PLANT-PARASITIC NEMATODES AND THEIR ASSOCIATED NATURAL ENEMIES WITHIN BANANA (MUSA SPP.) PLANTINGS IN HAWAII

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ABSTRACT

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A survey of banana fields was conducted on the Hawaiian islands of Kauai, Oahu, Maui, Lanai, Molokai and Hawaii in 2007 and 2008 to determine the most important plant-parasitic nematodes and their natural enemies associated with banana plantings in Hawaii. Plant-parasitic nematodes were surveyed from soil and banana root tissues collected at twenty seven banana farms among the Hawaiian islands. *Meloidogyne* spp., *Helicotylenchus* sp., followed by *Rotylenchulus reniformis* were the most frequently found plant-parasitic nematodes through soil assay. However, the bacterium *Pasteuria penetrans*, an obligate parasite of nematodes, was found attached to the cuticle of *Meloidogyne* juveniles at 26% of the sites surveyed. Root assay revealed that *Helicotylenchus multicinctus* reached higher abundance in banana root tissues compared to *Meloidogyne* sp., *R. reniformis, R. similis* and *Pratylenchus* sp. Elevated counts of *Pratylenchus* sp. and *R. similis* were only recorded from banana roots at one and two farm sites, respectively. Thus, *H. multicinctus* which was not considered an important plant-parasitic nematode in the past with respect to Hawaii banana fields should receive greater attention. Finally, the survey confirmed our assumption that potential natural enemies of plant-parasitic nematodes, including omnivorous and predatory nematodes, nematode-trapping fungi and *P. penetrans*, are commonly found. Any management practices developed to manage nematode problems in Hawaiian banana fields should be cautious of any ill effects on beneficial soil organisms.

Key words: Helicotylenchus multicinctus, *Meloidogyne*, nematode-trapping fungi, nematode survey, *Pasteuria penetrans*, predatory nematodes, *Pratylenchus*, *Radopolus similis*, *Rotylenchulus reniformis.*

RESUMEN

Wang, K.-H. and C. R. R. Hooks. 2009. Nematodos fitoparásitos y sus enemigos naturales en cultivos de banano (*Musa* spp.) en Hawaii. Nematropica 39:57-73.

Se llevó a cabo un censo en cultivos de banano en Hawaii, incluyendo las islas de Kauai, Oahu, Maui, Lanai, Molokai y Hawaii en 2007 y 2008, con el fin de identificar los nematodos fitoparásitos más importantes y sus enemigos naturales. Se colectaron muestras de suelo y de raíces en 27 plantaciones en las distintas islas. Los nematodos que se encontraron con mayor frecuencia en las muestras de suelo fueron *Meloidogyne* spp. y *Helicotylenchus* sp., seguidos de *Rotylenchulus reniformis.* Sin embargo, también se encontró la bacteria *Pasteuria penetrans*, un parásito obligado de nematodos, adherida a la cutícula de juveniles de *Meloidogyne* en el 26% de los sitios muestreados. Las muestras de raíces revelaron que *Helicotylenchus multicinctus* se encuentra con mayor abundancia en las raíces de banano que *Meloidogyne* sp., *R. reniformis, R. similis* y *Pratylenchus* sp. Sólo se encontraron cantidades altas de *Pratylenchus* sp. y de *R. similis* en muestras de raíces provenientes de una y dos plantaciones, respectivamente. Esto indica que debe brindarse mayor atención a *H. multicinctus* aunque tradicionalmente no se haya considerado como un nematodo de importancia en las planatciones de banano en Hawaii. Este estudio confirma que existe gran potencial de enemigos naturales, y que en plantaciones de banano se encuentran comúnmente nematodos omnívoros y depredadores, hongos atrapadores de nematodos, y *P. penetrans.* Las prácticas de manejo que se desarrollen para el control de nematodos fitoparásitos en Hawaii deben tener en cuenta el daño que pueda ocasionar a estos organismos benéficos.

Palabras clave: Helicotylenchus multicinctus, hongos atrapadores de nematodos, *Meloidogyne, Pasteuria penetrans,* nematodos depredadores, *Pratylenchus, Radopolus similis, Rotylenchulus reniformis.*

INTRODUCTION

Bananas (*Musa* spp.) are among the most important food crops in the world (Sharrock and Frison, 1999) and rank first among fruits with annual sales of approximately US 2.5 billion (Ploetz, 2001). Based on the 2006 statistic from FAO, banana is grown in more than 130 countries with an annual total production of 80 million tons (UNCTAD, 2009). Hawaii ranks number one in banana production (*Musa* sp.) within the United States. Commercial banana production occurs on all major Hawaiian islands with 80% of the production concentrated on the islands of Hawaii and Oahu (Constantinides and McHugh, 2003). In 2007, Hawaii growers generated 19.7 million pounds of fresh market banana, producing a farm gate value of $8 million (NASS, 2008). However, banana yields in Hawaii have declined since 2000 when 29 million pounds of fresh market banana were produced with a farm gate value of $10.4 million (NASS, 2008). Although this decrease has been largely contributed to *Banana bunchy top virus* (BBTV), many questions remain unanswered about the role of plant-parasitic nematodes in the decline of banana yields in Hawaii.

Most Hawaiian growers are unaware that nematodes are the cause of their production problems and fail to associate problems such as toppling of banana plants and yield reductions to nematode infestations. However, their impact on banana production in many other countries is well understood and documented (Davide and Marsigan, 1985; Speijer *et al.*, 1999). Among the many plant-parasitic nematode species associated with banana plantings, burrowing (*Radopholus similis* (Cobb) Thorne) and spiral (*Helicotylenchus multicinctus* (Cobb) Golden) nematodes are of greatest economic concern. *Radopholus similis* alone is considered one of the most damaging pathogens of *Musa* spp. worldwide (Gowen, 1995; Sarah, 1989; Araya, 1999; Gowen *et al.*, 2005). *Radopholus similis* and *H. multicinctus* are reportedly responsible for yield losses of 30-50% in Costa Rica and Panama, 40% in Africa, and 30-60% in India (Davide, 1995) and exceeding 50% in East Africa (Speijer and Kajumba, 1996; Kashaija *et al.*, 2004). Mixed populations of nematode species with different feeding habits normally coexist in banana plantations (Kashaija *et al.*, 1994). For example, Chabrier and Quénéhervé (2003) found during their study that five nematode species, *R. similis,* lance nematode (*Hoplolaimus seinhorstii* Luc), *H. multicinctus,* root-knot nematode (*Meloidogyne* sp.), and reniform nematode (*Rotylenchulus reniformis* Linford and Oliveira), caused more than 40% of toppling-over of banana plants between flowering and the last harvest by the second production cycle. Lesion nematode, *Pratylenchus* spp., is another genus of plant-parasitic nematodes damaging banana (Gowen *et al.*, 2005). Banana nematodes attack root and corm tissues causing damage that can reduce bunch size, shorten the life of production, prolong the vegetative cycle and cause banana plants to topple (McSorley and Parado, 1986; Bridge, 1988; Chabrier and Quénéhervé, 2003).

In 1966, Sher reported that *H. multicinctus* was found in a banana planting in Hilo, Hawaii, while Sugano *et al.* (2003) listed *Radopholus similis, Meloidogyne* spp., and *Rotylenchulus reniformis* as the top three nematode pests of bananas in Hawaii. There has been no official survey conducted to determine the nematode fauna associated with banana plantings in this production zone. Therefore, a survey is needed to determine the most important plant-parasitic nematodes of bananas in Hawaii.

In Hawaii banana is a relatively hardy and low input staple crop, and is typically grown continuously in the same fields for several years. If unabated by disease and properly watered, banana can continuously produce harvestable fruit with minimum input over an extended time period. Thus, in addition to plant-parasitic nematodes, there may be an opportunity for population build-up of predatory nematodes and other beneficial soil organisms (e.g., bacteria, fungi, etc.) that are likely to play important roles in regulating nematode populations. To help understand the severity of a nematode problem, it is also important to know the population densities of their natural enemies.

The objectives of this research project were to determine 1) the most prevalent plant-parasitic nematodes impacting banana plantings in Hawaii; and 2) the community of soil microorganisms associated with banana plantings that are natural enemies of plant-parasitic nematodes (e.g., nematode trapping fungi, *Pasteuria penetrans,* and omnivorous and predatory nematodes).

MATERIALS AND METHODS

Nematode survey

Nematode surveys were conducted at 27 banana fields distributed throughout the six major Hawaiian islands (Oahu, Hawaii, Maui, Lanai, Molokai, and Kauai) (Fig. 1). The field sites sampled were representative of banana growing regions in Hawaii. Brief descriptions of each farm (location, farm type, soil series, banana cultivars planted, and age of plants) are summarized in Table 1. Generally at each sampling site, fifteen mature banana plants were selected for sampling. Five soil cores were taken from the root zone (within 30-cm diameter from the pseudostem) of 5 individual mature banana plants (either at early flowering or at fruit baring stage) at a depth and diameter of 20 and 6.35 cm, respectively. Soil and roots contained in these five cores were composited into a single sample. This sampling was repeated three times, thus three composite samples (total of 15 plants) were collected from each location or field. In some farms where more discrete patches of banana were present, more than fifteen plants were examined. Numbers of sample collected from each location are listed in Table 2. Samples were stored in plastic bags, placed in a cooler and transported back to the laboratory for processing. A 250-cm^3 sub-sample of soil was removed from each sample and subjected to elutriation (Byrd *et al.*, 1976) and modified centrifugation methods. An aliquot of 1/5 of the nematode extracted from the soil were collected from the elutriation for counting. Root samples (approximately 236 cm^3) were cut into 2.5-cm pieces and incubated in a mist chamber (Barker, 1985) for 5 days to extract migratory nematodes from roots. Roots removed from the mist chamber were oven dried at 70°C for 3 days and the dry weight of each sample recorded. Total numbers of plant-parasitic nematodes collected were identified to the genus level and counted under an inverted microscope.

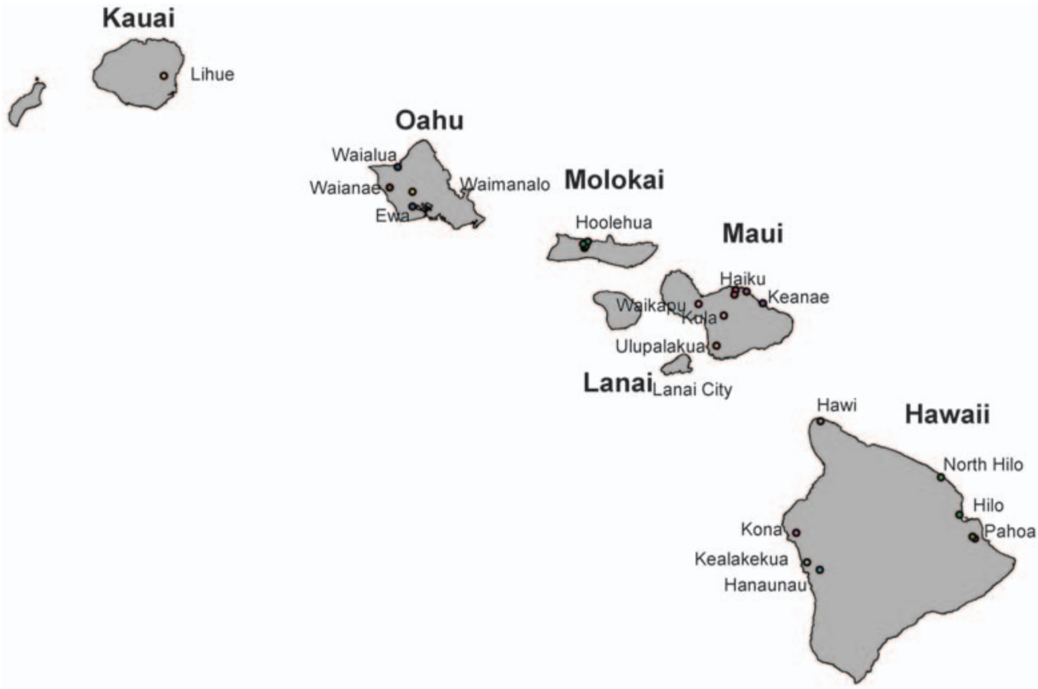

Fig. 1. Map of 27 banana farms being surveyed for nematodes in Hawaii.

Potential natural enemies of nematode pests

Omnivorous and predatory nematodes extracted from the soil samples were identified to genus level and counted. Feeding behavior of these nematodes was determined based on that categorized by Yeates et al. (1993). In addition, the number of *Meloidogyne* spp. with spores of *Pasteuria penetrans* attached on the cuticle was also recorded and converted to percent infestation.

Nematode-trapping fungi (NTF)

To estimate the occurrence of NTF, subsamples (10 g) of bulk soil collected from 18 of the farm sites distributed throughout 5 of the 6 islands were subjected to an assay for NTF as described by Jaffee *et al.* (1998). Soil was suspended in 20 ml sterile distilled water followed by a series of three 10 fold-dilutions. A 100 µl aliquot of each dilution was plated on 5.5-cm diameter Petri dishes containing ¼ th strength cornmeal agar (CMA/4) with 100 mg/L streptomycin giving 0.05, 0.005, and 0.0005 g/L dilution series. *Steinernema glaseri* were added to each plate as nematode-trapping fungus bait. At 3 weeks after plating, all plates were observed under an inverted microscope at 200 × magnifications. NTF were identified according to a key developed by Cooke and Godfrey (1964). Numbers of plates with NTF present were recorded. Population densities (propagules/g of soil) of each species were estimated by Most Probable Number program (Woomer *et al.*, 1990). Based on their ecological preferences and capabilities to trap nematodes, NTF were placed into two groups: saprophytic (formed adhesive nets) and parasitic (formed adhesive knobs and constricting rings) as suggested by Cooke (1963).

Table 1. Location, description of farm types, and soil types of the banana farms surveyed, and cultivars planted in each farm.

Location	Farm type[z]	Soil Series	Cultivars and age of plants (year)
Oahu			
Ewa	H	Ewa silty clay loam, fine, kaolinitic, isohyperthermic Aridic Haplustolls	Dwarf Brazilian (4-10)
Kunia	H	Kunia silty clay, fine, parasesquic, isohyperthermic Oxic Dystrustepts	Williams (4)
Waianae	H	Ewa silty clay loam, fine, kaolinitic, isohyperthermic Aridic Haplustolls	Dwarf Brazilian, Chinese Williams (1-5)
Waimanalo	H	Kabeohe Silty Clay Loam, very find, ferruginous, isohyperthermic, Rhodic Acrudox	Dwarf Brazilian (3-5)
Waialua 1	H	Waialua silty clay, very-fine, mixed, superactive, isohyperthermic Pachic Haplustolls	Dwarf Brazilian (6)
Waialua 2	H	Same as above	Dwarf Brazilian (3), Saba (5)
Hawaii			
North Hilo	L/O	Hilo silty clay loam, Medial over hydrous, ferrihydritic, isohyperthermic Acrudoxic Hydrudands	Dwarf Brazilian (13)
Hilo	H	Same as above	Dwarf Brazilian (>5)
Pahoa 1	H	Pahoa silty clay, Very-fine, parasesquic, isohyperthermic Torrertic Haplustolls	Dwarf Brazilian (>5)
Pahoa 2	H	Same as above	Dwarf Brazilian (>5)
Hawi	L/O	Hawi silty clay, very-fine, mixed, semiactive, isohyperthermic Pachic Haplustolls	Dwarf Brazilian, Ice Cream, Chinese Williams (7)
Hanaunau	L/O	Honaunau silty loam, very cobbly muck, Euic, isothermic, micro Lithic Udifolists	Dwarf Brazilian (1)
Kealakekua	H	Kealakekua silty clay loam, Hydrous, ferrihydritic, isothermic Typic Hydrudands	Dwarf Brazilian (5-10)
Kailua-Kona	L/O	Honaunau silty loam, very cobbly muck, Euic, isothermic, micro Lithic Udifolists	Chinese Williams, Dwarf Brazilian, Ice Cream, Raja Puri, Dwarf Red, Mysore, Cuban Red (1-5)
Lanai			
Lanai City	H	Waihuna clay, Very-fine, mixed, semiactive, isothermic Typic Haplusterts	Dwarf Brazilian (1-4)

[z]Farm type: H = high input with frequent application of synthetic fertilizer, herbicides (mostly glyphosate), and fungicides (such as benzimidazole, morpholine, strobilurins, triazoles, mancozeb, and chlorothalonil); L = low input, with minimum application of any fertilizer and pesticide, often left unattended; O = organic farming with application of organic fertilizer, weeds are mainly managed by mulches or hand weeding.

Table 1. (Continued) Location, description of farm types, and soil types of the banana farms surveyed, and cultivars planted in each farm.

Location	Farm type[z]	Soil Series	Cultivars and age of plants (year)
Maui			
Ulupalakua	L/O	Ulupalakua silty loam, medial over pumiceous or cindery, amorphic, isothermic Pachic Haplustands	Bluefields (> 15)
Haiku 1	H	Haiku clay, very-fine, ferritic, isohyper-thermic Ustic Palehumults	Valery (23)
Haiku 2	L/O	Same as above	Dwarf Brazilian, Tall Brazilian, Chinese Williams (>10)
Haiku 3	H	Same as above	Dwarf Brazilian (>5)
Waikapu	H	Waikapu silty clay loam, Fine, parases-quic, isohyperthermic Torroxic Haplustolls	Dwarf Brazilian (5)
Keanae	L	Hana hydrous, amorphic, isohyperthermic typic hydrudands	Dwarf Brazilian (>10)
Kula	H	Kula cobbly loam, Medial, amorphic, isothermic Humic Haplustands	Dwarf Brazilian (>10)
Molokai			
Hoolehua 1	L	Hoolehua silty clay, Fine, parasesquic, isohyperthermic Oxic Haplustepts	Dwarf Brazilian (2)
Hoolehua 2	L	Same as above	Williams, Bluefields, Dwarf Brazil-ian (0.5– 4)
Hoolehua 3	L	Same as above	San Juan, Saba, Dwarf Brazilian (3)
Hoolehua 4	L	Same as above	Dwarf Brazilian (12)
Kauai			
Lihue	H	Lihue silty clay, very-fine, ferruginous, isohyperthermic Rhodic Eutrustox	Dwarf Brazilian (2-4)

[z]Farm type: H = high input with frequent application of synthetic fertilizer, herbicides (mostly glyphosate), and fungicides (such as benzimidazole, morpholine, strobilurins, triazoles, mancozeb, and chlorothalonil); L = low input, with minimum application of any fertilizer and pesticide, often left unattended; O = organic farming with application of organic fertilizer, weeds are mainly managed by mulches or hand weeding.

Table 2. Abundance of omnivorous (O) and predatory (P) nematodes (per 250 cm^3 soil) in banana farms in Hawaii.

	n[y]	*Aporcelaimellus* (O)	*Butlerius* (P)	*Dorylaimellus* (O)	*Ecumenicus* (O)	*Mononchus* (P)	*Thornonema* (O)	*Timmus* (O)	*Tobrilus* (P)	*Tripyla* (P)	Total omnivore	Total predator
Ewa	3	0[z]	0	0	3 ± 3	0	0	0	0	0	3 ± 3	0
Kunia	3	0	0	0	0	0	0	0	0	0	0	0
Waianae	4	5 ± 5	0	0	10 ± 6	15 ± 9	0	0	3 ± 3	0	15 ± 10	20 ± 9
Waimanalo	3	39 ± 31	0	0	7 ± 7	7 ± 7	0	0	0	0	49 ± 25	7 ± 7
Wailua 1	3	17 ± 7	0	0	37 ± 23	23 ± 9	0	0	0	0	60 ± 29	27 ± 12
Wailua 2	2	5 ± 5	0	15 ± 15	0	5 ± 5	0	0	0	0	20 ± 10	5 ± 5
North Hilo	3	3 ± 3	0	0	0	0	0	0	0	0	43 ± 20	3 ± 3
Hilo	3	0	0	0	0	0	0	0	0	0	0	0
Pahoa 1	3	3 ± 3	0	0	0	0	0	0	0	0	3 ± 3	0
Pahoa 2	3	7 ± 7	0	0	0	0	0	0	0	0	7 ± 7	0
Hawi	3	0	0	0	10 ± 6	10 ± 6	0	3 ± 3	17 ± 12	0	10 ± 6	30 ± 17
Hanaunau	2	30 ± 20	0	0	35 ± 5	5 ± 5	0	0	20 ± 20	0	65 ± 25	30 ± 20
Kealakekua	3	7 ± 3	0	0	3 ± 3	0	0	0	3 ± 3	3 ±	10 ± 6	10 ± 6
Kailua-Kona	4	0	0	0	5 ± 5	0	0	0	0	0	5 ± 5	0
Ulupalakua	3	0	0	0	0	3 ± 3	0	0	0	0	0	3 ± 3
Haiku 1	4	0	0	0	3 ± 3	5 ± 3	0	0	0	0	3 ± 3	5 ± 3
Haiku 2	3	3 ± 3	37 ± 14	0	0	0	0	0	0	7 ± 7	3 ± 3	43 ± 17
Haiku 3	3	3 ± 3	0	0	0	10 ± 6	10 ± 6	7 ± 3	0	0	13 ± 9	10 ± 6
Waikapu	3	13 ± 9	0	0	0	17 ± 17	0	0	0	0	13 ± 9	17 ± 17
Kaenae	3	13 ± 7	0	0	3 ± 3	10 ± 10	3 ± 3	10 ± 6	0	27 ± 3	50 ± 23	37 ± 6
Kula	3	0	0	0	7 ± 3	0	0	0	0	0	7 ± 3	0
Lanai City	3	10 ± 10	0	0	20 ± 12	0	0	0	0	0	30 ± 21	3 ± 3
Hoolehua 1	3	217 ± 17	0	17 ± 17	133 ± 44	0	0	0	0	0	433 ± 60	0

[z]Means are average of ny replications for each location. Means are followed by ± standard error. Only means of the most abundant omnivorous and predatory nematodes (means ≥ 3) are presented.

Table 2. (Continued) Abundance of omnivorous (O) and predatory (P) nematodes (per 250 cm^3 soil) in banana farms in Hawaii.

	n[y]	*Aporcelaimellus* (O)	*Butlerius* (P)	*Dorylaimellus* (O)	*Ecumenicus* (O)	*Mononchus* (P)	*Thornonema* (O)	*Timmus* (O)	*Tobrilus* (P)	*Tripyla* (P)	Total omnivore	Total predator
Hoolehua 2	3	7 ± 7	0	0	37 ± 32	0	0	17 ± 17	0	0	43 ± 30	0
Hoolehua 3	3	17 ± 9	0	0	3 ± 3	0	0	0	0	0	20 ± 12	0
Hoolehua 4	3	3 ± 3	0	0	7 ± 3	3 ± 3	3 ± 3	7 ± 7	0	0	17 ± 7	7 ± 7
Lihuei	5	10 ± 4	0	2 ± 2	4 ± 2	0	2 ± 2	0	0	0	18 ± 4	0
% present		70.37	3.70	11.11	62.96	44.44	14.81	18.52	14.81	11.11	88.89	59.26
Means		15 ± 5	1 ± 0.9	1 ± 0.7	12 ± 3	4 ± 1	0.7 ± 0.3	1 ± 0.7	1 ± 0.7	1 ± 0.6	34 ± 9	9 ± 2

[z]Means are average of ny replications for each location. Means are followed by ± standard error. Only means of the most abundant omnivorous and predatory nematodes (means ≥ 3) are presented.

Statistical analysis

Means of the top five genera of plant-parasitic nematodes found in the soil and roots were presented. Since the objective of this project is to determine the most prevalent plant-parasitic nematodes impacting banana plantings in Hawaii and not to compare population densities among farm sites, standard error of each populations were presented instead of presenting mean separation among farm site. Correlation analysis based on Pearson Correlation coefficient was performed among the abundance of five of the most dominant genera of plant-parasitic nematodes, on percent *P. penetrans* infestation on root-knot nematodes, and on population densities of nematode-trapping fungi and omnivorous and predatory nematodes. All nematode abundance data was log transformed prior to the correlation analysis to obtain a normal distribution.

RESULTS

Plant-parasitic nematodes in soil

Dominant plant-parasitic nematodes extracted from the soils of banana fields included *Meloidogyne* sp. (100% of the farms surveyed), *H. multicinctus* (96.3%), *R. reniformis* (92.6%), and *R. similis* (37.0%) (Fig. 2). *Pratylenchus* sp. was less frequently found (7.4%), as were *Paratrichodorus* sp., *Hemicycliophora* sp., and *Mesocriconema* sp. (less than 15%). Although *Meloidogyne* spp. was detected in most banana farms, *Pasteuria penetrans* was associated with this nematode in 26% of the farms surveyed (Fig. 2A). Numbers of *Meloidogyne* sp. in the soil correlated positively with percent *P. penetrans* infestation (r = 0.3, P = 0.01, n = 73 where n is the number of observation). Soils in which populations of *Helicotylenchus* were detected commonly contained mixed species of *H. multicinctus* and *H. dihystera*

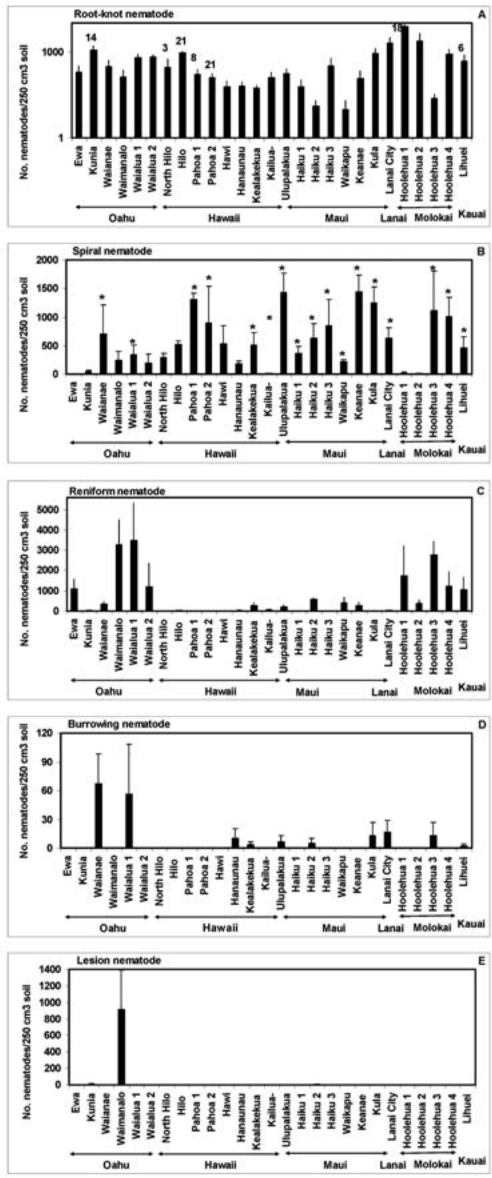

Fig. 2. Numbers of plant-parasitic nematodes found in soil sampled from 27 banana farms distributed on five Hawaiian islands; A) root-knot (*Meloidogyne* spp.), B) spiral (*Helicotylenchus* spp.), C) reniform (*Rotylenchulus reniformis*), D) burrowing (*Radopholus similis*), and E) lesion (*Pratylenchus* sp.) nematodes. Values on top of the columns in A indicate percentages of root-knot nematodes parasitized by *Pasteuria penetrans*. An * over a column in B indicates the presence of *Helicotylenchus multicinctus*.

(Cobb) Sher. However, *H. multicinctus* was the more prevalent species and was present in 63% of the soil samples, usually in farm sites with higher counts of spiral nematodes (Fig. 2B). Although *R. reniformis* was widely distributed, they were generally not detected or present at very low counts in most soils sampled on the Hawaii islands (Fig. 2C). On the other hand, although *Pratylenchus* was only found in two farms, population densities of this nematode reached 917/250cm^3 soil in one of these farms (Fig. 2E). Based on morphology, the only species of *Pratylenchus* found in these samples was *P. coffeae* Sher and Allen.

Plant-parasitic nematodes in roots

Banana root assays gave results similar to those found in soil assays (Fig. 3). *Meloidogyne* and *Helicotylenchus* were detected on 100 and 96.3% of the farms, respectively. However, root assays revealed higher percentages of farms infected by *R. similis* (48.2% in root vs 37% in soil) but lower percentages of farms infected by *R. reniformis* (63% in roots vs 92.6%) as compared to soil assay. Root assays detected similar number of farms infested with *H. multicinctus* (66.8% in roots vs 63% in soil) (Fig. 3B). Root assays indicated that *Helicotylenchus* occurred at higher abundance in banana fields than other plant-parasitic nematodes. While one of the farms reached approximately 1,700 *R. similis* per 10 g dry roots (Fig. 3D), 9 of the farms had *Helicotylenchus* spp. population densities with more than 1,700 per 10 g of dry roots (Fig. 3B). On the other hand, *Meloidogyne* sp. and *R. reniformis* were found in 2 and 1 farms, respectively, with more than 1,700/10 g dry root (Figs. 3A and 3C). All farms sampled on the island of Maui contained elevated counts of *H. multicinctus* (more than 5,000/10 g dry root weight). The greatest numbers were found in Keanae,

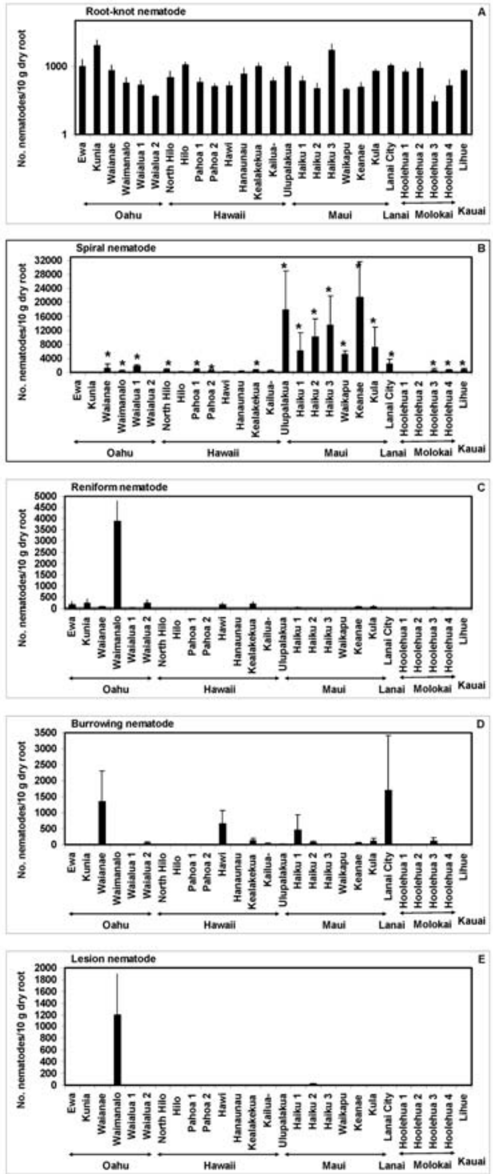

Fig. 3. Number of plant-parasitic nematodes extracted from fresh banana roots (equivalent to 10 g dry root weight) sampled from 27 banana farms distributed on five Hawaiian islands; A) root-knot, B) spiral, C) reniform, D) burrowing, and E) lesion nematodes An * over a column in B indicates the presence of *Helicotylenchus multicinctus*.

Maui where counts reached 21,556 /10 g dry root weight.

Omnivorous and predatory nematodes in soil

A total of 12 and 9 genera of omnivorous and predatory nematodes, respectively, were found during the survey (relatively abundant genera are presented in Table 2). The omnivorous nematodes encountered were *Aporcelaimellus, Axonchium, Dorylaimellus, Dorylaimoides, Dorylaimus, Ecumenicus, Hexactinolaimus, Mesodorylaimus, Paraxonchium, Prodorylaimus, Pungentus*, and *Timmus, Thornonema.* Predatory nematodes found included *Butlerius, Carcharolaimus, Cobbonchus, Discolaimus,* Diplogasteridae, *Mononchus, Nygolaimus, Tobrillus,* and *Tripyla.* Omnivorous and predatory nematodes were present in 88.9% and 59.3% of the farm sites (Table 2). Banana farms at the Hoolehua 1 site on the island of Molokai and the Haiku 2 site on the island of Maui contained the highest numbers of omnivorous and predatory nematodes, respectively (Table 2). Population densities of predatory nematodes were positively correlated with that of *Helicotylenchus* sp. (r = 0.23, P = 0.04, n = 84). Abundance of omnivorous nematodes were correlate with population densities of *Meloidogyne* spp. (r = 0.18, P = 0.09, n = 84). However the r value for both of these correlations is very low.

Nematode-trapping fungi (NTF)

Population densities of NTF were low in most farms (Tables 3 and 4). Seven species of NTF were detected; four of them are saprophytic whereas three are parasitic. Saprophytic NTF included *Dactylaria eudermata* Drechs. *Arthrobotrys oligospora* Fresenius, *Trichothecium flagrans* Dudd. and *A. pyriformis* (Juniper) Schenck, Kendr. & Pramer. They form adhesive nets to trap nematodes. Parasitic NTF included *Monacrosporium ellipsosporum* (Grove) Cooke and Dickson that formed adhesive knobs, and *Arthrobotrys brochopaga* (Drechs.) Schenk, Kendrick & Pramer and *A. dactyloides* Drechs. that formed constricting rings. The greatest abundance of saprophytic NTF was found in Pahoa 1 farm, whereas that of parasitic NTF was found in North Hilo farm. Numbers of parasitic and saprophytic NTF were correlated with the abundance of *Meloidogyne* spp. (r = 0.22, P = 0.08, n = 67) and *Helicotylenchus* sp. (r = 0.23, P = 0.06, n = 67). Although significant at the $P \leq 0.10$, the r values for both correlations are very low.

DISCUSSION

Nematode parasitism in banana plants is generally characterized by simultaneous infections of several species (Gowen *et al.*, 2005). Although several plant-parasitic nematodes were found during this survey, *Meloidogyne* spp. and *H. multicinctus,* followed by *R. reniformis,* were the most common nematodes inhabiting banana fields in Hawaii. Although similar results were obtained between soil and root assay for *Meloidogyne* spp., *H. multicinctus* and *P. coffeae,* slightly different results were obtained between these assays for *R. similis* and *R. reniformis.* Root assay can recover more endoparasitic nematodes such as *R. similis* and *P. coffeae,* whereas soil assay can recover more semiendoparasitic nematodes such as *R. reniformis* and endoparasitic nematodes that spend part of their life cycle in the soil such as *Meloidogyne* spp. and *H. multicinctus.* It is possible that higher recovery of *R. reniformis* from soil samples could be coming from occasional weeds close to banana plants, but in general, soil assay is more efficient way to detect *R. reniformis* (Wang *et al.*, 2001). This is because the root-parasitizing stages of *R. reniformis* are sedentary and could not be extracted by mist chamber that requite active movement of the nematodes. Despite the fact that our elutriation protocol can only

Table 3. Abundance of saprophytic nematode-trapping fungi (NTF) isolated from banana farms distributed on five islands in Hawaii.

Location	*Dactylaria eudermata*	*Arthrobotrys oligospora*	*Trichothecium flagrans*	*Arthrobotrys pyriformis*	Total saprophytic NTF[z]
Ewa	0.00[y]	0.00	0.00	0.00	0.00
Kunia	0.00	4.00 ± 2.32	0.00	0.00	4.00 ± 2.32
Waianae	1.32 ± 1.32	0.00	0.00	0.00	1.32 ± 1.32
Waimanalo	0.00	0.00	0.00	0.00	0.00
Wailua 1	0.00	0.00	0.00	0.00	0.00
North Hilo	0.00	2.98 ± 2.98	0.00	0.00	2.98 ± 2.98
Hilo	0.00	0.00	0.00	0.00	0.00
Pahoa 1	8.49 ± 8.49	0.00	8.51 ± 8.51	0.00	16.99 ± 8.50
Pahoa 2	0.00	0.00	0.00	0.00	0.00
Ulupalakua	0.00	5.95 ± 2.98	0.00	0.00	5.95 ± 2.98
Haiku 1	0.00	4.30 ± 2.58	0.00	0.00	4.30 ± 2.58
Haiku 2	0.00	7.36 ± 6.11	0.00	0.00	7.36 ± 6.11
Waikapu	0.00	0.00	0.00	5.18 ± 5.18	5.18 ± 5.18
Lanai City	5.95 ± 2.98	0.00	0.00	0.00	5.95 ± 2.98
Hoolehua 1	0.00	5.18 ± 5.18	0.00	0.00	5.18 ± 5.18
Hoolehua 2	0.00	0.00	0.00	0.00	0.00
Hoolehua 3	0.00	7.53 ± 4.00	0.00	0.00	7.53 ± 4.00
Hoolehua 4	0.00	5.18 ± 5.18	0.00	0.00	5.18 ± 5.18

[y]Means are average of 3 replications. Means are followed by ± standard error.
[z]Total saprophytic NTF was estimated by counting plates with the presence of any saprophytic NTF regardless of the species.

recover nematodes >10/250 cm^3 soil, higher recovery of *R. reniformis* was obtained from the soil assay than the root assay. Therefore, there is a need of performing both soil and root nematode assay in banana planting in Hawaiian soil ecosystem as *R. reniformis* is a commonly occurring nematode.

The distribution of different nematode species was generally not segregated by island. However, banana farms on Maui generally had higher populations of *H. multicinctus*. Most of the banana farms in Maui had been in production for many years (10 to 23 years) which may have allowed time for populations to build up. Several banana growers used boards and other props to prevent banana plants from toppling over but were unaware that nematodes were responsible for the poor root anchorage. Thus, continuously growing of nematode infected plants without administering management strategy may allow conditions for this nematode species to reach damaging levels.*Helicotylenchus* sp. (maximum of 21,556 per 10 g dry root), mainly composed of *H. multicinctus*, were extracted from banana roots in greater numbers than any other plant-parasitic nematode. Findings from this survey are similar to those reported by Brooks (2004) who conducted a similar nematode survey in banana fields in American Samoa,

Table 4. Abundance of parasitic nematode-trapping fungi (NTF) isolated from banana farms distributed on five islands in Hawaii.

Location	*Monacrosporium ellipsosporum*	*Arthrobotrys brochopaga*	*Arthrobotrys dactyloides*	Total parasitic NTF[z]
Ewa	0.00[y]	0.00	0.00	0.00
Kunia	9.24 ± 7.35	0.00	0.00	9.24 ± 7.35
Waianae	8.49 ± 8.49	0.00	0.00	8.49 ± 8.49
Waimanalo	0.00	0.00	0.00	0.00
Wailua 1	0.00	0.00	0.00	0.00
North Hilo	13.66 ± 7.41	1.32 ± 1.32	0.00	14.99 ± 8.50
Hilo	5.62 ± 1.65	0.00	2.53 ± 1.27	8.16 ± 2.59
Pahoa 1	1.32 ± 1.32	0.00	0.00	1.32 ± 1.32
Pahoa 2	0.00	0.00	0.00	0.00
Ulupalakua	0.00	0.00	0.00	0.00
Haiku 1	2.98 ± 2.98	0.00	0.00	2.98 ± 2.98
Haiku 2	0.99 ± 0.99	0.00	0.00	0.99 ± 0.99
Waikapu	1.32 ± 1.32	0.00	0.00	2.65 ± 2.65
Lanai City	7.28 ± 1.65	0.00	2.98 ± 2.98	10.25 ± 4.06
Hoolehua 1	2.65 ± 1.32	0.00	0.00	2.65 ± 1.32
Hoolehua 2	2.65 ± 1.32	0.00	0.00	2.65 ± 1.32
Hoolehua 3	0.00	3.97 ± 0	0.00	3.97 ± 0
Hoolehua 4	0.00	0.00	0.00	0.00

[y]Means are average of 3 replications. Means are followed by ± standard error.
[z]Total parasitic NTF was estimated by counting plates with the presence of any parasitic NTF regardless of the species.

another Pacific island. During that survey, Brooks (2004) found that *H. multicinctus* and *H. dihystera* population densities were much higher (5 times) than that of *R. similis* and two other species of *Pratylenchus.* Lower incidence and abundance of *R. similis* and *Pratylenchus* on banana planting in Hawaii as well as its neighboring Pacific islands such as American Samoa could be due to the source of introduction from planting materials to the geographic area. In the current survey, *R. similis,* which is considered the most important banana nematode pest worldwide, was found in greatest numbers on the island of Lanai at 1,706/10 g dry root. Damage thresholds are difficult to develop for banana plants because several factors may influence nematode populations on a perennial crop (Gowen, 1995). However, Gowen and Quénéhervé (2005) considered that 2,000 *R. similis*/100g fresh roots are a potential cause of yield loss in commercial cultivars worldwide. The level of *R. similis* in Lanai was well over this threshold level if we convert it to numbers per 100 g fresh root. We rely on root dry weight to avoid difference in root moisture content from farm to farm. While it is a common sampling procedure to sample nematodes from mature banana plants, Moens *et al.* (2001) reported that nematode densities and associated root necrosis and damage are higher in roots of banana suckers than in mother plants. This suggested that a greater abundance of nematodes might reach counts above the threshold level by the next crop harvest. McSorley and Parrado (1986) stated that *H. multicinctus* is the most serious nematode pest on banana where *R. similis* is absent. In addition, Ssango *et al.* (2004) demonstrated that numbers of *H. multicinctus* is indeed negatively correlated with banana bunch weight. Information on crop loss due to *H. multicinctus* per se is lacking possibly because banana plants are often infected by multiple pests concurrently.

Although *Meloidogyne* was found on all banana farms, *Pasteuria penetrans* was associated with this nematode in 26% of the farms surveyed and their infestation rate was positively correlated ($P < 0.05$) with the abundance of *Meloidogyne*. *Pasteuria penetrans* is an obligate, endospore-forming bacterial parasite of *Meloidogyne* spp. and has shown potential as an effective biological control agent against root-knot nematodes (Chen *et al.*, 1996; 1997). Chen et al. (1997) also reported that *P. penetrans* is a density dependent parasite. The Hoolehua site 1 on the island of Molokai had the highest counts (7,416/250 cm^3 soil) of *Meloidogyne* in the soil assay but only an intermediate infection level (543 *Meloidogyne*/10 g dry root) was detected from the root assay. It is possible that *P. penetrans* is keeping the *Meloidogyne* reproduction in check and thus preventing it from becoming a major nematode pest of bananas.

The banana crop profile for Hawaii listed *R. similis*, *Meloidogyne* spp. and *R. reniformis* as the top three nematode pests of banana, and *H. multicinctus* was not mentioned. In fact economic impacts of *R. reniformis* and *Meloidogyne* spp. on banana were not discriminately reported. This survey revealed that greater attention should be given to *H. multicinctus* which is a known contributor of yield loss in banana (Mukasa *et al.*, 2006). *Helicotylenchus mulcticinctus* was typically found in high numbers in farms that consisted of toppling banana plants. When plants within a mat (a cluster of banana plants or suckers originated from a single mother plant) start toppling, the chance that this mat will produce a harvestable bunch in the following cycle is reduced (Speijer *et al.*, 1999).

Omnivorous and predatory nematodes

Most surveys conducted to analyze nematode communities in banana or other perennial cropping systems focus mainly on plant-parasitic nematodes (Pinkerton *et al.*, 1999; Brook, 2004; Kumari *et al.*, 2005; Mukasa *et al.*, 2006). Omnivorous and predatory nematodes are potential natural enemies of plant-parasitic nematodes, although their potential in nematode suppression in banana agroecosystem has not been studied. The current study showed that the abundance of omnivorous nematodes correlated negatively with abundance of *Helicotylenchus* but positively with *Meloidogyne* sp. Omnivorous and predatory nematodes may have a greater opportunity to establish in perennial cropping systems as compared to annual systems where there may be continuous soil disturbances from plowing and other production practices (McSorley *et al.*, 2007; Sanchez-Moreno and Ferris, 2007). The banana agroecosystem offers one such opportunity. As expected, a diverse number of omnivorous and predatory nematodes were found in the soils of banana fields. Different field ages and cultural practices (Table 1) may have contributed to disparities among farms. Most farms that receive high input practices (except for Wailua 1 and Lanai) such as applying synthetic fertilizers, glyphosate and various types of fungicides (as described in Table 1) generally had lower abundance of omnivorous and predatory nematodes. Wailua 1 was a high input farm, but was not well attended for some time. Whereas farm in Lanai City use organic mulch around banana planting to avoid excessive weeds build up. The farm in Keanae did not receive organic amendments nor herbicide input, and was the least disturbed farm among those surveyed for more than 20 years. This farm site is also located in a high rainfall area where soil is naturally rich in microbial activities as reflected by the frequent encounter of earthworms during sampling. This is consistent with the relatively high numbers of both omnivorous and predatory nematodes found during the survey. Several farms surveyed that were certified as organic farms (e.g. Hanaunau, North Hilo, Hawi) or not certified as organic but practice organic farming (Hoolehua 1 and 2, and Haiku 2) had high counts of either omnivorous or predatory nematodes. However, dissimilarities in omnivorous and predatory nematode numbers among farms could also be in part due to high variation in soil types. For example, banana farms in Kailua-Kona and Ulupalakua (both are organic farms) were planted in areas with porous lava rocks. Although farmers at these locations avoided using synthetic fertilizer and herbicide, numbers of omnivorous and predatory nematodes were very low.

NTF

This study was not designed to determine the potential of NTF for suppressing plant-parasitic nematodes associated with banana, but a survey to document the abundance of NTF. NTF were recovered from 77.8% of the farms surveyed. We categorized NTF into two categories as suggested by Gray (1985). The saprophytic NTF (formed adhesive nets) are found in soil with low organic matter and low moisture due to their saprophytic nature (Gray, 1985). When nutrients or moisture condition improved, the saprophytic NTF are able to compete with other soil organisms by feeding on the expanding nematode population (Gray, 1985). In contrast, NTF that form rings and knobs are more common in soil with high organic matter and moisture (Gray, 1985). Parasitic NTF were most abundant in an organic farm located in North Hilo followed by a farm in Lanai City that frequently adding organic mulch or fertilizer to their banana. On the other hand, saprophytic NTF were most abundant in a conventional farm in Pahoa 1 that relied mostly on synthetic fertilizers.

This survey confirmed our assumption that potential natural enemies of plant-parasitic nematodes, including omnivorous and predatory nematodes, NTF and *P. penetrans*, are commonly found. It has been documented that chemical nematicides can negatively impact the fauna of predatory nematodes (Wang *et al.*, 2006) and nematode-trapping fungi (Wang *et al.*, 2003). Thus, any management practices developed to manage nematode problems in Hawaiian banana fields should be cautious of any ill effects on beneficial soil organisms.

Although plant-parasitic nematodes were collected in all the banana fields sampled, the full impact of these species on banana production remains unknown. The nematode species found during the survey are known to cause economic losses in other banana production areas of the world. However, until the impact of their presence on banana is quantified, farmers in Hawaii may choose to remain indifferent with regards to implementing management strategies to alleviate their presence. Specifically, a more concerted research effort is needed to help quantify their impact on banana quality and yield. Only then can we begin to convince growers about the extent of production lost attributable to their presence. Because of the importance of banana as a staple food and source of income for large and small scale farmers, we are hopeful that the information obtained during the survey will help bring greater attention to specific nematode pests in the soils of Hawaii banana fields and highlight the need for greater extension and research activity in this area.

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