption of water and nutrients, anchorage, synthesis of some plant hormones and storage (Lahav and Turner, 1989; Stover and Simmonds, 1987). The root system of banana consists of adventitious primary axes (Summerville, 1939). Secondary and tertiary roots develop from each primary root. The initiation and development of lateral roots (i.e. secondary and tertiary) are important as they increase the absorptive area and the volume of substrate exploited for water and nutrients (Charlton, 1996). Genotypic differences in roots of *Musa* spp. have been found. Swennen *et al.* (1986) found that dessert bananas (*Musa* AAA) have larger root systems than plantains (*Musa* AAB). Draye *et al.* (1999) reported genotypic

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differences in lateral root initiation. Thus, each variety may possess a different capacity to form primary, secondary and tertiary roots.

A few studies have investigated the relationships between root growth and the response of plants to nematodes. Seinhorst and Kozlowska (1977) studied the effect of *Rotylenchus uniformis* on carrots (*Daucus carota*). They found that the reduction of plant growth rate caused by nematodes depended on the number of nematodes per gram of root, and that tolerance to nematodes increased with age. With bananas, Menendez and Shepherd (1975) found differences in the numbers of roots and total root weight between synthetic tetraploids and Cavendish varieties infected with nematodes. Gowen (1976) found that roots of one of four tetraploids contained fewer *Radopholus similis* and *Helicotylencus multicinctus* than the others. Gowen (1996) suggested that varieties with a large number of roots may exhibit a greater tolerance to nematodes and that selection for this character should be a worthwhile breeding objective. However, improvement of the *Musa* root system through breeding has still been neglected.

To date, most research on the banana root system has focused on the roots of triploid varieties (*Musa* AAA Cavendish). However, none of those studies examined the relationship between root morphology and development, and resistance or tolerance to nematodes. Resistance is described as the effect of the host on nematode development and reproduction (Boerma and Hussey, 1992). It is a relative concept derived through genotype comparisons, and it frequently includes an indication of levels of resistance across a continuum of host-nematode interactions (Boerma and Hussey, 1992). Nematode tolerance in banana plants is defined as the ability to endure invasion without showing extreme disease symptoms such as uprooting or weak vegetative growth (Gowen, 1993).

Until now, only the variety Yangambi Km5 (*Musa* AAA) has been described as a source of resistance to both species of migratory endoparasitic nematodes, *R. similis* and *Pratylenchus goodeyi* (Fogain and Gowen, 1998). In a screening experiment, Kalorizou (2003) found differences among banana varieties in their potential to support reproduction of migratory nematodes. FHIA 17 and FHIA 03 seemed to be resistant since the number of nematodes they had could not be statistically distinguished from that of the known resistant variety Yangambi Km5. FHIA 01 and FHIA 25 both had an intermediate number of nematodes compared to Yangambi Km5 and a susceptible variety Williams, while FHIA 23 had the same response as Williams. The objectives of this study were therefore to examine how nematodes affect the roots of different banana varieties and to determine whether or not differences in root morphology among these varieties are associated with resistance to nematodes.

MATERIAL AND METHODS

Planting material

Triploid and tetraploid *Musa* varieties from different genomic groups and with different resistance to *R. similis* were selected (Table 1). Plants were propagated *in vitro* following the shoot/tip meristem culture technique (Vuylsteke, 1989). Rooted plants were transferred from aseptic culture conditions to a glasshouse for acclimatization

Table 1. Details of the *Musa* varieties evaluated.

Accession name	Experiment	Genome	Synonyms	Resistance to burrowing nematodes	Reference
Williams	2	AAA	Cavendish	Not resistant	Pinochet *et al.* (1998)
FHIA 23	1 and 2	AAAA	SH3444	Not resistant	Kalorizou (2003)
FHIA 01	1 and 2	AAAB	SH3481	Partially resistant	Pinochet *et al.* (1998); Kalorizou (2003)
FHIA 25	2	AAB	SH3775	Partially resistant	Kalorizou (2003)
FHIA 03	1	AABB	SH3565	Resistant	Kalorizou (2003)
FHIA 17	1 and 2	AAAA	SH3349	Resistant	Kalorizou (2003)
Yangambi Km5	1 and 2	AAA	Ibota	Resistant	Kalorizou (2003); Sarah *et al.* (1996); Fallas and Marbán-Mendoza (1994); Price (1994); Fogain and Gowen (1998)

(natural light and a mean air temperature of 27 °C). The nursery plants were planted into trays with vermiculite and were watered daily. After acclimatization (40 d), rooted plantlets were transplanted to 1-litre pots filled with vermiculite.

Plant husbandry

Experiment 1 was conducted between May and October 2001. It was a factorial block design with two nematode levels (with and without), three harvest times (202, 236, 270 days after planting, DAP) and five varieties (Table 1). There were four replicates per treatment combination. Twelve plants of each variety growing in 1-litre pots were inoculated with 4500 nematodes: a mixture of *R. similis* (5 %), *P. goodeyi* and *P. coffeae* (78 %) and *Helicotylenchus multicinctus* (17 %). *R. similis was* originally obtained from Uganda and cultured in the UK axenically on carrot discs. The other nematode species have been maintained in culture at the University of Reading, but their original source is not known. For each variety twelve (control) plants were not inoculated. For inoculation, a suspension of an axenic culture of *R. similis* (Ra 52), growing in carrot discs (Speijer and De Waele, 1997), and a mixture of *P. goodeyi*, *P. coffeae* and *H. multicinctus*, extracted from naturally infected banana roots and soil using a modification of Bearmann's technique and a maceration-sieving technique (Southey, 1986; Speijer and De Waele, 1997), were applied around the root system of each plant.

Fifteen days after inoculation the plants were transferred to a polytunnel at the University of Reading Plant Sciences Field Unit, UK. The plants were subsequently transplanted twice into 5-litre then 15-litre pots containing vermiculite, sand and gravel in the ratio 4:1:1. They were watered and fertilized by the incorporation of non-limiting amounts of Multicote 4 controlled-release fertilizer (Haifa Chemicals Ltd, Israel) into the mix at 119 DAP and a complete nutrient solution (N-14, P-10, K-27, MgO-2.5 and SO_3 11) daily from 202 DAP. The polytunnel was daylit with variable temperature. Air temperature was measured every two hours using miniature temperature data loggers (Tinytalk II, Gemini Ltd). The mean air temperature throughout Experiment 1 was 20.6 °C (average minimum and maximum air temperature 15.9 and 27.2 °C, respectively).

Experiment 2 was conducted between May and September 2002. It was a randomized block design of five replicate blocks each with a factorial combination of two nematode levels (with and without nematodes), six varieties (Table 1) and three harvest times (290, 320 and 350 DAP). One plant was harvested from each block at each harvest. The planting material was kept in a glasshouse for acclimatization and establishment. Fifteen plants per variety growing in 1-litre pots were inoculated with nematodes (1500 *P. goodeyi* and 250 *R. similis* (Ra 52) per plant) and the same number of plants per variety were used as a control. The plants were then transferred to a polytunnel at the Plant Environment Laboratory, University of Reading, UK. They were re-potted twice subsequently into 5-litre then 25-litre pots at monthly intervals to a mixture of vermiculite, gravel and sand in the ratio 4:2:1. The experiment was conducted under a constant temperature of 29/25 °C day/night with a 12-hour thermoperiod, average of 74 % relative humidity, natural sunlight and day length. At harvest 2 (320 DAP) the temperature was reduced to 25/20 °C. Plants were irrigated daily with a standard complete nutrient solution (Summerfield *et al.*, 1977).

Data collection

At each harvest in Experiment 1 and 2, plants were taken from the pots and all the potting media was removed. Root length, diameter, the number of the primary roots and root fresh weight were measured. Dry root weight was estimated using a sub-sample of about 10 % of the root fresh weight. Nematodes were extracted from a 100 g fresh weight root sample using the maceration-sieving technique and the number of *R. similis* + *Pratylenchus* spp., and *Helicotylenchus* spp. counted at all harvests except in Experiment 1, harvest 3.

Statistical analysis

Data were analysed using the SPSS statistical package (SPSS, 2001). Analysis of variance was used to assess treatment effects. The root dry weight data were transformed to $\log_{10}(x)$ before analysis to ensure homogeneity of residuals. Mean separation was made using the standard error of differences at the 5 % level when significant differences between treatments were found. In each experiment, the linear regression between resistance to nematodes (calculated as the number of nematodes for each variety as a proportion of the number of nematodes on the variety which had the least; Table 2) and the reduction in root dry weight due to nematodes (as a proportion of the dry weight of the control) was examined.

RESULTS

Number of nematodes

All varieties were successfully infected with nematodes in the nematode treatment. There was no effect of the interaction between variety and time on the number of *R. similis* and *Pratylenchus* spp. 100 g^{-1} of roots at harvest 1 and 2 in Experiment 1. The number of nematodes differed among varieties ($p = 0.01$), with the lowest number found on roots of FHIA01 and the greatest on YgKm5 (Figure 1). The numbers

Table 2. Average number of *R. similis*, *Pratylenchus goodeyi*, *P. coffeae* and *Helicotylenchus multicinctus* 100 g^{-1} root weight of each variety for the nematode treatment.

		Number of nematodes	
Experiment	Variety	*R. similis* and *Pratylenchus* spp.	*Helicotylenchus multicinctus*†
1	FHIA 01	77	43
	FHIA 03	154	115
	FHIA 17	311	127
	FHIA 23	136	53
	YgKm5	284	102
2	FHIA 01	890	
	FHIA 17	215	
	FHIA 23	519	
	FHIA 25	149	
	YgKm5	217	
	Williams	1231	

†Not tested in Experiment 2.

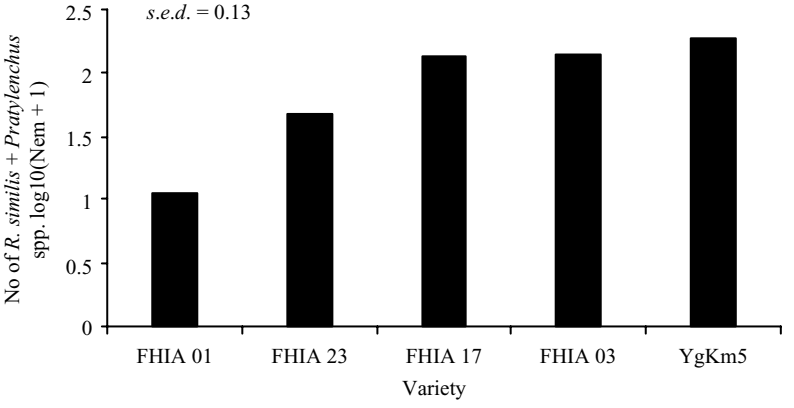

Figure 1. Number of *R. similis* and *Pratylenchus* spp. nematodes 100 g^{-1} of roots averaged across two harvest times in Experiment 1 (transformed to $\log_{10}$).

of *R. similis* and *Pratylenchus* spp. were the same at the two harvests. The number of *Helicotylenchus* spp. 100 g^{-1} of root was affected by the interaction between variety and time ($p = 0.001$). At harvest 1, FHIA 01 had the fewest nematodes, but other varieties did not differ from each other (Figure 2). Nematode numbers were similar between harvests for FHIA 01 and FHIA 23, but declined over time in the other varieties. FHIA 01 had the lowest number of nematodes.

In Experiment 2, there was no effect of the interaction between variety and time on the number of *R. similis* and *Pratylenchus* spp. 100 g^{-1} of roots at the three harvests. The number of nematodes differed among varieties ($p = 0.023$), with FHIA 17, FHIA 23, FHIA 25 and Ygkm5 having fewer nematodes than Williams (Figure 3). The

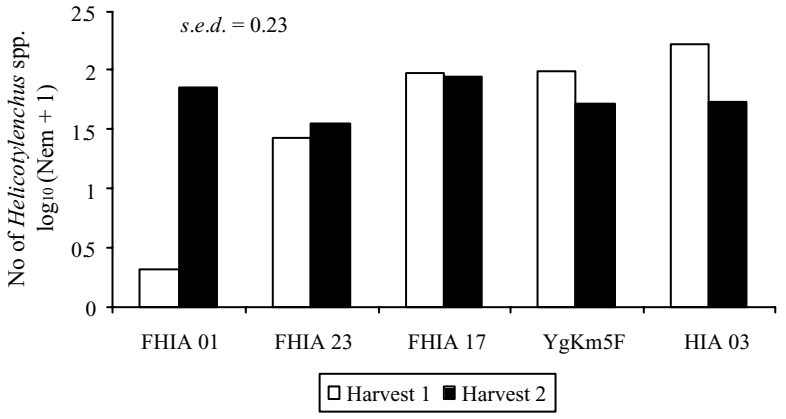

Figure 2. Number of *Helicotylenchus* spp. nematodes per 100 g^{-1} of roots of five banana varieties at two harvests in Experiment 1 (transformed to $\log_{10}$).

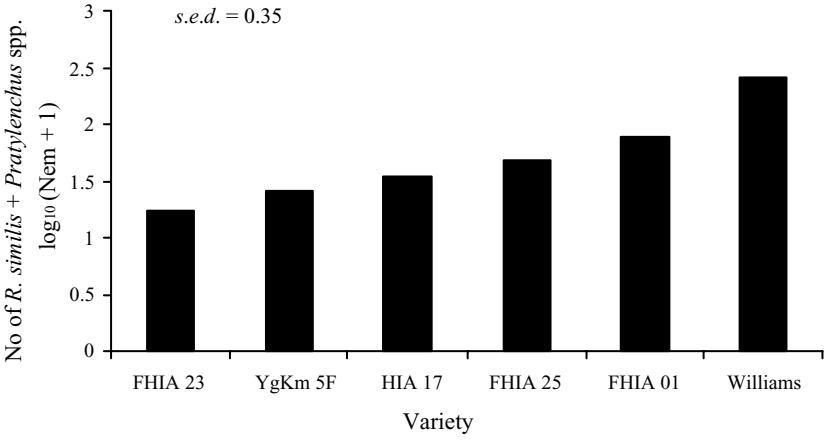

Figure 3. Number of *R. similis* and *Pratylenchus* spp. nematodes per 100 g^{-1} of roots of five banana varieties averaged across three harvests in Experiment 2 (transformed to $\log_{10}$).

average number of nematodes across all varieties was 108, 156 and 1347, at harvests 1,2 and 3 respectively ($p = 0.002$; $\log_{10}$ values of 2.03, 2.19, 3.13, *s.e.d.* = 0.17). The average number of nematodes per root sample across all harvests for each variety in Experiment 1 and 2 was calculated in order to examine the relationship with root weight, and these are presented in Table 2.

Root dry weight

In Experiment 1 the effect of the interaction between variety, nematode and time on root dry weight (RDW) was significant ($p < 0.001$), but inconsistent. Nematode-infected and control plants of FHIA 01, FHIA 17, FHIA 03 and YgKm5 had similar RDW at 202 and 270 DAP. At 236 DAP, nematode-infected plants of FHIA 01 and FHIA 17 had lower RDW than control plants, but the RDW of FHIA 23, FHIA 3

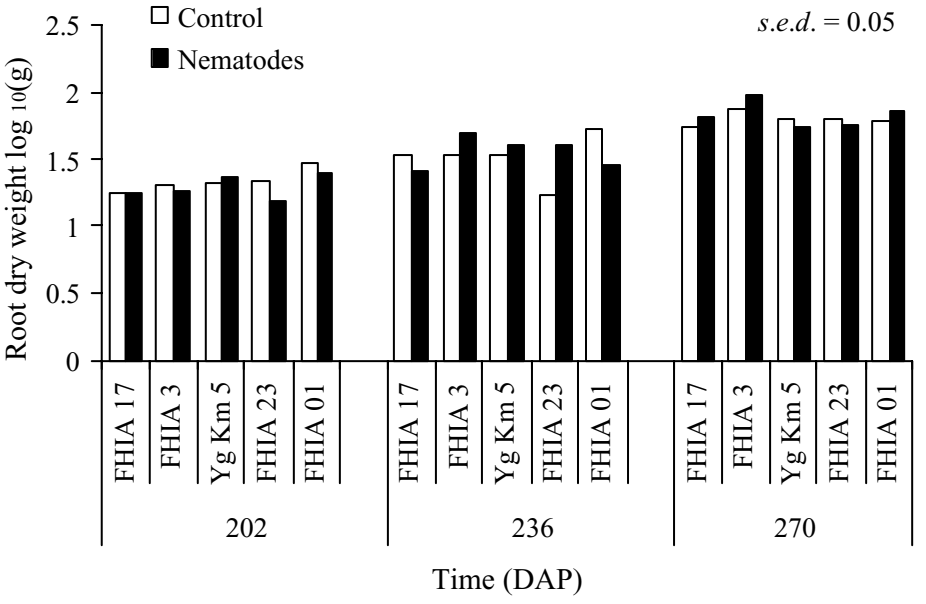

Figure 4. Effect of nematodes and banana variety on root dry weight in Experiment 1 at three harvests.

and Yg Km5 were highest in nematode-infected plants (Figure 4). Root dry weight was also affected by the interaction between variety and time ($p = 0.025$). FHIA 01 had greater RDW than the other FHIA varieties at 202 DAP (Table 3). FHIA 17 had the smallest weight throughout. Varieties FHIA 01, FHIA 03 and YgKm5 had the greatest RDW on average. There was no linear correlation between the relative number of nematodes per root system and the percentage reduction in RDW due to nematodes ($p = 0.407$).

In Experiment 2, no interactions affected the RDW. Varieties differed in RDW ($p < 0.001$). Williams and FHIA 23 had a lower RDW (179.6 g and 185.8 g respectively at 350 DAP) than the other FHIA varieties and YgKm5 (209.7 g). FHIA 17 (244.7 g) and FHIA 25 (306.8 g) had the greatest RDW. Nematodes had no effect on RDW ($p = 0.131$). There was no linear correlation between the relative number of nematodes per root system and the percentage reduction in the RDW caused by nematodes ($p = 0.477$).

Primary root number

The effect of the interaction between variety, nematode and time on the primary root number was not significant in either experiment. In Experiment 1, varieties differed and these differences were affected by the interaction between variety and time ($p = 0.03$). FHIA 17 had fewer roots at 202 DAP than FHIA 01, FHIA 03 and YgKm5 (Table 3). YgKm5 had more roots at 236 DAP than FHIA 01 and FHIA 03. All varieties had the same root number by 270 DAP. FHIA 01, FHIA 17 and FHIA 03 initiated primary roots throughout, but YgKm5 and FHIA 23 formed no more roots

Table 3. Effect of variety on primary root number, root length and root diameter per plant, and on the root dry weight at three harvests in Experiment 1. Values in brackets are $\log_{10}$ (root dry weight).

Time (DAP)	Variety	Primary root number	Primary root length (m)	Primary root diameter (mm)	Root dry weight (g)
202	FHIA 17	25.1	0.19	4.55	17.6 (1.24)
	FHIA 23	32.5	0.18	4.87	18.7 (1.26)
	FHIA 03	33.5	0.18	4.85	19.5 (1.28)
	FHIA 01	35.1	0.21	5.34	27.6 (1.43)
	YgKm5	38.6	0.26	4.86	22.5 (1.35)
236	FHIA 17	56.1	0.22	5.52	30.2 (1.46)
	FHIA 23	57.3	0.22	5.94	30.1 (1.42)
	FHIA 03	45.4	0.23	5.99	42.6 (1.61)
	FHIA 01	49.3	0.23	6.55	41.6 (1.59)
	YgKm5	68.0	0.26	5.89	38.3 (1.57)
270	FHIA 17	59.0	0.23	6.70	61.5 (1.78)
	FHIA 23	57.1	0.25	6.80	62.0 (1.78)
	FHIA 03	61.3	0.23	7.17	86.2 (1.92)
	FHIA 01	58.1	0.24	7.38	67.0 (1.82)
	YgKm5	66.8	0.32	5.68	61.2 (1.77)
d.f. (variety × time)		8	8	8	8
s.e.d. ($P = 0.05$) (variety × time)		3.27	0.01	0.07	(0.025)

after 236 DAP. Nematode infection reduced the number of primary roots by 9.5 %, from 52 to 47 primary roots for control and nematode-infected, respectively, averaged across all varieties ($p = 0.004$, *s.e.d.* 1.69).

The effect of the interaction between variety and time on primary root number was also significant in Experiment 2 ($p = 0.013$). FHIA 17 and FHIA 25 had more roots than FHIA 01 and FHIA 23 at 290 DAP (Table 4). FHIA 17 had more roots at 320 DAP than FHIA 01 and FHIA 23. At 350 DAP, YgKm5 and FHIA 17 had the most primary roots.

Primary root length

In Experiment 1, there was no effect of the interaction between variety, nematode and time on the primary root length ($p = 0.72$), but the interaction between variety and time affected root length ($p = 0.02$). YgKm5 had the longest roots at each harvest (Table 3). Root length FHIA 01 was greater than for FHIA 03 and FHIA 23 at 202 DAP, but by 236 DAP all the FHIA varieties had the same root length. Nematodes did not affect the primary root length ($p = 0.16$).

In Experiment 2, there was also no effect of the interaction between variety, nematode and time on the primary root length ($p = 0.39$). The length of the primary roots increased over time and was subject to interaction with variety ($p = 0.01$). YgKm5 had the longest roots, which were greater than the FHIA varieties at all times (Table 4). FHIA 17 had shorter roots than FHIA 25, Williams and YgKm5 at 290 and 320 DAP. Nematodes did not affect primary root length ($p = 0.08$).

Table 4. Effect of variety on primary root number, root length and root diameter per plant at three harvests in Experiment 2.

Time (DAP)	Variety	Primary root number	Primary root length (m)	Primary root diameter (mm)
290	FHIA 23	49.6	0.21	6.27
	FHIA 01	55.2	0.23	6.40
	Williams	58.6	0.24	5.62
	FHIA 25	63.7	0.25	6.22
	YgKm5	62.6	0.29	5.03
	FHIA 17	63.8	0.19	6.26
320	FHIA 23	83.0	0.31	7.36
	FHIA 01	86.5	0.33	7.43
	Williams	96.5	0.33	6.69
	FHIA 25	90.0	0.31	6.90
	YgKm5	91.1	0.41	6.15
	FHIA 17	100	0.29	7.77
350	FHIA 23	107	0.34	7.91
	FHIA 01	128	0.32	7.85
	Williams	130	0.41	6.25
	FHIA 25	129	0.35	6.95
	YgKm5	159	0.41	5.58
	FHIA 17	155	0.31	7.66
d.f. (variety × time)		10	10	10
s.e.d. ($p = 0.05$) (variety × time)		4.5	0.01	0.17

Primary root diameter

In both experiments, the interaction between variety, nematode and time did not affect the primary root diameter ($p = 0.447$ and $p = 0.947$ for Experiments 1 and 2, respectively). In Experiment 1, the effect of the interaction between variety and time was significant ($p = 0.003$). At 202 DAP, varieties had similar root thicknesses (Table 3). At 236 and 270 DAP, FHIA 01 had the thickest roots. YgKm5 had the thinnest roots and differed from FHIA 03 and FHIA 23 at 236 DAP, and from all the FHIA varieties at 270 DAP. The FHIA varieties had more roots with diameters in the range 6–9 mm than YgKm5.

In Experiment 2, the primary root diameter varied among varieties at each time and was affected by the interaction between variety and time ($p < 0.001$). Root diameter increased between 290 and 320 DAP, but was similar thereafter (Table 4). YgKm5 always had the thinnest roots. FHIA 01, FHIA 23 and FHIA 17 had similar root diameters, and these were greater than FHIA 25 and Williams at 290 and 350 DAP.

DISCUSSION

Nematodes affected the root dry weight of banana varieties in Experiment 1 when they reduced the root dry weight of FHIA 23 at the first harvest, and of FHIA 01 and FHIA 17 at the second of the three harvests. These results are consistent with Seinhorst and Kozlowska's (1977) observation that the effect of the nematodes on the growth of plants changes gradually, but stops suddenly. After that, plants increase their

weight at the same rate as equally large plants without nematodes. Nematodes also reduced the number of primary roots by 9.5 %.

Although root morphology depends to a certain extent on environmental factors (Lassoudiére, 1971), it is likely that the differences in root morphology observed here among banana varieties reflected differences in genotype. In the present study, YgKm5 and FHIA 17 had the most primary roots and YgKm5, Williams and FHIA 25 had longer roots than the other FHIA varieties. FHIA 01, FHIA 17 and FHIA 23 had thicker roots than YgKm5, Williams and FHIA 25. Varieties also differed in root dry weight. In Experiment 1, FHIA 01, FHIA 03 and YgKm5 had greater root dry weights than the other varieties. In Experiment 2, FHIA 25 and FHIA 17 had greater root dry weights than the other varieties. YgKm5 had a similar root dry weight to FHIA 17 and FHIA 01.

It is likely that root characteristics are related to plant resistance or tolerance to nematodes. Hahn *et al.* (1996) found a linear correlation between the final number of nematodes per gram of root and the decrease in root weight due to nematodes. They showed that a reduction in root dry weight could be used as an indicator of specific pathogenicity of the burrowing nematode populations. In the current study, varieties differed in the number of nematodes per root system and in nematode reproduction rate, but (with the exception of FHIA 23, FHIA 01 and FHIA 17 in Experiment 1) nematodes did not reduce root dry weight. Across varieties there was no linear correlation between relative nematode density and the proportional reduction in root weight. Thus, there was no simple relationship between resistance (indicated by the relative number of nematodes on the root system of a variety) and tolerance (indicated by root growth of that variety in the presence of nematodes). Some differences in root morphology among varieties were associated with the degree of resistance to nematodes (Table 1). The resistant varieties YgKm5 and FHIA 17 had more roots, and YgKm5 had longer roots, than the partially resistance and susceptible varieties. Root dry weight was greatest for resistant varieties Yg Km5 and FHIA 03, and least for susceptible varieties FHIA 23 and Williams. Thus, resistance to nematodes was associated with varieties with greater root mass, and more and larger primary roots.

Some tetraploid bananas (*Musa* AAAA) bred in Jamaica in the 1960s were found to have significantly fewer nematodes than the standard Cavendish *Musa* AAA varieties (Robusta and Valery) but were considered to be tolerant rather than resistant (Gowen, 1993). Tolerance was manifest in the greater root mass, root number, pseudostem girth and primary root diameter which was expressed in the field by less toppling. It may be argued that a greater root mass provides more resources for endoparasitic nematodes, but this may not be important considering that the life of individual roots is relatively short. Under ideal growing conditions, however, a banana 'shoot' will flower after 5–7 months and root growth ceases as dominance of the next flowering shoot (with a new root system) takes over.

According to Loomis and Connor (1992), the specification of a crop model or a plant ideotype (a conceptual model of an ideal phenotype) offers a way in which various traits concerning the development of new improved varieties can be evaluated. The root

morphology characteristics identified here in the resistant varieties could form a part of a plant ideotype for resistance to nematodes. The use of controlled environments to study root characteristics of banana is not ideal due to possible constraints on root growth imposed by the rooting volume of the 25-litre pots. This is countered in some part by the advantage for variety comparisons of controlling water and nutrition at optimal levels, and the uniformity of the potting media for the growth and extraction of roots in such a controlled environment system. Nevertheless, it would be useful to repeat the experimental design in a field-based investigation. Characteristics of the above ground parts of bananas which could contribute to a plant ideotype that is resistant or tolerant to nematodes are examined in an accompanying paper (Kalorizou *et al.*, 2007).

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