SEASONAL VARIATION OF NEMATODE ASSEMBLAGES AND DIVERSITY ON SELECTED SOIL GROUPS IN KENYA: VERTISOLS, CAMBISOLS AND ARENOSOLS †

[VARIACIONES ESTACIONALES DEL ENSAMBLAJE DE NEMATODOS Y DIVERSIDAD EN GRUPO DE SUELOS SELECCIONADOS EN KENIA: VERTISOLES, CAMBISOLES Y ARENOSOLES]

A.K. Thuo[1], G.N. Karuku[2*], J.W. Kimenju[1], G.M. Kariuki[3], P. K. Wendot[3] and H. Melakeberhan[4]

[1]Department of Plant Science and Crop Protection, University of Nairobi, P.O Box 30197-00100, G.P.O, Nairobi, Kenya.
[2]Department of Land Resource and Agricultural Technology, University of Nairobi, P.O Box 30197-00100, G.P.O, Nairobi, Kenya. emails: karuku_g@yahoo.com or gmoe54321@gmail.com or gmoe@uonbi.ac.ke.
[3]Kenyatta University, Department of Agricultural Science and Technology, P.O. Box 43844-00100 Nairobi, Kenya.
[4]Agricultural Nematology Laboratory, Department of Horticulture, Michigan State University (MSU), East Lansing, MI 48824, USA.
**Corresponding author*

SUMMARY

Background. Soil health assessment has been based on narrow disciplinary approaches that overlook the multiple and interacting biological processes that are the basis of sustainable crop productivity. **Objective**. Determine the influence of seasonal variations in nematode assemblages in different soil groups, sites and disturbance levels as an indicator of soil health. **Methodology**. Sampling was done in areas characterized by small scale subsistence agriculture in Kenyan Northern sites and Southern sites over three distinct seasons. The sampling points included disturbed (tilled) and the adjoining undisturbed (untilled) soils within three soil groups, namely Vertisols, Cambisols and Arenosols. Nematodes were extracted using the centrifugal-floatation technique, enumerated and assigned to their respective trophic groups. **Results.** Total nematode abundance in the three seasons varied significantly ($p \leq 0.05$) with a mean of 68, 93 and 52 nematodes in 200 cm^3 of soil in seasons I, II and III, respectively. Nematodes abundance in the undisturbed soils was significantly higher (98) compared to the disturbed soils (62) nematodes per 200 cm^3). Mean abundance of nematodes was highest in Cambisols. In addition, nematode abundances, in all trophic levels across the three seasons, were significantly higher ($p \leq 0.05$) in the northern compared to the southern sites. Bacterivores (28%) had the highest percentage frequency of detection followed by herbivores (27%) and fungivores (21%) while omnivores (11%) had the least. **Implications**. Nematode communities do respond variably to different soil groups and seasonal changes. **Conclusion.** Nematodes can therefore be utilized as viable bio-indicators of soil health and quality.

Key words: Soil health; soil groups; disturbance level; nematode assemblages.

RESUMEN

Antecedentes. La evaluación de la salud del suelo se ha basado en enfoques disciplinarios que pasan por alto los procesos biológicos múltiples e interactivos que son la base de la productividad sostenible de los cultivos. **Objetivo.** Determinar la influencia de las variaciones estacionales en los conjuntos de nematodos en diferentes grupos de suelos, sitios y niveles de perturbación como un indicador de la salud del suelo. **Metodología.** El muestreo se realizó en áreas caracterizadas por la agricultura de subsistencia a pequeña escala en los sitios del norte de Kenia y los sitios del sur durante tres estaciones distintas. Los puntos de muestreo incluyeron suelos perturbados (labranza) y adyacentes no perturbados (sin labranza) dentro de tres grupos de suelos, Vertisoles, Cambisoles y Arenosoles. Los nematodos fueron extraídos usando la técnica de flotación centrífuga, enumerados y asignados a sus respectivos grupos tróficos. **Resultados.** La abundancia total de nematodos en las tres estaciones varió significativamente ($p \leq 0.05$) con una media de 68, 93 y 52 nematodos en 200 cm^3 de suelo en las estaciones I, II y III, respectivamente. La abundancia de nematodos en los suelos no perturbados fue significativamente mayor (98) en comparación con los suelos perturbados (62) (nematodos por 200 cm^3). La abundancia media de nematodos fue mayor en los cambisoles. Además, la abundancia de nematodos, en todos los niveles tróficos en las tres estaciones, fue significativamente

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mayor ($p \leq 0.05$) en los sitios del norte en comparación con los del sur. Los bacterívoros (28%) tuvieron el porcentaje de frecuencia de detección más alto, seguidos por los herbívoros (27%) y los fungívoros (21%), mientras que los omnívoros (11%) tuvieron el menor. Trascendencia. Las comunidades de nematodos responden de manera variable a diferentes grupos de suelos y cambios estacionales. Conclusión. Por lo tanto, los nematodos pueden utilizarse como bioindicadores viables de la salud y la calidad del suelo.
Palabras clave: salud del suelo; grupos de suelos; nivel de perturbación; ensamblajes de nematodos.

INTRODUCTION

A number of pertinent issues arise pertaining to the optimal utilization of Kenya's agricultural land, which include; the impacts of land use change on soil degradation, biological diversity and support of human needs through available biological systems (Kimenju *et al.,* 2009). Increase in anthropogenic activities needs to be addressed with the aim of bridging this deficit in available arable land (Kaihura and Stocking, 2003; Maitima *et al.*, 2004a). As such, soil degradation in Kenya needs to be addressed to help realize the country's full agricultural potential. An organism occurring either singly or in a community set up, which can reliably depict the condition of an ecosystem, is termed as a bio-indicator (Rosa and Nahum, 2012). There exists some soil properties, chemical and physical, that are responsive to farm management though some are discrete in their response (Zhang *et al.,* 2012a; Mendoza *et al.,* 2008) and thus inadequate in detecting potential biological fluctuations in an ecosystem (Zhang *et al.*,2012b; Suter II, 2001). Soil health which is best used to refer to the condition of a soil as a result of its management can be investigated by application of these nematode communities as they form a key resource that is yet to be fully tapped into (Andre *et al*., 1994, 2001; Wheeler *et al*., 2004; Science Editors, 2004). Nematodes are known to respond differently to environmental fluctuations over time in their diversity and abundance (Yeates *et al*., 2009).

Most studies have overlooked the need to investigate nematode assemblage in different agro-ecosystems over durations (Friedel and Gabel, 2001; Martini *et al.,* 2004; Monokrousos *et al*., 2006; Maria *et al*., 2007). Baseline studies conducted by Karuri *et al*. (2010) recommend the need to examine other important variables like seasons and types of crops in a farm, and in addition assessment of known soil physical and chemical parameters that influence nematode assemblage (Mendoza *et al.,* 2008). Soil groups have variable characteristics and influences according to past studies (Ferris and Matute, 2003; Sánchez –Moreno *et al.,* 2006; Sánchez –Moreno *et al.,* 2008) due to their inherent chemical, physical and biological components (Van Diepeningen *et al.,* 2006). Increase or decrease in nematode assemblages can be utilized in their descriptive aspects (ecosystem change attributes) through body mass to determine effect of soil disturbance levels (Fiscus and Neher, 2002; Ferris, 2010; Mills and Adl, 2011). Wardle (1995) observed that nematode assemblages respond differently to tillage practices where large and smaller nematodes decrease and increase respectively to continued intensive cultivation (DuPont *et al.,* 200; Zhang *et al.,* 2012). In addition, nematodes in natural ecosystems influence spatial and temporal diversity of plant-associated communities both above and below-ground (De Deyn and Van der Putten, 2005).

Nematode diversity indices have therefore been formulated to assess different ecosystems (Neher and Darby, 2009). Abundance of nematodes in an ecosystem is referred to as species richness (Rosa and Nahum, 2012) and comparative contribution made by an individual species' of the total number of organisms present in a given community is synonymously referred to as the Shannon-Weaver Index [H'] (Shannon and Weaver, 1949). These indices are not only used in measuring ecosystem changes in their absolute terms, but also assess the nematode genera loads in relation to the entire ecosystem population (Rosa and Nahum, 2012). An ecosystem is said to be thriving if its diversity is high with numerous taxa since many trophic levels that are complementary to each other are formed (Metting and Blaine, 1993). This study aimed at determining the effect of soil groups (Vertisols, Cambisols and Arenosols), disturbance levels and seasonal variations on nematode assemblages in different sites.

MATERIALS AND METHODS

Site selection and sampling

The study was conducted in Murang'a, Machakos and Makueni Counties of Kenya. A total of 576 soil samples were collected over three consecutive seasons, namely, cold/dry season (August 2012), warm/rainy season II (December 2012) and hot/dry season III (March 2013) in Makuyu to the North and Machakos and Makueni to the South of the Equator as in Table 1. Three soil groups; Vertisols, Cambisols and Arenosols were chosen and the sampling sites included tilled and untilled soil in each soil group. Classification of soil groups was based on the soil classification system (WRB,

2014) and verification of the sampling points was done through the global positioning system (GPS) coordinate system. Sampling bags and flags were labeled with numeric codes prior to sampling then the pre-labeled flags were placed in a systematic order at individual sampling hills. GPS co-ordinates and soil temperature were then recorded using a Garmin GPS 60 receiver and a soil thermometer, respectively, at each sampling points and a composite soil sample of 1kg collected using a 600 cm^3 soil auger at 20 cm depth. The samples were placed in zip-lock plastic bags, stored in cool boxes and then transported to the laboratory. A total of 192 samples were collected during each season. The GPS coordinates were used to trace the exact sampling points in subsequent samplings in each season.

Sample processing and identification of nematodes

Laboratory analyses involved thorough mixing of each samples, sieving through a 4 mm mesh into a holding pan and partitioning into sub-samples for nematode analysis and storage. Nematodes were extracted from 200 cm^3 soil sub-sample using the centrifugal-floatation method described by Jenkins (1964). The sample was suspended in 5 litres of tap-water in a 20 litre-bucket and stirred by hand for 10 seconds to release the nematodes from the soil. The slurry of water was then decanted through a 2 mm mesh sieve into a second bucket and the filtrate ran through a series of fine aperture sieves of 250, 150 and then 38 µm mesh. The residue collected on the 38 µm aperture sieve was backwashed and concentrated to form a 30 ml volume that was transferred into 50 ml-centrifuge tubes. This suspension (of water and soil) underwent the first spin by centrifuging at 1750 rpm for 7 minutes. The supernatant formed after the first spin was discarded and the pellet was re-suspended by topping up to the 30 ml mark using sucrose solution (450 g/l water). A second spin was conducted at 1750 rpm for 3 minutes for each individual sample. The supernatant formed after the second spin was poured into excess water to lower the high osmotic pressure in the sugar suspension, and then concentrated using the 38 µm mesh sieve to make a 3 ml nematode suspension. Nematodes in each sample were then killed and immobilized (fixed) using a modification of the technique described by Hooper (1986) by adding 3 ml of hot (70^0C) double Triethanolamine Formaldehyde (TAF) solution (14 ml 40% formalin: 4 ml tri-ethanolamine: 91 ml distilled water) to make a 6 ml final fixed nematode suspension.

Table 1. Monthly average temperature and rainfall for Murang'a, Machakos and Makueni counties from April 2012 to April 2013.

Year	Month	Muranga (Makuyu)		Machakos (Makutano)		Makueni (Sultan Hamud)	
		Average (ºC)	Rainfall (mm)	Average (ºC)	Rainfall (mm)	Average (ºC)	Rainfall (mm)
2012	April	21	243	21	243	24	116
	May	20	193	20	193	23	37
	June	18	41	18	41	21	12
	July	18	13	18	13	20	13
	August*	**19**	**4**	**19**	**4**	**21**	**14**
	September	20	35	20	35	23	9
	October	21	57	20	35	24	57
	November	21	43	21	43	24	133
	December*	**20**	**119**	**20**	**119**	**23**	**164**
2013	January	20	42	20	42	23	88
	February	21	1	20	42	24	14
	March*	**21**	**82**	**21**	**82**	**25**	**171**
	April	21	137	21	137	24	182

Weather data obtained for rainfall and temperature through Nairobi University Kabete campus synoptic station for Makuyu, Makutano and Sultan Hamud areas. Sampling took place during the months followed by (*) in the periods of August (Sn1/cold & dry), December (Sn2/warm & rainy) and in March (Sn3/hot & dry).

The processed samples were then stored at 20^0C to allow the fixed nematodes in them to adequately settle at the bottom of the vial after which enumeration and identification was done in a microscope-mounted nematode counting chamber. Nematode identification was based on morphological and morphometric features observed under a compound microscope (Motic B SERIES) at ×400-000 magnification. The nematodes were identified up to genera level using standard nematode identification keys that included, The Pictorial Key to Genera of Plant Parasitic Nematodes (Mai *et al.,* 1968), C.I.H. Description of Plant-parasitic Nematodes and the 'Interactive Diagnostic Key to Plant-parasitic and free-living nematodes which is available from their identification website (http://nematode.unl.edu/konzlistbutt.htm).
Nematode quantification was achieved by tallying the nematode three times by taking a 1 ml aliquot each time. The mean count was used to calculate the total number of nematodes in the original 3 ml as a representative count for each soil sample. Unidentifiable nematodes were not included in the enumeration while all nematodes identified were enumerated then grouped into trophic levels of herbivore, fungivore, bacteriovore, omnivore and predator using the methods described by Yeates *et al.* (1993) and Bongers and Bongers (1998). The total number of nematodes in each trophic group from the aliquot of 200 cm^3 soil was expressed as abundance and the percentage of each trophic group within the community was expressed as percentage frequency of occurrence.

Statistical analyses

Three nematode diversity indices were calculated, namely, species richness (N_0= number of species present) using the formula described by Hill (1973), Shannon diversity index ($H' = -\Sigma pi\ (ln\ Pi)$), where *Pi* is the proportion of taxa in the total population (Shannon, 1949) and species evenness ($J' = H'/ln(s)$, where *s* is the number of individual species present (Pielou, 1966) were computed. N_0 was used to compare the number of all species within the community. Shannon diversity index (H′) was used to investigate for rare and sensitive genera, and J′ was used to compare homogeneity of the genera in the systems. Data was subjected to a two-way analysis of variance (ANOVA) to investigate the effect and interactions between the different seasons, soil groups, sampling sites and disturbance levels. General Linear Model (PROC GLM) procedures in SAS version 9.2 (SAS Institute Inc. Cary, NC) were used to analyze and distinguish nematode abundance and frequency in the seasons, soil groups, sites and disturbance levels. Significantly different means ($p \leq 0.05$) were separated using the Tukey-Kramer comparison test.

RESULTS

Total nematode abundance in different seasons, soil groups, sites and disturbance levels

The abundance of nematodes differed significantly ($p \leq 0.05$) between seasons, sites, soil groups and disturbance levels (Table 2). The nematode abundance increased significantly ($p \leq 0.05$) from season I to season II and subsequently decreased from season II to season III. The Northern sites had a significantly higher ($p \leq 0.05$) nematode abundance of 88 nematodes in 200 cm^3 of soil compared to the Southern sites (54). Cambisols had a significantly high ($p \leq 0.05$) nematode abundance whereas Arenosols had the lowest. Undisturbed (natural) soils had a significantly higher nematode abundance unlike the disturbed (tilled) soils. This could probably be due to differences in organic matter content and different nutrition levels in the soils. Cambisols tend to have more organic carbon compared to Arenosols hence the marked difference. Again, the nutrient content such as TN, P and K were higher in Cambisols as well as in undisturbed soils hence better nutrition that gave rise to higher nematodes numbers. Hu & Qi (2010) reported similar findings where total abundance of nematode was positively correlated with the content of soil organic matter, TN, available P and K.

Arenosols had the highest significant omnivore abundances than both the Vertisols and Cambisols, respectively while both Cambisols and Vertisols had significantly higher herbivore abundances than Arenosols (Table 3). The mean abundance of omnivores and fungivores was highest in season 2 and lowest in season 1 while the mean abundance of predators and bacterivores was highest in season 2 but lowest in season 3. Mean abundance of all trophic groups was significantly highest in the northern sites than in the southern sites. Natural soils had also significantly higher omnivore, predator, bacterivore and herbivore abundances than the tilled soils.

Influence of site conditions on abundance of different nematode feeding groups

The abundance of omnivores differed significantly ($p \leq 0.05$) across the three seasons in both the northern and southern sites (Table 4). Omnivores, predators, herbivores and bacterivores were significantly abundant ($P \leq 0.05$) in the undisturbed compared to the tilled soils in the Southern sites. Predators had a significantly different abundance

across the seasons, soil groups and disturbance levels in the North with high abundances being observed in season II, undisturbed sites and in Cambisols soil group (5.6, 6.2 and 4.8 nematodes/ 200 cm^3 soil, respectively. The predator abundance in the southern region was significantly different between the natural and tilled soils but no significant differences were observed amongst seasons and soil groups. The abundance of bacterivores differed significantly among seasons and soil groups in all regions. The natural soils in the North had a relatively higher but insignificant bacterivore abundance compared to tilled soils. In the southern region, significantly higher bacterivore abundance was observed in season I compared to seasons II & III of 70, 34 and 38 nematodes/200 cm^3 soil, respectively. In the northern region, Cambisols and Arenosols had significantly higher mean bacterivore abundances of 90 and 102 nematodes/200 cm^3 soil, respectively compared to 60 nematodes/200 cm^3 soil for Vertisols. This different from the southern region where both Vertisols and Cambisols had significantly higher bacterivore abundances of 55.7 and 47.8 nematodes/200 cm^3 soil, respectively compared to 34 nematodes/200 cm^3 soil in Arenosols. Significant differences were observed in fungivore abundance across the seasons and soil groups in both sites. In the north, high fungivore abundances of 26 nematodes/200 cm^3 soil were observed in season II, that were significantly different compared to seasons I and II at 7 and 9 nematodes/200 cm^3 soil, respectively and which were not significantly different from each other. The highest mean fungivore abundance in the south were observed in season II and III at 11 and 10 nematodes/200 cm^3 soil, respectively and which were significantly different compared to season I. The soil groups in both sites had significantly different mean fungivore abundance with the highest mean being observed in Arenosols at 16 nematodes/200 cm^3 soil in the north compared to the abundance of 13 and 10 nematodes/200 cm^3 soil, respectively in the south where Vertisols and Cambisols had significantly highest fungivore abundance compared to a low of 4.1 nematodes/200 cm^3 soil observed in the Arenosols. The natural and tilled soils had no significant differences in fungivore abundance in both sites.

Herbivores were significantly different in abundance across the seasons and soil groups in both natural and tilled soils. Data indicated that mean herbivore abundance in the northern region was significantly higher in season II at 54 nematodes/200 cm^3 soil compared to seasons I & III at 33 and 39 nematodes/200 cm^3 soil, respectively. When compared to the southern region, no significant difference was observed across the seasons. However, both regions had significantly different herbivore abundance between the natural and tilled soils with the natural having more herbivores in both regions at 101 and 49 nematodes/200 cm^3 soil, respectively. Vertisols and Cambisols had significantly higher herbivore abundance compared to the Arenosols which had low mean herbivore abundance in both regions.

Table 2. Total nematode abundances in different seasons, soil groups, sites and disturbance levels.

Variable		P Value	Mean
Seasons (n=192)	Season I	< 0.0001	68.38[b]
	Season II		93.01[a]
	Season III		51.61[c]
Sites (n=288)	North	< 0.0001	88.23[a]
	South		53.77[b]
Soil Groups (n=192)	Vertisols	0.003	65.75[b]
	Cambisols		82.07[a]
	Arenosols		65.17[b]
Disturbance (n=144)	Natural	< 0.0001	97.74[a]
	Tilled		62.08[b]

Means followed by different superscripts along a column between different seasons, sites, soil groups and disturbance levels indicate significantly different means at $P \leq 0.05$ where n= sample size.

Seasonal abundance of different nematode feeding groups

Significant differences ($P \leq 0.05$) were observed in seasonal abundance of nematode feeding groups across soil groups and seasons in both natural and tilled soils as indicated in Table 5. Mean omnivore abundance was highest in Arenosols in season I & III at 3 and 4 nematodes/200 cm^3 of soil, respectively. This was significantly higher than omnivore abundance in Vertisols and Cambisols in the two seasons. In season II, a high mean omnivore abundance of 7 nematodes/200 cm^3 soil was observed in Vertisols and was significantly higher than in Cambisols and Arenosols. Between the two sites, significant differences ($p \leq 0.05$) in omnivore abundance were observed in the first two seasons unlike season III. The natural landscape generally had significantly higher mean omnivore abundance in all three seasons compared to the tilled landscape where low abundances were observed. Predators showed significant differences across the soil groups only in season II where Cambisols had the highest mean abundance of 4 nematodes/200 cm^3 soil. Across the

sites, significant differences in mean predator abundance was observed only in season I & II where the northern sites had a higher predator abundance in both seasons (4.2 and 5.6 nematodes/200 cm^3 soil, respectively) compared to season III with slightly higher mean predator abundance of 2.8 nematodes/200 cm^3 soil was observed in the south. However, there was no significant difference in mean predator abundance in season III. The untilled soils had significantly high predator abundance in all seasons compared to the tilled soils.

Significant differences were observed in bacterivore abundance in season I and II across the soil groups. In season I, the highest mean bacterivore abundance was observed in Cambisols (95 nematodes/200 cm^3 soil) and in season II, Arenosols had the highest abundance (81.4 nematodes/200 cm^3 soil) compared to other soil groups which had lower bacterivore means. Furthermore, significant differences in bacterivore abundances between the untilled and tilled soils was observed in season II and III with a high bacterivore abundance in the natural (122 and 61 nematodes/200 cm^3 soil, respectively) than the disturbed ecosystems which had 58.6 and 36.9 nematodes/200 cm^3 soil, respectively. The abundance of fungivores was significantly different across the soil groups in season I and III where mean fungivore abundances in Cambisols and Vertisols were 8 and 14 nematodes/200 cm^3 soil, respectively. Across the two sites, the north had significantly ($p \leq 0.05$) higher fungivore abundance in season I and II. Subsequently, significant differences in mean fungivore abundance was only observed in season II between the natural and tilled soils whereby more fungivores were observed in the untilled soils than the tilled. Herbivore abundance was significantly ($p \leq 0.05$) different across the soil groups in all seasons. Cambisols had significantly ($p \leq 0.05$) higher herbivore abundance in season I and III. In season II, significantly ($p \leq 0.05$) higher mean herbivore abundance was observed in Vertisols and Cambisols at 52.2 and 54.0 nematodes /200 cm^3 soil, respectively compared to Arenosols 23.7 nematodes /200 cm^3 soil). Between the two sites, herbivores differed significantly only in season II and III with the north generally having higher herbivore abundance (53.5 and 38.7 nematodes/200 cm^3 soil, respectively) than the south (30.8 and 27.2 nematodes/200 cm^3 soil, respectively). Furthermore, herbivores were significantly higher in the natural compared to the tilled landscape across the seasons.

Table 3. Mean Interaction effects between seasons, disturbance levels and soil groups on nematodes feeding groups in the Northern and Southern Sites.

Variables		OM	PD	BV	FV	HV
Soil Groups (n = 192)	Vertisol	3.6^{ab}	3.3^{a}	57.8^{a}	10.9^{a}	39.9^{a}
	Cambisols	3.3^{b}	3.6^{a}	65.6^{a}	10.7^{a}	48.7^{a}
	Arenosols	4.1^{a}	3.2^{a}	58.6^{a}	8.4^{a}	22.1^{b}
	Mean	3.7	3.4	60.7	10	36.9
Seasons (n = 192)	Season I	2.4^{c}	3.6^{a}	75.2^{a}	5.9^{c}	32.7^{a}
	Season II	6.1^{a}	3.8^{a}	70.5^{a}	16.9^{a}	40.7^{a}
	Season III	3.2^{b}	2.8^{b}	41.8^{b}	9.6^{b}	32.4^{a}
	Mean	3.9	10.2	62.5	10.8	35.3
Sites (n = 288)	North	4.5^{a}	4.1^{a}	82.0^{a}	12.2^{a}	40.8^{a}
	South	2.9^{b}	2.8^{b}	44.7^{b}	8.0^{b}	30.1^{b}
	Mean	3.7	3.5	63.4	10.1	35.5
Disturbance (n = 144)	Natural	7.1^{a}	5.9^{a}	86.8^{a}	10.0^{a}	70.5^{a}
	Tilled	2.9^{b}	2.7^{b}	53.7^{b}	9.9^{a}	27.7^{b}
	Mean	5	4.3	70.3	9.95	49.1

Means followed by different superscripts in each trophic group along a column between different seasons, sites, soil groups and disturbance levels indicate significantly different means at $P \leq 0.05$ where **n**= sample size. (**HV**: herbivores, **BV**: bacterivores, **FV**: fungivores, **PD**: predators, **OM**: omnivores).

Frequencies of occurrence of total nematodes across the seasons

Seasonal percentage frequencies of occurrence of nematodes are presented in Figure 1. There was a general increase of omnivores from season I to II and a decrease in season III at 20%, 64% and 35%, respectively. A similar trend was observed for predators at 44%, 46% and 32%, respectively, fungivores at 52%, 85% and 76% and herbivores at 91%, 94% and 92%, respectively in the three seasons. However, the bacterivores showed a different trend where their frequency first decreased in season 1 to 98% and tended to a constant in seasons II and III at 96%.

Occurrence of different nematode feeding groups

The occurrences of different nematode feeding groups are presented in Figure 2. Bacterivores and herbivores had higher frequency of occurrence at 28% compared to the other groups of predators and omnivores with significantly lower frequencies of occurrence at 12% and 11%, respectively.

Among the soil groups, significant frequency differences ($P \leq 0.05$) were observed between omnivores and fungivores with Arenosols having a higher omnivore frequency. Subsequently, fungivore frequencies were highest in Cambisols (Table 6). However, between the seasons, significant differences ($P \leq 0.05$) in nematode frequencies were observed in omnivores, predators and fungivores where all these feeding groups showed the highest frequencies in season II. Furthermore, abundance of omnivore, predator, fungivore and herbivore feeding groups in the two sites were significantly different apart from bacterivores. Comparing the two landscapes, it was observed that frequencies of omnivore, predators, bacterivores and herbivores were significantly higher ($P \leq 0.05$) in the natural untilled soils compared to the disturbed soils. However, fungivore frequencies showed no significant differences ($P \leq 0.05$) between the two landscapes.

Diversity of Nematodes

The genus richness in both Vertisols and Cambisols was significantly different ($P \leq 0.05$) in all the three seasons where it increased from season I to II followed by a decrease in season III (Table 7). Shannon diversity and genus richness indices in the natural untilled soils differed significantly ($P \leq 0.05$) in all the three seasons where both indices were highest in season II followed by season III, respectively. Shannon diversity and genus richness indices in the northern sites also varied significantly ($P \leq 0.05$) over three seasons. The Shannon diversity index was high in season II at 1.9 followed by season III at 1.7. In addition, genus richness was significantly higher ($P \leq 0.05$) in season II at 11.7 followed by season III at 9.5. Genus evenness in the soil groups, disturbance levels and different sites were not significantly affected by the seasons**.**

DISCUSSION

Nematode abundance

The study has established that total nematode abundance varies significantly based on soil groups, across seasons and sites. The natural soils had the greatest abundance of nematodes. A high abundance of nematode populations may be related to soil fertility coupled with high net primary productivity (Kergunteuil *et al*., 2016). Thus, higher nematode population densities in the non-tilled compared to the tilled soils indicates possible favorable conditions for nematodes (Table 3). Nematode populations increased from the cold/dry season to the warm/rainy season and decreased in the hot/dry season. These population dynamics could have been influenced by temperature and moisture changes in the soil and the inherent difference in reproductive activity of various soil nematodes during the study period. Temperature shifts may kill or cause infertility in certain nematode species, which may skew diversity estimates of nematode assemblages (Takemoto *et al*., 2010). Nematode abundance may have been minimal in season III in both sites and ecosystems because some nematodes are known to enter an inactive stage of anhydrobiosis brought about by unfavorable environmental conditions such as low soil moisture (Treonis and Wall, 2005). This inactive stage enables nematodes to survive until favorable conditions of moisture and temperature resume (Freckman *et al*., 1979; Treonis and Wall, 2005). Water indirectly stimulates primary production and determines the carbon contribution to the ecosystem that affects microbial diversity (Dutta and Dutta, 2016). Moisture availability acts as a trigger for changes in food resources such as bacteria, fungi and plants for the nematodes in different trophic levels. However, this factor has varying effects in that water availability regulates the development and germination of spores and the growth rate of the mycelia of saprophytic fungi (Le Pioufle and Declerck, 2018; Trey *et al*., 1999).

In this study, total nematode abundances and diversity were higher in the Northern than in the Southern sites where bacterivores were the dominant group in the North. Also the nematode abundance was higher in undisturbed compared to the disturbed/tilled soils. Neher *et al*. (2004) suggested that fluctuation of nematodes during vegetation shifts is influenced by

several biotic and abiotic factors such as temperature, annual rainfall, type of soil and plants, organic substances, microflora and management practices. Pei-Pei Xue *et al*. (2018) found that soil properties contributed the most to the microbial distribution, while other environmental factors (e.g., temperature, elevation) showed lesser impact. Also, it indicated that agricultural activities reduced the variation of the microbial communities, though its influence was local and much less than the overall influence of soil properties. Omnivore and predatory nematodes have been found to be more abundant in recently abandoned fallow fields than in cultivated or semi-natural and meadow lands in previous studies (Hanel, 2003). The results of this study indicate that the varied total nematode abundance based on soil disturbance levels depends on the assemblage composition meaning that no general patterns can be drawn without analyzing the taxa and functional group responses. For example, Liphadzi *et al.* (2005) reported general increase in nematode abundance in tilled plots due to the predominance of fungal feeders (up to 90%) in the assemblages he studied. According to Dabur and Bajaj (2002), the populations of omnivores were significantly higher ($P \leq 0.05$) in undisturbed than in tilled fields. A study by Lenz and Eisenbeis (2000) showed total nematode density was reduced after the first tillage, with bacterivores dominating in tilled plots and herbivores being more abundant in no-tilled plots. On the contrary, a study by Wang *et al*. (2004) show that 25 years of tillage did not strongly affect predators but reduced numbers of fungivores.

Frequency of occurrence of nematodes

This study demonstrated that the frequency of occurrence of herbivores increased from season I through to season III. This can be attributed to the increasing soil humidity from season I to II, and in addition to new root resources availability that favor growth, reproduction and colonization by herbivores. This might have led to the herbivores being the second most dominant trophic group in the study in all soil types both in tilled and untilled. This is in agreement with results by Yeates and Bird (1994). In addition, Freckman and Ettema (1993) found the bacterial feeders to be dominant in annual grass as well as perennial cropping systems, followed by herbivores and fungivores, thus agreeing with the findings of this study. The seasonal population variations pattern suggests that the ecological conditions, particularly their interaction with various soil variables is unfavorable for the multiplication and development of the nematodes in season III while season I provides a slightly favorable condition and season II the ideal condition. Similar observations with regard to the population of parasitic nematodes (*Hoplolaimus* and *Helicotylenchus* spp.) in citrus rhizosphere were made by Siddiqui (1963) who attributed the decline in number to the unfavorable soil temperature. Furthermore, an increase in nematode numbers can be attributed to maximum nematode metabolism, production and energy turnover which probably occurred during the period when the range of soil moisture and temperature were optimal for nematode activity. Nematode frequency of occurrence reached a maximum in each soil group due to the high frequency and abundance of bacteriovorous nematodes. This is in agreement with findings by Vanette and Ferris (1997) who observed an increase of bacterivores in the soil. Bacterivores ingest bacteria by sucking them up from suspensions.

A large number of plants lose some of their leaves on a seasonal basis. This detritus enriches the soil with available organic matter leading to microbial community build-up (Berg and Steinberger, 2008) followed by an increase in fungivore and bacteriovore nematodes.

Omnivorous nematodes feed on bacteria and fungi in addition to other components of the faunal community. A decrease in occurrence of bacterial or fungal communities would naturally result in a decline in bacterivores and fungivores, while omnivores can feed on alternative food sources (Neher, 2010).

Nematode diversity

All nematode diversity indices except genus evenness were significantly different ($P \leq 0.05$) based on seasons, soil groups and location and soil disturbance levels. The nematode diversity was highest in the Northern compared to the Southern sites. This was attributed to the environmental and climatic differences between the two sites and the duration at which land had been under cultivation (Todd *et al*., 2006). High nematode population densities and high diversity occur in almost all soils but changes in nematode diversity shown by values of the Shannon-Weiner index (H) often reflect environmental differences (Yeates and Bongers, 1999). The variability observed in genus diversities between the two sites (North and South) indicate the soil groups did not have much impact on nematode diversity with regard to the Shannon-Weiner index. Effects of disturbance on soil fauna are inferred by nematode abundance and diversity in agricultural fields (Wardle, 1995; Ettema, 1998; Porazinka *et al*., 1999; Ekschmitt *et al*., 2003). Data from the study show untilled soils had a higher nematode

Table 4. Interaction effects between seasons, disturbance levels and soil groups on nematodes feeding groups in the Northern and Southern Sites.

Seasons/ Disturbance Levels/Soil groups	OM			PD			BV			FV			HV		
	North	**South**	Mean	**North**	**South**	Mean	**North**	**South**	Mean	**North**	**South**	Mean	**North**	**South**	Mean
Season I	2.6^{b}	2.2^{c}	2.4^{c}	4.2^{b}	3.0	3.6^{a}	81.0^{b}	69.9^{a}	75.5^{a}	7.3^{b}	4.7^{b}	6.0^{c}	32.8^{b}	32.7	32.8
Season II	9.3^{a}	3.9^{a}	6.6^{a}	5.6^{a}	2.5	4.1^{a}	145.1^{a}	34.0^{b}	89.6^{a}	25.6^{a}	11.1^{a}	18.4^{a}	53.5^{a}	30.8	42.2
Season III	3.5^{b}	2.9^{b}	3.2^{b}	2.7^{c}	2.8	2.8^{b}	46.7^{c}	37.5^{b}	42.1^{b}	9.4^{b}	9.7^{a}	9.6^{b}	38.7^{ab}	27.2	32.9
Mean	5.1	3.3		4.2	2.8		90.9	47.1		14.1	8.5		41.7	30.2	
Natural	9.5^{a}	5.2^{a}	7.4^{a}	6.2^{a}	5.6^{a}	5.9a	85.0^{a}	88.6^{a}	86.8^{a}	11.7	8.5	10.1	100.9^{a}	49.2^{a}	75.1^{a}
Tilled	3.4^{b}	2.4^{b}	2.9^{b}	3.5^{b}	2.1^{b}	2.8b	81.0^{a}	35.5^{b}	58.3^{b}	12.4	7.9	10.2	30.1^{b}	25.6^{b}	27.9^{b}
Mean	6.5	3.8		4.9	3.9		83.0	62.1		12.1	8.2		65.5	37.4	
Vertisol	4.2	3.2	3.7^{ab}	3.5^{b}	3.1	3.3	60.0^{b}	55.7^{a}	57.4	9.4^{b}	12.6^{a}	11.0	46.6^{a}	34.2^{a}	40.4^{a}
Cambisols	4.1	2.6	3.4^{b}	4.8^{a}	2.6	3.7	89.8^{a}	47.8^{a}	68.8	11.9^{ab}	9.6^{a}	10.8	50.5^{a}	47.0^{a}	48.8^{a}
Arenosols	5.3	3.1	4.2^{a}	4.0^{ab}	2.6	3.3	102.2^{a}	33.5^{b}	67.9	16.2^{a}	4.1^{b}	10.2	28.8^{b}	16.9^{b}	22.9^{b}
Mean	4.5	3.0		4.1	2.8		84.0	45.7		12.5	8.8		42.0	32.7	

Means followed by different superscripts are significantly different at $P \leq 0.05$ along the columns; means with no letters are not significantly different. (OM- omnivores, PD- predators, BV- bacterivores, FV-fungivores, HV- herbivores)

Table 5. Interaction effects between soil groups, sites, and disturbance levels on abundance of nematode feeding groups in different seasons.

Soil groups/Sites/ Disturbance levels	OM				PD				BV				FV				HV			
	SnI	SnII	SnIII	mean	SnI	SnII	SnIII	mean	SnI	SnII	SnIII	mean	SnI	SnII	SnIII	mean	SnI	SnII	SnIII	mean
Vertisols	2.2^{b}	7.3^{a}	2.8^{b}	4.1^{ab}	3.5	3.9^{ab}	2.6	3.3	76.5^{ab}	56.0^{c}	45.0	59.2	5.8^{ab}	15.0	14.4^{a}	11.7	35.8^{b}	52.2^{a}	34.1^{ab}	40.7^{a}
Cambisols	2.2^{b}	5.5^{b}	2.7^{b}	3.5^{b}	3.4	4.3^{a}	3.1	3.6	94.9^{a}	76.7^{b}	38.6	70.1	7.7^{a}	18.6	8.4^{b}	11.6	53^{a}	54^{a}	40.4^{a}	49.1^{a}
Arenosols	2.8^{a}	5.6^{b}	4.3^{a}	4.2^{a}	3.8	3.3^{b}	2.6	3.2	58.6^{b}	81.4^{a}	42.2	60.7	4.5^{b}	17.3	7.2^{b}	9.7	18.3^{c}	23.7^{b}	24.8^{b}	22.3^{b}
mean	2.1	5.1	3.2		2.9	3.4	2.8		57.8	54.0	32.2		4.8	13.2	8.3		27	33	25.6	
North	2.6^{a}	9.3^{a}	3.5	5.1^{a}	4.2^{a}	5.6^{a}	2.7	4.2^{a}	81.0	145.1^{a}	46.7	91.0^{a}	7.3^{a}	25.6^{a}	9.4	14.1^{a}	32.8	53.5^{a}	38.7^{a}	41.7^{a}
South	2.2^{b}	3.9^{b}	2.9	3.0^{b}	3.0^{b}	2.5^{b}	2.8	2.8^{b}	69.9	34.0^{b}	37.5	47.0^{b}	4.7^{b}	11.1^{b}	9.7	8.5^{b}	32.7	30.8^{b}	27.2^{b}	30.2^{b}
Mean	2.4	6.6	3.2		3.6	4.1	2.8		75.5	89.6	42.1		6.0	18.4	9.6		32.8	42.2	33	
Natural	3.6^{a}	15.4^{a}	6.1^{a}	8.4^{a}	7.4^{a}	6.0^{a}	4.5^{a}	6.0^{a}	87.9	122.1^{a}	60.8^{a}	90.3^{a}	4.7	23.7^{a}	8.5	12.3	62.2^{a}	105^{a}	53.7^{a}	73.6^{a}
Tilled	2.1^{b}	4.4^{b}	2.5^{b}	3.0^{b}	2.7^{b}	3.3^{b}	2.3^{b}	2.8^{b}	71.4	58.6^{b}	36.9^{b}	55.6^{b}	6.3	15.1^{b}	10.0	10.5	26.4^{b}	29.5^{b}	27.4^{b}	27.8^{b}
mean	2.9	10.0	4.3		5.1	4.7	3.4		79.7	90.4	48.9		5.5	19.4	9.3		44.3	67.3	40.6	

Comparisons are shown for each season if seasons, soil groups, sites and ecosystems interaction was significant at $P \leq 0.05$, and comparison shown for main effect if no interaction effect was observed. Means followed by different letters along columns indicate the significant differences at $P \leq 0.05$; means with no letters are not significantly different. (OM= omnivores, PD=predators, BV= bacterivores, FV= fungivores, HV= herbivores, SnI= season 1, SnII = season 2, SnIII = season 3)

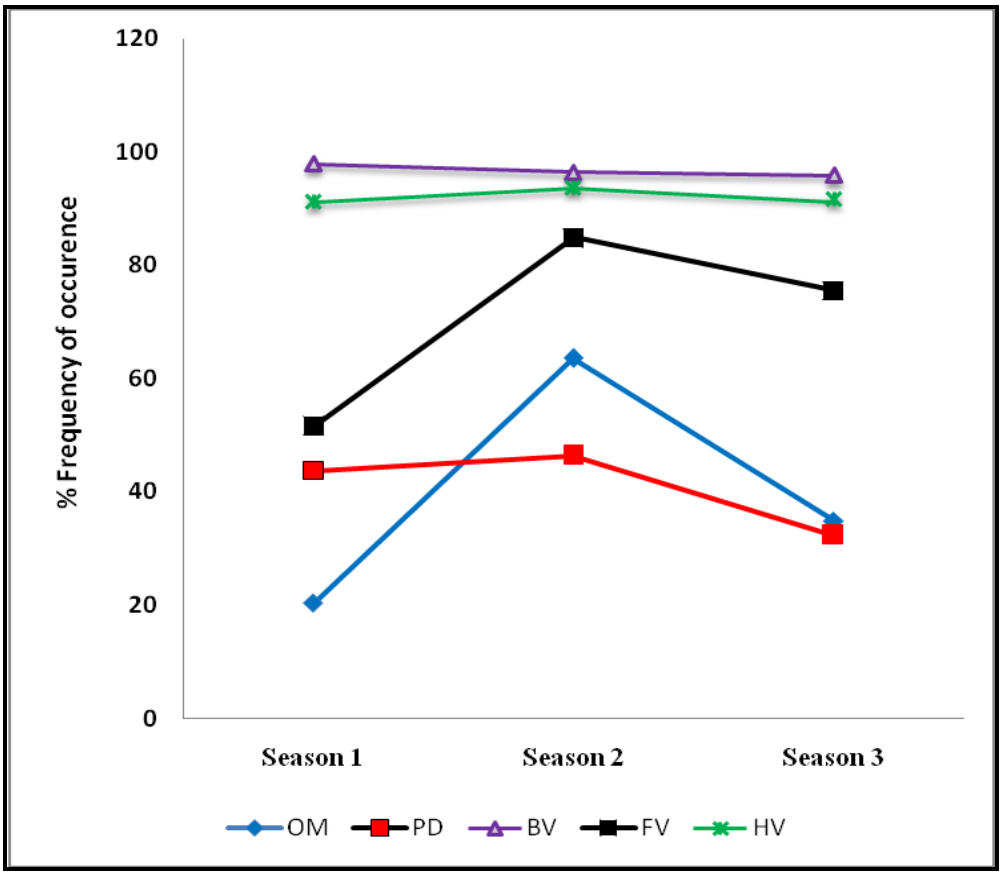

Figure 1. Seasonal trends in ffrequencies of occurrence of different nematode feeding ggroups (OM: omnivores, PD: predators, BV: bacterivores, FV: fungivores, HV: herbivores).

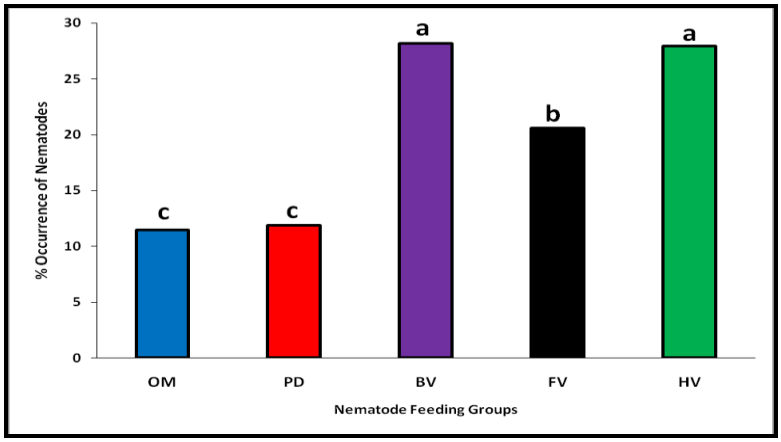

Figure 2. Frequency of occurrence of different nematode feeding ggroups in all the three soil groups across all the three seasons (OM: omnivores PD: predators, BV: bacterivores, FV: fungivores, HV: herbivores). Bars headed by different letters indicate means that are significantly different at $P \leq 0.05$.

Table 6. Mean frequencies of occurrence in nematode feeding groups observed in different soil groups, seasons and sites.

		OM	PD	BV	FV	HV
Soil Group	Vertisols	2.52^{b}	2.63	4.30	3.46^{ab}	4.30
	Cambisols	2.47^{b}	2.64	4.28	3.57^{a}	4.26
	Arenosols	2.75^{a}	2.55	4.36	3.28^{b}	4.28
Season	Season 1	2.12^{c}	2.68^{a}	4.36	2.89^{c}	4.28
	Season 2	3.22^{a}	2.75^{a}	4.30	3.90^{a}	4.28
	Season 3	2.46^{b}	2.41^{b}	4.28	3.59^{b}	4.28
Sites	North	2.78^{a}	2.92^{a}	4.36	3.66^{a}	4.35^{a}
	South	2.38^{b}	2.32^{b}	4.27	3.22^{b}	4.22^{b}
Disturbance	Natural	3.27^{a}	3.42^{a}	4.44^{a}	3.48	4.44^{a}
	Tilled	2.36^{b}	2.37^{b}	4.27^{b}	3.42	4.23^{b}

Means followed by different letters indicate the significant differences at $P \leq 0.05$; means with no letters are not significantly different. **(**OM=omnivores, PD=predators, BV=bacterivores, FV=fungivores, HV=herbivores)

Table 7. Diversity Indices across the seasons in different soil groups, disturbance levels and sites.

Variables			Shannon Index (H')	Genus Richness (N_0)	Genus Eveness (J')
Soil Groups	Vertisols	Season I	1.67	8.44^{b}	0.80
		Season II	1.75	10.41^{a}	0.79
		Season III	1.66	8.84^{b}	0.80
	Cambisols	Season I	1.68	9.23^{b}	0.79
		Season II	1.84	11.02^{a}	0.82
		Season III	1.67	9.41^{b}	0.79
	Arenosols	Season I	1.59	8.27	0.79
		Season II	1.65	9.38	0.80
		Season III	1.76	9.13	0.82
Disturbance Levels	Natural (Untilled)	Season I	1.87^{b}	10.63^{c}	0.80
		Season II	2.07^{a}	14.5^{a}	0.78
		Season III	1.94^{ab}	12.0^{b}	0.79
	Tilled	Season I	1.58	7.99	0.79
		Season II	1.64	8.85	0.80
		Season III	1.61	8.17	0.81
Sites	North	Season I	1.66^{b}	9.17^{b}	0.78
		Season II	1.91^{a}	11.73^{a}	0.78
		Season III	1.68^{b}	9.47^{b}	0.77
	South	Season I	1.64	7.38	0.81
		Season II	1.60	7.34	0.81
		Season III	1.71	8.34	0.84

Means along columns with different letters indicate significantly different indices at ($P \leq 0.05$). SnI= Season 1, SnII = Season 2, SnIII = Season 3.

diversity and species richness compared to the tilled land/soil. Soil disturbance cause changes in physical and biological properties of the soil and these influence the distribution of nematodes (Freckman and Baldwin, 1990). The findings of this study are in agreement with those of Hanel (2003) who observed that nematode fauna are usually more abundant in non-cultivated lands and their diversity increases in the soil when arable fields are abandoned.

Recommendation

Having established that seasons, soil groups and disturbance levels influence nematode abundance, it is recommended that further work should also be done to determine how different soil groups influence nematode assemblages at the species level.

CONCLUSIONS

Significant differences in soil nematode abundance and diversity were observed among different soil groups in the untilled and tilled soils in the northern and southern sites of Kenya across the three seasons. Nematodes can be utilized as viable bio-indicators of soil health and quality.

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