

Diversity of nematodes on banana (*Musa* spp.) in Kenya linked to altitude and with a focus on the pathogenicity of *Pratylenchus goodeyi*

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Summary – Bananas (*Musa* spp.) are considered the most important fruit crop in Kenya, grown mostly by smallholder farmers. However, in the past two decades production has declined and has largely been attributed to plant pathogens, including plant-parasitic nematodes. To assess the understanding and awareness that banana farmers have of nematodes, a survey was conducted. The incidence, abundance and distribution of nematodes in relation to altitude were determined for different banana types on 180 farms and the pathogenicity of *Pratylenchus goodeyi*, originating from three different altitudinal locations, was compared on two banana cultivars. Just 2.3% of farmers were aware of nematode damage and symptoms, none of whom applied any management measures. The highest abundance of nematodes was recorded at an altitude range of 1601-2000 m a.s.l., with *Pratylenchus*, *Meloidogyne* and *Helicotylenchus* being the predominant genera. Across all altitudinal locations, cooking banana had higher densities of nematodes than dessert bananas. In pots, *P. goodeyi* populations from Embu (1300 m a.s.l.) appeared more aggressive and with higher levels of multiplication than the population from Oyugis (1100 m a.s.l.). Cooking banana ('Ng'ombe') was more susceptible than dessert banana ('Sukari Ndizi'). Nematode damage is more prominent in areas at higher altitude and on cooking banana cultivars. The findings provide key information in guiding informed and suitable management decision thresholds in relation to potential climate change.

Keywords – altitudinal gradient, climate adaptation, East African Highland banana, *Helicotylenchus*, *Meloidogyne*, nematode survey, smallholder farmers, yield loss.

In East and Central Africa, bananas (*Musa* spp.) are an immensely important staple food crop, fruit crop and source of income for millions of people. In Kenya, bananas are the most important fruit crop, accounting for 35.6% of the total fruit production, and represent the top fruit income earner (Kneoma, 2018). Bananas are often grown across a range of environments, providing a cost-effective source of food energy year-round as well as an ideal infant food when other crops are off-season (Mbaka *et al.*, 2008). Both dessert and cooking types are grown

on an estimated 82 000 ha with a total production of 1.43 million MT (Kneoma, 2018). The most important areas of production include Meru (14%), Kirinyaga (12%), Embu (10%), Bungoma (8%), Taita Taveta (7%), Kisii (7%) and Murang'a (6%) (Ministry of Agriculture, Fisheries and Livestock, 2017). Production is mainly under smallholder conditions (Ng'ang'a *et al.*, 2011).

The current rapid rate of population growth in Kenya, combined with evolving changes in food behaviour, provides an ideal opportunity for increasing banana produc-

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tion in the country. Despite showing great production potential, however, banana yields have declined significantly over the past two decades (FAO, 2015). This reduction has been attributed to increased incidence of pests and diseases, including plant-parasitic nematodes (Reddy *et al.*, 2007), worsened by a lack of effective control strategies (Inzaule *et al.*, 2005).

Globally, nematodes are reported as major pests of banana (Coyne & Kidane, 2018), causing yield losses of 30-60% (Kamira *et al.*, 2013; Sikora *et al.*, 2018). This yield reduction is especially notable in Africa, where nematodes may cause up to 50% loss in East African highland bananas ('EAHB') (Gaidashova *et al.*, 2009; Coyne *et al.*, 2018). In Kenya, a community of nematode species remains a threat to banana production, with *Radopholus similis*, *Pratylenchus goodeyi* and *Helicotylenchus multicinctus* reported as the main pathogenic nematodes affecting *Musa* spp. (Gichure & Ondieki, 1977; Inzaule *et al.*, 2005; Reddy *et al.*, 2007; Waweru *et al.*, 2014). When nematodes attack roots they create tissue damage, exposing the roots to secondary infections from fungal, bacterial and viral pathogens (Okafor *et al.*, 2015; Smiley, 2015). Damaged roots are also less able to access adequate water and nutrients (Risède *et al.*, 2010), suppressing plant growth, lengthening the fruiting period, reducing bunch weight and shortening the production life of mats (Wachira *et al.*, 2013). Due to poor anchorage from damaged root systems, fruit-bearing plants may easily topple, especially during storms and strong winds (Coyne & Kidane, 2018).

Crop productivity is heavily influenced by climate, which also strongly affects pest and disease infestation (Das *et al.*, 2011). Historical records demonstrate an increase in global temperatures since the late 19th century (Kirtman *et al.*, 2014) with Africa identified as probably the most vulnerable continent to climate change and climate variability (Niang *et al.*, 2014). Consequently, changing climates will enable pests and diseases to colonise new localities and to survive outside their historic ranges (Harvell *et al.*, 2002), including nematodes (Talwana *et al.*, 2015; Erima *et al.*, 2017).

Traditionally, some species of nematodes infecting banana have been distributed through a conspicuous temperature gradient, such as *R. similis*, which is traditionally found at lower altitudes with warmer temperatures (Blomme *et al.*, 2012), while *P. goodeyi* traditionally occurs at higher altitudes where temperatures are cooler (Kashaija *et al.*, 1994; Luambano *et al.*, 2018). It is worth noting that these two species have different damage poten-

tials as they present different levels of aggressiveness, with *R. similis* reported to be more damaging than *P. goodeyi* (Price, 2006; Plowright *et al.*, 2013). Given that banana responds poorly to climate change, in relation to impacts on food and nutritional security assessments, the quantification of the climatic conditions for banana production is of particular importance to assess banana's climate sensitivity and, thereafter, to predict the potential impacts of climate change on banana production systems (Varma & Bebbber, 2019).

Owing to the shift in temperatures (King'uyu *et al.*, 2000) along the altitudinal gradient linked to climate change in the East African Highlands, it is possible that the distribution of *R. similis* to higher altitudes, overlapping with *P. goodeyi*, will detrimentally impact 'EAHB' productivity (Coyne *et al.*, 2018). To determine the incidence, abundance and distribution of nematodes at different altitudes on bananas in Kenya, both cooking and dessert type bananas were assessed for nematodes in key banana-growing localities. The differential pathogenicity of three populations of *P. goodeyi* recovered from three different altitudinal zones was also assessed.

Materials and methods

FIELD SAMPLING IN MID (1100-1600 M A.S.L.) AND HIGH (1601-2000 M A.S.L.) ALTITUDE AREAS

Banana farms from 12 major banana-producing areas of Kenya were sampled in Kisii (1100-1600 m a.s.l.), Migori (1100-1600 m a.s.l.), Homabay (1100-1600 m a.s.l.), Kakamega (1601-2000 m a.s.l.), Embu (1100-1600 m a.s.l.), Meru (1601-2000 m a.s.l.), Kiambu (1601-2000 m a.s.l.), Murang'a (1601-2000 m a.s.l.), Kirinyaga (1100-1600 m a.s.l.), Nyeri (1601-2000 m a.s.l.), Busia (1100-1600 m a.s.l.) and Bungoma (1601-2000 m a.s.l.) between November 2018 and July 2019 (Fig. 1). In each area, 15 distant farms were selected for sampling, resulting in a total of 180 sampled farms. In each farm, soil and roots were collected from two banana types: 'EAHB' (cooking type) and 'Cavendish' (dessert type), from a hole measuring 20 × 20 × 20 cm dug using a spade *ca* 1 m from the banana plant/mat. Five functional roots measuring *ca* 10 cm each were also sliced longitudinally to assess percentage root damage using the Root Necrosis Index (RNI) according to Speijer & De Waele (1997) and Coyne *et al.* (2014). The geographical coordinates and altitude were recorded for each farm.

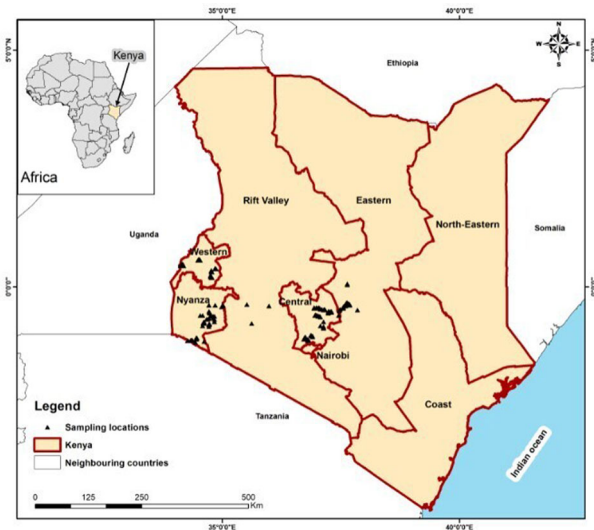


Fig. 1. Map of Kenya showing the sampling locations (▲).

AWARENESS OF PLANT-PARASITIC NEMATODES ON BANANAS AND NEMATODE EVALUATION

The study assessed farmers' knowledge levels and perceptions of nematodes as pests affecting banana production. This was executed through a structured questionnaire with each of the 180 selected farmers.

EXTRACTION AND PROCESSING OF PLANT-PARASITIC NEMATODES

In the laboratory, banana roots were washed, blotted dry on tissue paper, then chopped to *ca* 1 cm length pieces. Nematodes were extracted from 5 g roots and 100 cm³ of soil for 48 h, using the modified Baermann technique (Coyne *et al.*, 2014). Nematodes were counted and examined under a Leica MZ12 dissecting microscope with under-stage lighting at $\times 20$ magnification. Nematodes were killed using the hot water bath method at 65°C (Roy *et al.*, 2014) and fixed in 4% formalin (Coyne *et al.*, 2014) to facilitate identification. Nematodes were identified to genus level using a Leica 2500 compound microscope at 40 \times magnification, based on morphological features described by Hooper *et al.* (2005). Photos were captured at 40 \times magnification.

PATHOGENICITY POT TRIAL ASSESSMENT

The reproductive potential and pathogenicity of three populations of *P. goodeyi* were assessed in pots on two banana cultivars (dessert type 'Sukari Ndizi' and cooking type 'Ng'ombe') at two locations, the International

Centre for Insect Physiology and Ecology (*icipe*), Nairobi (1600 m a.s.l.), and at an identified farm in Kisii (1300 m a.s.l.). Three populations of *P. goodeyi* were recovered from separate locations at different altitudes: Oyugis (1100 m a.s.l.), Embu (1300) and Nairobi (1600). Banana tissue culture plantlets were obtained from Jomo Kenyatta University of Agriculture and Technology at the hardening stage and transplanted into 1.5 l plastic pots filled with steam-sterilised loamy textured soil. Plants were inoculated with 2000 nematodes (pot)⁻¹ using infected banana root tissue segments containing predominantly *P. goodeyi*. Roots were bulk harvested from a farm from each of the three locations where high densities of mainly *P. goodeyi* were observed. Nematode densities were calculated as above and root weights equating to 2000 *P. goodeyi* used to inoculate each pot. The root segments were split longitudinally, cut to *ca* 1 cm length and mixed homogeneously. The cut root segments were applied within a 3 cm radius furrow around the plant and covered with soil. A non-inoculated control using autoclaved banana root segments was included and treatments were replicated ten times in a completely randomised design. The banana plantlets were maintained under shade and irrigated twice weekly. The experiments were terminated at 120 days post-inoculation. At harvest, root fresh weight and shoot fresh weight were recorded; RNI and nematode densities in the soil and roots were assessed and the nematode reproductive factor (RF) calculated:

$$\text{RF} = (\text{Final population}/\text{Initial population})$$

DATA ANALYSIS

Data from questionnaires were coded and analysed using Statistical Package for Social Sciences (SPSS) version 16.0. The nematode count data were transformed by $\log_{10}(x + 1)$ to reduce the coefficient of variation. Percentage RNI from the survey and pot trials were transformed by arcsine (\sqrt{x}) to ensure that data conformed to normal distribution. All data were subjected to analysis of variance (ANOVA) using R version 3.5.1 (R Core Team, 2015) system statistical software and means separated by Tukey's multiple comparison test of significance at ($P \leq 0.05$). Correlation between *P. goodeyi* densities in banana roots and root damage was computed using the Spearman's rank correlation coefficient. Descriptive statistics were used to summarise data.

Table 1. Plant-parasitic nematodes recovered from banana farms at different altitude ranges in Kenya.

Order	Sub-order	Family	Genus	Altitudinal range ¹
Tylenchida	Tylenchina	Pratylenchidae	<i>Pratylenchus</i>	Mid, High*
			<i>Radopholus</i>	Mid
		Hoplolaimidae	<i>Hoplolaimus</i>	Mid, High
			<i>Rotylenchus</i>	Mid
			<i>Helicotylenchus</i>	Mid*, High
			<i>Scutellonema</i>	Mid, high
			<i>Aphelenchoides</i>	Mid, High
		Aphelenchoididae	<i>Aphelenchus</i>	Mid
		Aphelenchidae	<i>Meloidogyne</i>	Mid*, High
		Meloidogynidae	<i>Tylenchus</i>	Mid, High
		Tylenchulidae	<i>Filenchus</i>	Mid, High
Tylenchorhynchidae	<i>Tylenchorhynchus</i>	Mid		
Dorylaimida	Dorylaimina	Longidoridae	<i>Longidorus</i>	Mid
Triplonchida	Diphtherophorina	Trichodoridae	<i>Trichodorus</i>	Mid

¹ Mid altitude = 1100-1600 m a.s.l., high altitude = 1601-2000 m a.s.l. An asterisk indicates that genus occurrence was significantly greater in the altitudinal range.

Results

AWARENESS BY FARMERS OF PLANT-PARASITIC NEMATODES ON BANANAS

The majority of the farmers growing bananas (97.8%) did not know that nematodes are pests of bananas, with just 2.2% of farmers being aware. None of the interviewed farmers was aware that their banana fields were infested and damaged by nematodes, even though some (2%) were familiar with bananas toppling over but were unaware of the cause. The majority (98%) of farmers had not noticed bananas toppling in their farms.

EFFECT OF ALTITUDE AND BANANA TYPE ON ROOT DAMAGE

Root necrosis was greater ($P < 0.05$) at higher altitudes (14.9%), in comparison to the mid altitudes (8.5%), although there were no differences ($P > 0.05$) between 'EAHB' (12.5%) and 'Cavendish' (11.0%).

OCCURRENCE OF PLANT-PARASITIC NEMATODE GENERA

Fourteen nematode genera belonging to eight families in the orders Tylenchida, Dorylaimida and Triplonchida were found associated with banana (Table 1). *Pratylenchus goodeyi* was the most commonly recovered (66.1%) species followed by *H. multicinctus* (16.3%) and

Meloidogyne spp. (8.9%), while *R. similis* (0.3%) was rarely observed (Table 2). These nematodes were recovered from both soil and roots across altitudinal ranges and in both 'EAHB' and 'Cavendish' bananas (Figs 2, 3). On the effect of altitude on plant-parasitic nematode density, cooking banana showed greater densities ($P < 0.05$) of *P. goodeyi* isolated from high altitude banana-producing areas than from mid altitudes (Fig. 2). *Helicotylenchus multicinctus* was recorded in greater ($P < 0.05$) densities in mid altitude than in higher altitudes, while *Meloidogyne* spp. were recovered in greater ($P < 0.05$) densities from mid altitudes in comparison to high altitude areas (Fig. 2). *Radopholus similis* was barely detectable in mid altitudes and it was not recovered from high altitude areas. On 'Cavendish', *P. goodeyi* densities were similar ($P > 0.05$) in both high and mid altitude areas (Fig. 3) and *H. multicinctus* was recorded in greater densities ($P < 0.05$) in mid altitude than in the high altitude areas (Fig. 3). *Meloidogyne* spp. densities were greater ($P < 0.05$) in mid altitude in comparison to high altitude areas, whilst *R. similis* registered extremely low densities in mid altitudes and was absent at high altitude banana-growing areas (Fig. 3).

DISTRIBUTION OF PLANT-PARASITIC NEMATODES ACROSS BANANA PRODUCTION AREAS IN KENYA

Greater densities ($P < 0.05$) of nematodes were associated with banana in Kakamega, a high altitude banana production area (>1600 m a.s.l.), than other areas. In Kakamega, greater nematode densities were associated

Table 2. Mean density and percentage incidence of nematode species/genera recovered from banana production areas in Kenya.

Nematode	Mean density (5 g root) ⁻¹	Percentage incidence
<i>Pratylenchus goodeyi</i>	105 ± 56.67	66.1
<i>Helicotylenchus multicinctus</i>	26 ± 18.91	16.3
<i>Meloidogyne</i> spp.	14 ± 12.31	8.9
<i>Hoplolaimus</i> spp.	4 ± 3.01	2.6
<i>Filenchus</i> spp.	4 ± 2.71	2.3
<i>Longidorus</i> spp.	2 ± 1.61	1.3
<i>Trichodorus</i> spp.	2 ± 0.87	0.9
<i>Aphelenchoides</i> spp.	1 ± 0.54	0.4
<i>Rotylenchus</i> spp.	0.49 ± 0.21	0.3
<i>Radopholus similis</i>	0.40 ± 0.18	0.3
<i>Tylenchus</i> spp.	0.33 ± 0.06	0.1
<i>Aphelenchus</i> spp.	0.31 ± 0.07	0.1
<i>Tylenchorhynchus</i> spp.	0.27 ± 0.02	0.1

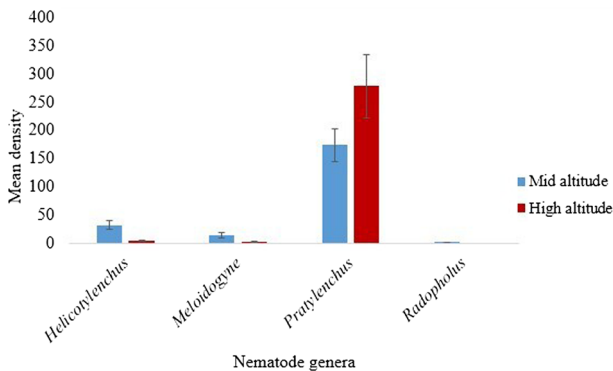


Fig. 2. Mean densities (5 g fresh root)⁻¹ of plant-parasitic nematode genera associated with East African Highland cooking banana ‘EAHB’ in mid and high altitude banana production areas in Kenya.

with ‘EAHB’ than ‘Cavendish’ (Fig. 4), as was the case in Embu, Meru and Kisii (Fig. 5). The opposite was observed in Bungoma and Homabay, where ‘Cavendish’ supported greater nematode densities than ‘EAHB’.

EFFECT OF BANANA TYPE ON PLANT-PARASITIC NEMATODE DENSITY

‘EAHB’ supported higher ($P < 0.05$) densities of *P. goodeyi* than ‘Cavendish’ at both the high and mid altitude ranges, whilst there was no significant difference between banana types for *H. multicinctus* or *Meloidogyne* spp. (Fig. 6) in high altitude ranges. However, *H. multicinctus*

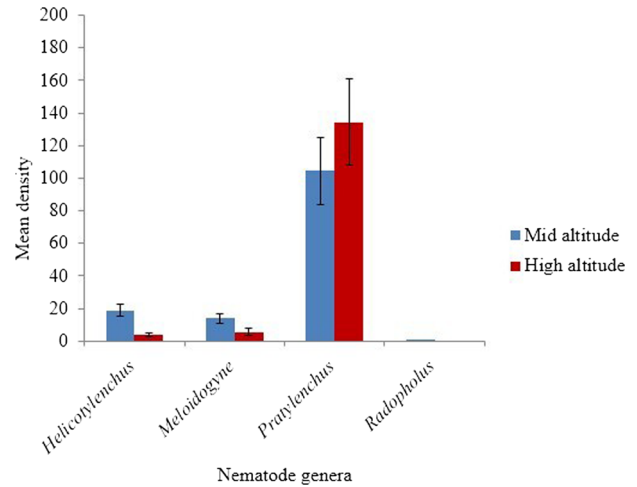


Fig. 3. Mean densities (5 g fresh root)⁻¹ of plant-parasitic nematode genera associated with dessert bananas (‘Cavendish’) in mid and high altitude banana production areas in Kenya.

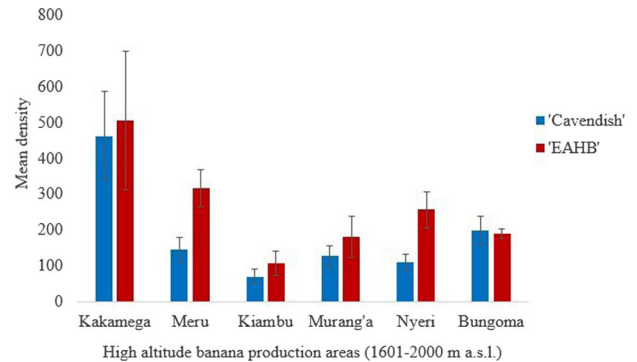


Fig. 4. Mean densities (5 g fresh root)⁻¹ of plant-parasitic nematodes from dessert (‘Cavendish’) and East African Highland cooking banana (‘EAHB’) roots at high altitude (1601-2000 m a.s.l.) banana production areas in Kenya.

was recovered in greater ($P < 0.05$) densities on ‘EAHB’ than ‘Cavendish’ at the mid altitude ranges, whilst *R. similis* was not recovered from banana at the high altitude ranges (>1600 m a.s.l.) on either ‘Cavendish’ or ‘EAHB’, and were negligible in mid altitudes (Fig. 7).

EFFECT OF *PRATYLENCHUS GOODEYI* POPULATIONS ON BANANA ROOT DAMAGE

The percentage root necrosis following inoculation with the three populations of *P. goodeyi* did not differ ($P > 0.05$) between the two study sites at Nairobi and Kisii (Table 3) or between banana type ($P > 0.05$). However, root necrosis caused by the three *P. goodeyi* populations varied and was significantly ($P =$

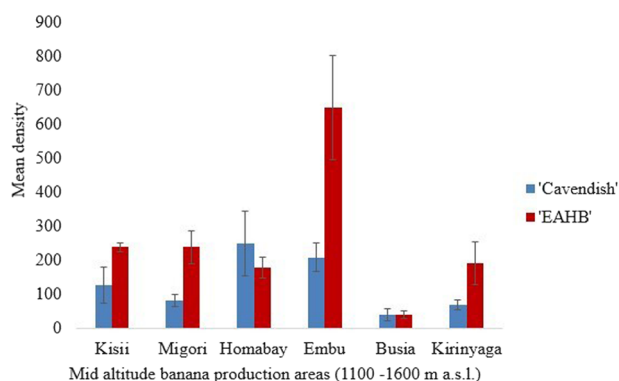


Fig. 5. Mean densities (5 g fresh root)⁻¹ of plant-parasitic nematodes from dessert ('Cavendish') and East African Highland cooking banana ('EAHB') roots at mid altitude (1100-1600 m a.s.l.) banana production areas in Kenya.

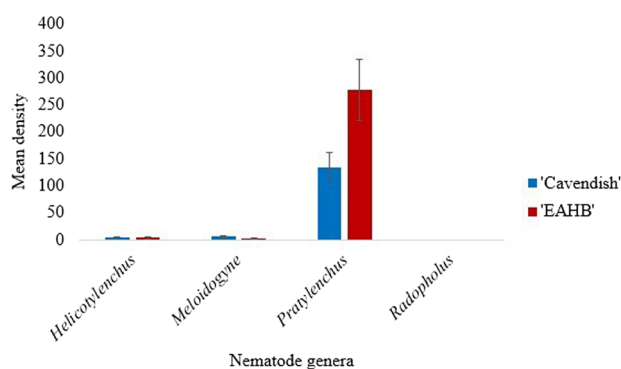


Fig. 6. Mean densities (5 g fresh root)⁻¹ of plant-parasitic nematodes from dessert ('Cavendish') and East African Highland cooking banana ('EAHB') roots at high altitude regions in Kenya (1601-2000 m a.s.l.).

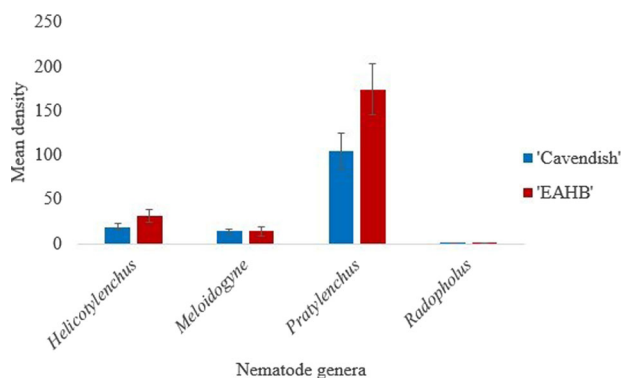


Fig. 7. Mean densities (5 g fresh root)⁻¹ of plant-parasitic nematodes from dessert ('Cavendish') and East African Highland cooking banana ('EAHB') roots at mid altitude regions in Kenya (1100-1600 m a.s.l.).

Table 3. Effect of *Pratylenchus goodeyi* populations on cooking ('Ng'ombe') and dessert banana ('Sukari Ndizi') genotypes at two trial sites in Kenya.

	Mean percentage necrosis	<i>t</i> value	<i>P</i> value
Trial site			
Kisii	5.8 ± 9.01	1.25	0.218
Nairobi	8.5 ± 11.93		
Banana genotype			
'Ng'ombe'	6.9 ± 5.12	0.25	0.817
'Sukari Ndizi'	7.4 ± 8.75		
Population		<i>F</i> -value	
Embu	8.3 ± 11.60	9.86	0.273
Nairobi	15.1 ± 14.08		
Oyugis	4.7 ± 10.62		

Non-inoculated control had no nematodes and differed significantly (*P* < 0.05) from three *P. goodeyi* populations.

0.003) greater for the Nairobi population than the Oyugis population with a difference of 10.4% (Table 4). The severity of root necrosis was not significantly different between the Nairobi and Embu populations, or between the Oyugis and Embu populations (Table 4).

EFFECT OF BANANA CULTIVAR AND TRIAL SITE ON *PRATYLENCHUS GOODEYI* POPULATION DENSITY

Across the two trial sites, the mean density of *P. goodeyi* was 346 (5 g root)⁻¹ for Nairobi and 266 (5 g root)⁻¹ for Kisii, although there was no significant difference (*P* = 0.479) (Table 5). The mean *P. goodeyi* density on 'Ng'ombe' was significantly (*P* = 0.002) greater compared with 'Sukari Ndizi' but did not differ among the three populations (*P* > 0.05) (Table 5). A post ANOVA test showed variations in mean densities of *P. goodeyi* across the three populations, although these variations were not significant (*P* > 0.05) (Table 6).

REPRODUCTIVE FACTOR OF THREE *PRATYLENCHUS GOODEYI* POPULATIONS ACROSS TWO TRIAL SITES

From the two trial sites, the RF was similar for the three *P. goodeyi* populations in Kisii, compared with Nairobi (*P* > 0.05) (Table 7). However, the RF differed significantly between banana cultivars, with 'Ng'ombe' recording a greater (*P* < 0.0048) RF compared to 'Cavendish' (Table 7), but with no differences between *P. goodeyi* populations (*P* = 0.1728) (Table 7).

Table 4. Post analysis of variance test results of banana root necrosis damage by *Pratylenchus goodeyi* populations originating from three altitudinal locations in Kenya.

Population	Contrast difference	SE	<i>t</i>	<i>P</i> > <i>t</i>	95% Confidence interval
NRB vs EMB	6.87	2.78	2.47	0.069	−0.36 14.10
OYG vs EMB	3.55	2.86	1.24	0.600	−10.99 3.88
OYG vs NRB	10.43	2.92	3.56	0.003	−18.03 2.83

EMB = Embu; NRB = Nairobi; OYG = Oyugis; SE = standard error. Non-inoculated control had no nematodes and differed significantly ($P < 0.05$) from three *P. goodeyi* populations.

Table 5. Density of *Pratylenchus goodeyi* populations originating from three altitudinal locations on cooking ('Ng'ombe') and dessert banana ('Sukari Ndizi') genotypes.

	Mean	<i>t</i> value	<i>P</i> value
Trial site			
Kisii	266 ± 78.28	−0.7	0.479
Nairobi	346 ± 63.01		
Banana genotype			
'Ng'ombe'	487 ± 62.65	−3.25	0.002
'Sukari Ndizi'	134 ± 20.03		
Population		<i>F</i> -value	
Embu	557 ± 49.81	4.76	0.671
Nairobi	271 ± 51.79		
Oyugis	376 ± 39.97		

Non-inoculated control had no nematodes and differed significantly ($P < 0.05$) from three *P. goodeyi* populations.

CORRELATION BETWEEN *PRATYLENCHUS GOODEYI* DENSITIES IN BANANA ROOTS AND ROOT DAMAGE

A positive ($r = 0.177$) and significant ($P < 0.05$) correlation was observed between nematode density in the root system and root necrosis.

Discussion

The current study shows clearly that *P. goodeyi* is the most prominent nematode at higher altitude areas (>1600 m a.s.l.) of Kenya, compared to its occurrence in mid altitude areas (<1600 m a.s.l.), reflecting previous studies from across the region (Kashaija *et al.*, 1994; Gaidashova *et al.*, 2004; Reddy *et al.*, 2007; Kamira *et al.*, 2013). However, recent findings by Luambano *et al.* (2017) show that both *P. goodeyi* and *P. coffeae* occur at lower altitudes, such as on the islands of Zanzibar and across the Tanzanian coast. Luambano *et al.* (2018) further reported *P. coffeae* on banana in mainland Tanzania, where the nematode had previously not been reported.

Therefore, *Pratylenchus* species, and in particular *P. goodeyi* (Mgonja *et al.*, 2019), appear to be shifting from their 'known' distribution in East Africa to outside their traditional ranges. Previous studies have demonstrated an altitudinal demarcation for *P. goodeyi* distribution (Talwana *et al.*, 2003; Gaidashova *et al.*, 2009; Kamira *et al.*, 2013), while the current study shows *P. goodeyi* occurring at lower altitudes in the mid altitude belt. *Pratylenchus goodeyi* was seldom observed in low altitudinal elevations in East Africa until recently when the nematode was encountered in Tanzania (Luambano *et al.*, 2017), raising questions as to whether variations in ecotypes, which are more tolerant of higher temperatures, are developing (Coyne, 2009). Although *P. goodeyi* infection can affect banana root efficiency (Wang *et al.*, 2009) and expose plants to secondary infections (Tanimola *et al.*, 2013; Smiley, 2015) at high altitudes, it is yet to be determined how this impacts bananas at higher temperatures in lower altitudes.

From the current study, *H. multicinctus* was recovered from elevations above 1600 m a.s.l., unlike earlier reports (Kashaija *et al.*, 1994; Gaidashova *et al.*, 2004) where the nematode was observed in all sites below 1600 m a.s.l. but not above. This could relate to the mixed banana production systems observed in most of the farms surveyed. *Helicotylenchus multicinctus* is recognised as a key nematode constraint to *Musa* production, especially plantain in West Africa (Coyne, 2009) but also on 'EAHB' (Hartman *et al.*, 2010). Comparatively, *H. multicinctus* is not viewed as being as aggressive as *R. similis*, but where it occurs in high populations it can cause severe root damage (Tanimola *et al.*, 2013).

Meloidogyne spp. was widely distributed in both mid and high altitude areas (<1600 m a.s.l.) in low densities. Although *Meloidogyne* spp. have been similarly encountered in mid altitude areas in the region (Kamira *et al.*, 2013), the nematodes have not regularly been encountered at high altitudes but are more prevalent at lower altitudes (<1400 m a.s.l.) (Kashaija *et al.*, 1994; Talwana *et al.*, 2003; Reddy *et al.*, 2007). Whilst studies have shown that

Table 6. Post analysis of variance test results for *Pratylenchus goodeyi* densities of populations originating from three altitudinal locations.

Population	Contrast difference	SE	<i>t</i> value	<i>P</i> > <i>t</i>	95% Confidence interval
NRB vs EMB	-285.66	149.56	-1.91	0.228	-674.06 102.73
OYG vs EMB	-180.50	153.85	-1.17	0.645	-580.05 219.03
OYG vs NRB	105.15	157.27	0.67	0.909	-303.28 513.59

EMB = Embu; NRB = Nairobi; OYG = Oyugis; SE = standard error. Non-inoculated control had no nematodes and differed significantly ($P < 0.05$) from three *P. goodeyi* populations

Table 7. Reproductive factor (RF) of three *Pratylenchus goodeyi* populations originating from three altitudinal locations on cooking ('Ng'ombe') and dessert banana ('Sukari Ndizi') genotypes at two trial sites in Kenya.

	Mean RF	SE	<i>t</i> value	<i>P</i> value
Trial site				
Kisii	0.23	0.05	0.95	0.3455
Nairobi	0.35	0.11		
Banana genotype				
'Ng'ombe'	0.46	0.12	2.87	0.0048
'Sukari Ndizi'	0.12	0.02		
Population			<i>F</i> -value	
Embu	0.45	0.16	1.78	0.1728
Nairobi	0.19	0.03		
Oyugis	0.23	0.06		

SE = standard error.

Meloidogyne spp. can affect bunch weight (Van den Bergh *et al.*, 2000) and cause root galling (Coyné *et al.*, 2014), *Meloidogyne* spp. are generally not considered a major pest of bananas in East Africa (Tanimola *et al.*, 2013).

Interestingly, *R. similis*, a damaging species and prevalent elsewhere in the region, was rarely detected in the current study, further supporting observations by Reddy *et al.* (2007) who observed it infrequently. This observation could be ascribed to the increasing use and popularity of tissue culture plants in Kenya, which would limit the spread of *R. similis* as the distribution of this species results mainly from the dissemination of infected banana planting materials (Price, 2006; Blomme *et al.*, 2012). *Radopholus similis* has also traditionally been found at altitudes below 1400 m a.s.l. (Kashaija *et al.*, 1994; Gaidashova *et al.*, 2004; Reddy *et al.*, 2007) where temperatures are higher, although in the current study the nematode was detected only infrequently across all survey sites.

The current study identified more species of nematodes on cooking banana than on dessert bananas, with high

densities of the dominant *P. goodeyi* observed on 'EAHB' compared to 'Cavendish', confirming earlier findings (Reddy *et al.*, 2007), where more lesion nematodes were observed on 'EAHB' in most Kenyan districts surveyed. This observation could be explained in part by the endemic and dominant cultivation of 'EAHB' in the cooler highlands (Karamura *et al.*, 1998), as opposed to lowland areas (Gaidashova *et al.*, 2004).

In the pathogenicity study of *P. goodeyi* populations, the higher densities of *P. goodeyi* from the Nairobi trial (1600 m a.s.l.), compared to that of Kisii (1300 m a.s.l.), could be due in part to the existence of an inherent degree of variability in aggression and infectivity between temperatures and within the pathogen biology (Talwana *et al.*, 2003). This current observation of *P. goodeyi* at altitudes of 1300 m a.s.l. indicates that the temperature range of the nematode is shifting, as it is now occurring in areas at lower altitudes where it has previously not been reported (Luambano *et al.*, 2017; Mgonja *et al.*, 2019), challenging observations that the nematode is confined to higher altitudinal ranges above 1500 m a.s.l. (Kamira *et al.*, 2013). The higher root necrosis observed in Nairobi compared with Kisii may be related to the higher average altitude of Nairobi (>1600 m a.s.l.) compared to Kisii (<1300 m a.s.l.). Greater nematode densities and RF was recorded from 'Ng'ombe' but, interestingly, with lower root damage, while 'Sukali Ndizi' had lower nematode densities and RF but greater root damage. Although root damage varied across sites on both cultivars, 'Sukali Ndizi' would appear to be less tolerant of *P. goodeyi* than 'Ng'ombe'. These observations reflect the views of Marin *et al.* (2009) that reproductive fitness of the nematode and the amount of root damage caused on the host may not always be related, suggesting that these attributes could be under the control of different genes (Shaner *et al.*, 1992). In the current study, it was noted that a demonstrable degree of variability in nematode aggressiveness exists and that infection levels vary between temperatures within sites and among the three *P. goodeyi* populations. This

damage could be influenced by factors such as plant cultivar or climate (Gauggel *et al.*, 2005), confirming reports by Talwana *et al.* (2003). The future of banana production in the region, therefore, would benefit from the long-term development of management thresholds to cope with these changing threats.

The variability of root necrosis among the three *P. goodeyi* populations observed across sites mirrors those found by Speijer & De Waele (1997) and Nega & Fetena (2015), who observed that overall nematode damage levels displayed large variability among different sites in Uganda and Ethiopia. This observation suggests that in rolling out breeding programmes for nematode resistance, banana cultivars that maintain a strong root system when infected with high nematode densities provide a good source of nematode management (Barekye *et al.*, 2000). Comparatively, the Embu population isolated from a temperature of 20°C had a significantly greater RF than the Nairobi (24°C) or Oyugis (26°C) populations. While these observations typify the multiplication indices of plant-parasitic nematodes at higher temperatures (Talwana *et al.*, 2003; Coyne *et al.*, 2014; Wu *et al.*, 2014), they contradict the thermophobic character of *P. goodeyi*. Further, the results from the current study indicate that *P. goodeyi* is adapted to a wide range of temperatures despite showing thermal sensitivity in aggressiveness. The current findings indicate that *P. goodeyi* is spreading geographically, regardless of climatic conditions or altitudinal elevation (Coyne *et al.*, 2018; Mgonja *et al.*, 2020).

The current study has demonstrated that the vast majority of banana growers in Kenya are not aware of nematodes as pests infecting their bananas. These findings confirm other studies (Brooks, 2004; Wang & Hooks, 2009; Chitamba *et al.*, 2016), where most growers are unaware of nematodes as a major cause of *Musa* production problems and have only limited knowledge of banana nematodes as a pest. In addressing the nematode challenge, therefore, there is a need to raise farmers' awareness and promote the use of healthy, nematode-free planting materials (Coyne, 2009).

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