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## Host status of twelve commonly cultivated crops in the Cameroon Highlands for the nematode *Pratylenchus goodeyi*

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*Pratylenchus goodeyi* is a recognized pest of bananas and plantains in African highland regions. To evaluate the crop host status of *P. goodeyi* in the Cameroon Highlands, a field experiment was conducted in a field previously cropped with banana, using 12 crops planted in a randomized design with four replicates. The site was at Mbouroukou near Melong at 1200 m above sea level on volcanic soils. Banana was the susceptible reference crop. Sampling of roots and rhizosphere soil was undertaken at 4 months after planting. A non-parametric ANOVA revealed significant differences in *P. goodeyi* root population densities among the treatments (crops). Crops were classified as good hosts of *P. goodeyi* when their mean root densities were statistically similar to banana. When mean *P. goodeyi* root densities were significantly lower than banana but higher than 1000 100 g<sup>-1</sup> FRW, crops were classified as intermediate hosts. Crops with a mean *P. goodeyi* root density significantly lower than banana and lower than 1000 nematodes 100 g<sup>-1</sup> FRW were classified either as poor hosts (>20 *P. goodeyi* 100 g<sup>-1</sup> FRW) or very poor hosts (≤20 *P. goodeyi* 100 g<sup>-1</sup> FRW). Beans and maize (cv. CMS 8704) were good hosts of *P. goodeyi*; watermelon and onion were intermediate hosts; maize (cv. Kasafi), taro, okra, Irish potato and sweet potato were poor hosts, while cocoyam and tomato were very poor hosts.

**Keywords:** alternative hosts; banana lesion nematode; crop rotation; host range; tropical agriculture

### 1. Introduction

Bananas and plantains (*Musa* spp.) are important crops in Cameroon and in other Central African countries. As a staple, plantain is the most important food crop with the second highest consumer preference after yam (Dury et al. 2002). Bananas and plantains play a vital role for food security and rural household incomes, while bananas are also an important export cash crop. In 2005, over 855,000 tonnes of bananas and 1335,000 tonnes of plantain were produced in Cameroon (FAO 2007). In smallholder farms, both bananas and plantains are traditionally planted in mixed cropping systems.

Root nematodes are a serious constraint upon *Musa* production worldwide (Gowen et al. 2005). Following a nematode survey of plantains on smallholder farms in Cameroon, Bridge et al. (1995) identified 13 endoparasitic nematode species associated with plantain. Based on root damage the most important nematode species were *Helicotylenchus multicinctus* (Cobb, 1893) Golden, 1956, *Pratylenchus coffeae* (Zimmerman, 1898) Filipjev & Schuurmans Stekhoven, 1941, *Pratylenchus goodeyi* Sher & Allen, 1953 and *Radopholus similis* Cobb, 1913. The

dominant nematode species in the Cameroon Highlands on bananas and plantains is the root-lesion nematode *P. goodeyi* (Price and Bridge 1994; Fogain 2001; Jacobsen et al. 2004). This nematode species has been identified as a pest in commercial banana plantations in Australia (New South Wales), Crete and the Canary Islands (De Guiran and Vilardébo 1962; Pattison et al. 2002), but is more commonly known as a pest of bananas and plantains in small-scale farmers' fields in highland Africa (Speijer et al. 1993; Bridge et al. 1995; Bridge et al. 1997; Speijer and De Waele 2001; Talwana et al. 2003).

In Cameroon, various organophosphate and organocarbamate non-fumigant nematicides can be bought over the counter (Cohan et al. 2004). These products are cholinesterase inhibitors that interfere with hatching, root penetration and development of plant parasitic nematodes (Sipes and Schmitt 1998). Nematicides rarely completely eliminate nematodes and, due to their mode of action, they pose a major threat to the health of untrained users. A survey carried out in Cameroon by Matthews et al. (2003) showed that most pesticides were applied without the use of protective clothing. Acute financial constraints, cost,

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availability and environmental concerns result in the limited use of nematicides by small-scale farmers in the Cameroon Highlands, necessitating the adoption of alternative control methods such as crop rotation.

The effect of crop rotation on nematode communities depends on the specificity of the host status of crops within the rotation to the various plant parasitic nematode species. By changing crops from a good host crop to a poor or immune host crop, nematode population densities will decline. Weeds present in the field may act as a potential refuge, but in general effective management of nematode population densities may be achieved using poor or immune, completely resistant, host crops by reducing the nematode population densities below damage threshold levels.

The aim of this study was to determine the host status of commonly cultivated crops in the Cameroon Highlands and to identify which crops could be cultivated in rotation with banana and plantain by small-scale farmers to reduce *P. goodeyi*.

## 2. Materials and methods

### 2.1. Experimental site and set-up

The experiment was conducted at the Mbouroukou Research Station (5°06'N, 9°89'E, Littoral Province, Cameroon) at 1200 m above sea level. Average daily temperature is 20°C and average annual rainfall is 1900 mm, with the rainy season commencing in April and ending in October. Soils are volcanic dark-brown loams with a pH of 4.9 (Sama-Lang, unpublished). The site is situated on the slopes of Mount Manengouba in the forest-savannah transition area. Fallow and weed vegetation was dominated by *Aspilia africana* (Pers.) C.D. Adams, *Cyperus* spp., *Mariscus* spp., *Mimosa* spp. and *Pennisetum* spp.

A field previously cultivated to banana for several years was cleared, and 48 sub-plots (4.5 × 3.8 m) were prepared during July and August 2004. The infestation level of *P. goodeyi* on the existing banana plants was 8500 nematodes 100 g<sup>-1</sup> fresh root weight (FRW). Other nematode species present in the roots were *Meloidogyne* spp. Goeldi, 1892 (240 nematodes 100 g<sup>-1</sup> FRW), *Helicotylenchus* spp. Steiner, 1945 (17 nematodes 100 g<sup>-1</sup> FRW) and *Hoplolaimus* spp. von Daday, 1905 (5 nematodes 100 g<sup>-1</sup> FRW).

Each sub-plot was planted with one of 12 crops at their normally recommended spacing: (1) *Allium cepa* L. (onion, local variety); (2) *Citrullus lunatus* (Thunb.) Matsumura & Nakai (watermelon, cv. Sugar baby); (3) *Colocasia esculenta* (L.) Schott (taro, local variety); (4) *Abelmoschus esculentus* (L.) Moench. (okra, local variety); (5) *Ipomoea batatas* (L.) Lam (sweet potato, cv. TIB1); (6) *Lycopersicon esculentum* Mill. (tomato, cv. Roma); (7) *Musa* sp. (AAA group, cv. Grande Naine); (8) *Phaseolus vulgaris* L. (bean, local variety); (9) *Solanum tuberosum* L. (Irish potato, local variety);

(10) *Xanthosoma sagittifolium* (L.) Schott (cocoyam, local variety); (11) *Zea mays* L. (maize, cv. Kasai); (12) *Zea mays* L. (maize, cv. CMS 8704). The banana was included in the experiment as the susceptible reference crop. Nine tissue-culture propagated banana plants were planted per sub-plot (1.9 × 2.3 m).

The experiment was arranged in a completely randomized design with four replicates. Fertilizer (NPK: 12:14:19) was applied once at 3 months after planting according to local practices: 7 g NPK per stand of beans (300 kg ha<sup>-1</sup>), Irish potato (300 kg ha<sup>-1</sup>), maize (100 kg ha<sup>-1</sup>), okra (200 kg ha<sup>-1</sup>), onion (235 kg ha<sup>-1</sup>), sweet potato (145 kg ha<sup>-1</sup>), tomato (250 kg ha<sup>-1</sup>) and watermelon (100 kg ha<sup>-1</sup>); 15 g NPK per stand of banana (100 kg ha<sup>-1</sup>), cocoyam and taro (both 430 kg ha<sup>-1</sup>). Manual weeding was conducted as necessary.

### 2.2. Nematode population density assessment

Sampling of roots and rhizosphere soil was carried out at 4 months after planting when the population densities of *P. goodeyi* on banana averaged 9000 nematodes 100 g<sup>-1</sup> FRW. Roots and rhizosphere soil were collected from at least one-third of all plants per plot, which were randomly selected. One bulk sample was combined, for roots and rhizosphere soil respectively, per sub-plot.

Nematode extraction from the roots was done by maceration and sieving (Hooper 1990). In the laboratory, each root sample was washed, cut in 0.5-cm pieces and mixed by hand. A 50-g sub-sample (or all roots if less than 50 g were available) was taken from each sample and macerated in a kitchen blender with tap water. The sample was then poured through nested sieves of 200, 125, 50 and 32- $\mu$ m apertures, rinsed and nematodes collected from the 50 and 32- $\mu$ m sieves into a beaker and diluted to 100 ml with tap water.

Nematode extraction from the rhizosphere soil was conducted by gravitation and decanting (Hooper 1990). In the laboratory, soil samples of 250 ml were mixed in a 10-l capacity bucket half-filled with tap water, left to settle for 30 s and the suspension was poured over nested sieves of 50 and 32- $\mu$ m apertures. Nematodes were collected from the 50 and 32- $\mu$ m sieves into a beaker and diluted to 100 ml with tap water.

Following extraction, nematode suspensions were cleaned through centrifugal flotation (Hooper 1990), by adding 5 g of kaolin per 100 ml of suspension and centrifuging at 2500–3000 rpm. The supernatant was discarded and 15 ml of MgSO<sub>4</sub>-solution ( $\delta = 1.15$ ) added to the pellet. This mixture was further centrifuged for 5 min at 2500–3000 rpm. The supernatant was retained and the pellet discarded. The nematode suspension was rinsed through a 32- $\mu$ m aperture sieve, collected and diluted to 100 ml with tap water.

Nematode densities were assessed from three 1-ml aliquots and examined under a light microscope. Taxonomical verification was done in collaboration with the Nematology Unit, ARC-Plant Protection Research Institute, Queenswood, South Africa.

### 2.3. Statistical analysis

Levene's test was used to show heterogeneity of variances between groups (crops). Examination of the normal probability plots and the Kolmogorov–Smirnov test for normality revealed non-normality of the data.  $\text{Log}(x + 1)$  transformation of the density data failed to normalize them. When transformations are unsuccessful in bringing the distributions of the error terms close enough to normality to meet the assumptions ANOVA a nonparametric inference procedure can be useful (Kutner et al. 2005). A Kruskal–Wallis analysis of ranks (nonparametric ANOVA equivalent) was, therefore, used to examine the effect of treatment (crop) on the root population densities of *P. goodeyi*. A Mann–Whitney test (non-parametric *t*-test equivalent) was used to assist in the host status classification of the crops.

Crops were classified as good hosts of *P. goodeyi* when their mean root densities were similar to banana ( $P \leq 0.05$ ). When mean *P. goodeyi* root densities were lower ( $P \leq 0.05$ ) than banana but higher than 1000  $100 \text{ g}^{-1}$  FRW, crops were classified as intermediate hosts. Crops with a mean *P. goodeyi* root density lower ( $P \leq 0.05$ ) than banana and lower than 1000 nematodes  $100 \text{ g}^{-1}$  FRW were classified either as poor hosts ( $> 20 P. goodeyi$   $100 \text{ g}^{-1}$  FRW) or very poor hosts

( $\leq 20 P. goodeyi$   $100 \text{ g}^{-1}$  FRW). Statistical analyses were performed using SPSS for Windows, Student Version 14.0 (SPSS, Chicago, IL, USA).

### 4. Results

*Pratylenchus goodeyi* population densities extracted from roots were significantly ( $\chi^2_{1,11} = 31.31$ ;  $P \leq 0.001$ ) different among the crops tested (Table 1). Population densities of *P. goodeyi* on bean and maize cv. CMS 8704 did not differ from those on the susceptible reference crop, banana cv. Grande Naine. On maize cv. CMS 8704 and banana *P. goodeyi* was the dominant species (more than 50% of all plant parasitic nematodes extracted were *P. goodeyi*). *Pratylenchus goodeyi* was not the dominant plant parasitic nematode species on bean, although the highest maximum *P. goodeyi* population density was found on this crop (31,190 nematodes  $100 \text{ g}^{-1}$  FRW, Table 1). Bean and maize cv. CMS 8704 can be classified as good hosts of *P. goodeyi*. The mean population densities of *P. goodeyi* on watermelon and onion were significantly ( $P \leq 0.05$ ) lower than those on banana. However, their relatively high maximum *P. goodeyi* densities (almost 9000 nematodes  $100 \text{ g}^{-1}$  FRW, Table 1) show that these crops are capable of sustaining *P. goodeyi* populations. Watermelon and onion are therefore classified as intermediate hosts of *P. goodeyi*. The mean population densities of *P. goodeyi* on the other crops were also significantly ( $P \leq 0.05$ ) lower than those on banana. Maize cv. Kasai, taro, okra and Irish potato only supported relatively small populations of *P. goodeyi* (58–145 nematodes  $100 \text{ g}^{-1}$  FRW, Table 1),

Table 1. Mean and maximum *Pratylenchus goodeyi* root population densities  $100 \text{ g}^{-1}$  fresh root weight, the proportion (%) of *P. goodeyi* in the plant parasitic nematode root community and host status of 12 commonly cultivated crops in the Cameroon Highlands for *P. goodeyi*.

Crop <sup>1</sup>	Mean density <sup>2</sup>	Maximum density <sup>2</sup>	% <i>P. goodeyi</i>	Pair-wise comparison <sup>4</sup> <i>P</i> -value	Host status
Bananas cv. Grande Naine	12787	17500	86.67	–	Good host
Beans	11883	31190	20.82	0.56	Good host
Maize cv. CMS'8704	7523	15227	90.70	0.15	Host
Watermelon cv. Sugar baby	2991*	8789	57.23	0.02	Intermediate host
Onion	2474*	8800	29.94	0.02	Intermediate host
Maize cv. Kasai	308*	567	18.01	0.02	Poor host
Taro	145*	300	1.67	0.02	Poor host
Okra	92*	238	0.44	0.02	Poor host
Irish potato	58*	200	1.74	0.02	Poor host
Sweet potato cv. TIBI	20*	79	0.50	0.02	Very poor host
Cocoyam	8*	33	0.64	0.02	Very poor host
Tomato cv. Roma	8*	33	0.15	0.02	Very poor host
Significance <sup>3</sup>	$P < 0.001$ ; $\chi^2_{1,11} = 31.31$				

<sup>1</sup>Local variety unless otherwise stated.

<sup>2</sup>Mean ( $n = 4$ ) and maximum *P. goodeyi* root population densities  $100 \text{ g}^{-1}$  fresh root weight.

<sup>3</sup>Kruskal–Wallis analysis of ranks.

<sup>4</sup>Mann–Whitney pair-wise comparison of *P. goodeyi* root population densities  $100 \text{ g}^{-1}$  fresh root weight per crop compared to those found on banana.

\*Mean *P. goodeyi* root population densities differ significantly from those found on banana at  $P \leq 0.05$ .

and are classified as poor hosts of *P. goodeyi*. Both the mean and maximum population densities of *P. goodeyi* on cocoyam, tomato and sweet potato were very low ( $\leq 20$  and  $\leq 100$  nematodes  $100\text{ g}^{-1}$  FRW, respectively, Table 1). These crops are therefore classified as very poor hosts of *P. goodeyi*. *Pratylenchus goodeyi* was extracted from the roots of all crops but was not found in the rhizosphere soil of onion, maize cv. Kasai, Irish potato and tomato.

In addition, species belonging to seven plant parasitic nematode genera were recorded across crops (Table 2). *Meloidogyne* spp. and *Helicotylenchus* spp. were recovered from both the roots and the rhizosphere soil of all crops. *Scutellonema* spp. Andrassy, 1958 were recovered from the roots of all crops but were not found in the rhizosphere soil of okra. *Helicotylenchus* spp. were the most common nematode species found in the roots of bean, Irish potato, maize cv. Kasai, tomato and onion; *Meloidogyne* spp. in the roots of cocoyam and okra; *Scutellonema* spp. in the roots of sweet potato and taro. *Mesocriconema* spp. Andrassy, 1965 were extracted only from the roots of bean, but were found in the rhizosphere soil of banana, bean, Irish potato, both maize cultivars, okra, sweet potato and tomato. Trace numbers of *Aphelenchoides* spp. Fischer, 1894 (extracted from the roots of onion and maize cv. CMS 8704), *Psilenchus* spp. deMan, 1921 (extracted from the roots of bean) and *Pratylenchus coffeae* (extracted from the roots of taro) were also found.

## 5. Discussion

A total of 123 plant species have been screened so far for their host status for *P. goodeyi* (Price 1994; Mbwana et al. 1995; Prasad et al. 1995; Namaganda et al. 2000; our study). Only about 10% of these plant species were classified as good hosts of *P. goodeyi* by one or more authors: four food crops (banana, plantain, onion and watermelon), one medicinal crop, (*Plectranthus barbatus*), one fodder crop (*Tripsacum laxum*) and six weeds (*Cynodon* sp., *Cyperus esculentus*, *Hyperrhenia rufa*, *Leonotis mollisina*, *Solanum incanum* and *Tridax* sp.). Therefore, our study reflects previous reports (Price 1994; Mbwana et al. 1995; Namaganda et al. 2000) that *P. goodeyi* has a relatively narrow host range, especially in comparison to other *Pratylenchus* spp. However, we also concur with the cautionary remarks of Prasad et al. (1995), that the host range of *P. goodeyi* is wider than previously thought.

Of the 123 plant species screened to date, 10% have been classified as good hosts and also as (very) poor hosts or non-hosts of *P. goodeyi*, which includes cassava, okra, taro, bean, tomato, Irish potato, sorghum and maize, the agroforestry crop *Leucana leucocephala* and four weeds *Bidens pilosa*, *Commelina benghalensis*, *Digitaria scalarum* and *Solanum nigrum*.

Table 2. Plant parasitic nematode taxa composition and population densities on the roots of 12 crops commonly cultivated in the Cameroon Highlands.

Crop	Nematode spp. in roots	Mean density $100\text{ g}^{-1}$ fresh root weight
Bananas cv. Grande Naine	<i>Pratylenchus goodeyi</i>	12787
	<i>Helicotylenchus</i> sp.	716
	<i>Meloidogyne</i> sp.	507
Beans	<i>Scutellonema</i> sp.	397
	<i>Helicotylenchus dihystra</i>	25682
	<i>Meloidogyne</i> sp.	17365
	<i>Pratylenchus goodeyi</i>	11883
	<i>Scutellonema</i> sp.	1450
	<i>S. clathricaudatum</i>	
	<i>Mesocriconema</i> sp.	42
Cocoyam	<i>Ditylenchus</i> sp.	nd
	<i>Psilenchus</i> sp.	nd
	<i>Meloidogyne</i> sp.	1210
	<i>Helicotylenchus</i> sp.	64
Irish potato	<i>Scutellonema</i> sp.	25
	<i>Pratylenchus goodeyi</i>	8
	<i>Helicotylenchus</i> sp.	2484
	<i>Meloidogyne</i> sp.	494
	<i>Scutellonema</i> sp.	191
	<i>Pratylenchus goodeyi</i>	58
Maize cv. CMS 8704	<i>Pratylenchus goodeyi</i>	7523
	<i>Helicotylenchus</i> sp.	450
	<i>H. dihystra</i>	
	<i>Meloidogyne</i> sp.	132
	<i>Scutellonema</i> sp.	50
Maize cv. Kasai	<i>Aphelenchoides</i> sp.	nd
	<i>Helicotylenchus</i> sp.	1064
	<i>H. dihystra</i>	
	<i>Pratylenchus goodeyi</i>	308
	<i>Scutellonema</i> sp.	231
Okra	<i>Meloidogyne</i> sp.	100
	<i>Meloidogyne</i> sp.	15976
	<i>Helicotylenchus</i> sp.	3822
	<i>H. dihystra</i>	
Onion	<i>Scutellonema</i> <i>clathricaudatum</i>	764
	<i>Pratylenchus goodeyi</i>	92
	<i>Helicotylenchus</i> sp.	3345
	<i>Pratylenchus goodeyi</i>	2474
	<i>Scutellonema</i> sp. <i>S. bradys</i>	1864
	<i>S. clathricaudatum</i>	
	<i>Meloidogyne</i> sp.	232
Sweet potato cv. TIB1	<i>Aphelenchoides</i> sp.	nd
	<i>Scutellonema</i> sp. <i>S. bradys</i>	2040
	<i>S. clathricaudatum</i>	
	<i>Helicotylenchus</i> sp.	1487
Taro	<i>Meloidogyne</i> sp.	227
	<i>Pratylenchus goodeyi</i>	20
	<i>Scutellonema</i> sp.	3563
	<i>S. clathricaudatum</i>	
	<i>Meloidogyne</i> sp.	2728
	<i>Helicotylenchus</i> sp.	1777
Tomato cv. Roma	<i>Pratylenchus goodeyi</i>	145
	<i>Pratylenchus coffeae</i>	nd
	<i>Helicotylenchus</i> sp.	4156
	<i>Meloidogyne</i> sp.	1233
Watermelon cv. Sugar baby	<i>Scutellonema</i> sp.	205
	<i>Pratylenchus goodeyi</i>	8
	<i>Pratylenchus goodeyi</i>	2991
	<i>Helicotylenchus dihystra</i>	995
	<i>Meloidogyne</i> sp.	621
	<i>Scutellonema</i> sp.	568

nd, Nematode species present but exact nematode population density of this species not determined.



The contradictions among these five studies suggest that the host status classification of crops should be studied carefully before advising rotation crops to farmers. This classification might be influenced by several factors including host response differences among cultivars, differences in pathogenicity among nematode populations and methodological differences among studies. In the five studies mentioned above different cultivars were used. Similarly, the pathogenicity of the *P. goodeyi* populations may have differed in the regions where the studies were carried out. It has been suggested (Bridge et al. 1997) that differences in pathogenicity may be present between *P. goodeyi* populations from Uganda and Tanzania. Inter- and intraspecific variation has been observed within the genus *Pratylenchus* (Andrès et al. 2000; Waeyenberge et al. 2000) and it has been proposed that genetic segregation within the species *P. goodeyi* may exist, as the isozyme pattern of *P. goodeyi* from Cameroon differed from that of *P. goodeyi* from other regions (Andrès et al. 2000). Finally, methodological differences such as the time of sampling and the extraction method used may also have contributed to the observed differences in host status among the five studies.

Most farmers in the Cameroon Highlands plant mainly in mixed cropping systems (Jacobsen et al. 2004). The long-term stability of these systems derives from the diversity of crops and cultivars used, which reduces the risks of pest accumulation inherent to long-term cultivation (Bridge 1996). Another important source of plant parasitic nematodes on bananas and plantains are infested suckers. Nematode management programmes aiming to reduce *P. goodeyi* in these mixed cropping systems should therefore recommend rotation mixtures of poor hosts in combination with clean planting materials, such as hot-water (Colbran and Saunders 1967) or boiling-water (Hauser 2007) treated suckers, to achieve the best results. Cocoyam, groundnut and sweet potato were consistently identified as (very) poor hosts of *P. goodeyi* (Price 1994; Mbwana et al. 1995; Prasad et al. 1995; Namaganda et al. 2000; our study) indicating that they could be suitable rotation crops especially if appropriate cultivars are used. The trace numbers of *P. goodeyi* recorded on sweet potato in our study agree with the results obtained by Namaganda et al. (2000) that this crop is not immune, as reported by Price (1994) and Mbwana et al. (1995), but rather, a very poor host. In general, only crops with a similar (very) poor host status should be grown together in mixed cropping rotations (Bridge 1996). To correctly evaluate the suitability of the rotation crops for the management of *P. goodeyi*, validation trials should be carried out over a sufficiently long period of time before advising these crops on a large scale to farmers.

Plant parasitic nematodes often occur in multiple species communities and efforts to control *P. goodeyi*

may enhance population densities of other nematode species (Luc et al. 2005). *Helicotylenchus multicinctus* was not found in the root samples examined during this study, which is surprising as it is frequently identified in association with bananas and plantains, specifically where *P. goodeyi* is abundant (Sikora et al. 1989; Barekye et al. 2000). On some crops included in our study, *Meloidogyne* spp. and *Helicotylenchus* spp. can reach relatively high population densities. Although the pathogenicity to bananas and plantains of these nematode taxa is not clear, there are indications that under certain conditions they can cause considerable damage to the roots of bananas and plantains resulting in substantial yield losses. Root damage to *Musa* spp. caused by *H. multicinctus* has been reported (McSorley and Parrado 1986; Davide 1996; Chau et al. 1997; Moens et al. 2006). Speijer and Fogain (1999), Parvatha Reddy (1994) and Brentu et al. (2004) observed yield reductions ranging from 19 to 34%. Stunted growth, thinner pseudostems and smaller fruit bunches of bananas caused by *Meloidogyne* spp. have also been reported (Sudha and Prabhoo 1983; Lin and Tsay 1985; Razak 1994). Davide and Marasigan (1985) and Brentu et al. (2004) observed yield reductions ranging from 26 to 57%.

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