

Plant parasitic nematode assemblages associated with sweet potato in Kenya and their relationship with environmental variables

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Abstract Sweet potato is one of the most important staple food crops consumed in Kenya and throughout Africa but yields are greatly reduced by plant parasitic nematodes (PPN). The aim of this study was to determine the prevalence of PPN in Kenyan sweet potato fields and their relationship with soil and climatic variables. Soil samples were collected from sweet potato fields in Busia, Teso, Kisii, Embu and Makueni counties. Thirteen nematode genera were identified across the five counties with *Meloidogyne*, *Pratylenchus* and *Rotylenchus* being the most prevalent. There was a significant ($P < 0.05$) relationship between PPN abundance and sodium, calcium and iron. Canonical correspondence analysis of climatic variables revealed that the relationship between rainfall and nematode genera was significant ($P < 0.05$) while

maximum and minimum temperatures were not significant. This description of PPN assemblages associated with sweet potato in Kenya and their relationship with environmental variables provides a starting point from which appropriate nematode management strategies can be implemented.

Keywords *Ipomoea batatas* · Soil properties · Nematode diversity

Introduction

Plant parasitic nematodes (PPN) cause substantial yield losses of agricultural crops (Strange and Scott 2005) with a resultant global cost of > \$120 billion p.a. (Chitwood 2011). The nematodes, *Meloidogyne* spp., *Heterodera* spp., *Globodera* spp., *Radopholus similis*, *Ditylenchus dispaci*, *Bursaphelenchus xylophilus*, *Rotylenchulus reniformis*, *Xiphinema index*, *Nacobus aberrans* and *Aphelenchoides besseyi* are considered as the top 10 plant parasitic by nematologists (Jones et al. 2013). Due to its capability of rapidly spreading to and colonizing new localities (Bebber et al. 2014) and wide host range, root knot nematode (RKN, *Meloidogyne* spp), is ranked as the most economically damaging (Jones et al. 2013). Twenty *Meloidogyne* species occur in Africa with *M. incognita*, *M. javanica* and *M. arenaria* being the most prevalent (Onkendi et al. 2014).

Plant parasitic nematodes are widely distributed in Kenyan agro-ecosystems (Waceke 2007; Maina et al. 2011; Mwangi et al. 2014; Nzesya et al. 2014). In Kenya, sweet potato is an important subsistence crop that is grown by smallholder farmers in most agro-ecological zones (AEZ) (Mwololo et al. 2007). Sweet potato is a preferred staple crop in developing countries due to its low cost of production and its ability to grow in a range of environments (Woolfe 2002). However,

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sweet potato yield and quality are reduced by PPN infection (Coyne et al. 2003; Olabiyi 2007). The presence of PPN in sweet potato growing AEZ in Kenya may be an important production constraint and the situation may deteriorate due to an increase in nematode abundance and a shift in distribution as a result of changes in temperature and moisture. Population trends of PPN and the relationship between nematodes and plants are affected by environmental conditions (Griffin et al. 1996). At both global and continental scales, nematode community structure is influenced by temperature and rainfall (Bakonyi et al. 2007; Nielsen et al. 2014). Temperature and moisture may directly or indirectly affect nematode abundance and distribution. Temperature directly affects different nematode processes such as rate of feeding (Boag 1980), and root penetration (Roberts et al. 1979), while nematode infection rate is directly impacted by moisture (Colagiero and Ciancio 2011). A risk analysis of climate change on coffee nematodes in Brazil, suggested that high temperature would result in an increase in the area infested with *Meloidogyne* spp. by 2060 as a result of increased nematode reproduction rates (Ghini et al. 2008). An increase in temperature has also been correlated with increased rate of development and reproduction of *Meloidogyne* (Bird 1972) and *Pratylenchus* (Duyck et al. 2012). The objective of this study was to therefore determine the current environmental drivers and distribution of parasitic nematodes associated with sweet potato in Busia, Teso, Kisii, Embu and Makueni counties in Kenya.

Materials and methods

Soil sampling sites

In April 2015, rhizosphere soil was collected from sweet potato fields in five counties that represent the main agro-ecological zones where sweet potato is grown in Kenya (Table 1; Fig. 1). Busia, Teso, Kisii, Embu and Makueni counties are located at altitudes of 1220 m, 1140 m, 1700 m, 1300 m and 1260 m respectively. The sampled areas were fields that were exclusively cultivated with sweet potato for 5 years or more. Classification of the Kenyan agro-ecological zones is as described by Jaetzold and Schmidt (1983) and it is based on the probability of major crops achieving their water and temperature requirements. For each location, samples were collected from 10 sweet potato fields at a depth of 25 cm using a 3.5 cm diameter soil auger. In each field, soil samples were collected along three separate W shaped “sample walks” (25 kg of soil from each “sample walk”) with 30 sampling points where the distance between two points was 10 m. Subsequently three 200 g sub-samples from each walk were used for nematode extraction (Wiesel et al. 2015).

Nematode extraction and identification

Nematodes were extracted from 200 g of soil for 48 h using the modified Baermann technique (Hooper 1990). Nematodes were fixed in formalin-acetic fixative before identification (Stamps and Linit 1998). The nematodes were enumerated and identified to genus level using a Leica compound microscope. Physical and chemical properties of soil (pH, clay, sand, silt, calcium, copper, iron, magnesium, manganese, phosphorous, potassium, sodium, zinc, total nitrogen and organic carbon) were evaluated at Kenya Agricultural and Livestock Research Organization (KALRO), Nairobi, Kenya.

Temperature and rainfall data collection

Monthly rainfall, maximum and minimum temperature data for the sampling sites during April 2015 was provided by the Kenya Meteorological Department (KMD). To investigate the long term trend in temperature and rainfall in the sampling sites, data was obtained from KMD as indicated in Table 2. Analysis of nematode data was performed on the average of the three 200 g soil sub-samples. Differences in nematode genera abundance between the counties (pooled nematode data per county) were determined by analysis of variance (ANOVA) using Genstat v 17.1 statistical software (VSN International Ltd) with the Fisher's LSD post hoc analysis. The absolute frequency (Number of samples containing a nematode genus/Number of samples collected) X 100, prominence values (Absolute density X square root (absolute frequency)); Absolute density = Mean number of nematodes/100 cm³ soil) and relative prominence values (Prominence value of a nematode genus/sum of prominence values for all nematode genera X 100) of nematode genera were calculated (Norton 1978). The nematode data was transformed by log (x + 1) before analysis to reduce heterogeneity of variances. Hierarchical cluster analysis based on Bray-Curtis dissimilarity matrix and Ward's clustering algorithm which produces well defined clusters was used to infer the structure of plant parasitic nematodes (PPN) populations in sampled sweet potato fields from 28 villages. The ‘heatmap.2’ function was used to pair the dendrograms with a heat map of nematode abundance using the gplots package of R (R Development Core Team 2013). Differences in soil physical and chemical properties were analyzed using ANOVA. Canonical correspondence analysis (CCA) was used to investigate relationships between PPN and soil properties, rainfall, maximum and minimum temperature (for weather data collected in April 2015 during collection of soil samples) using vegan in R package. Seasonal and annual trends for long term rainfall and temperature data were analyzed using the Mann-Kendall non-parametric test with the ‘Kendall’ package in R environment. Seasons were considered as March, April, May (MAM), June, July, August (JJA), September, October,

Table 1 Geographic location of soil sampling sites in Kisii, Busia, Teso, Embu and Makueni Counties, Kenya

Province	County	Sub-county	Village	Sampled field	Latitude	Longitude
Nyanza	Kisii	Mosocho	Nyabungututu	Field 1	0°38'58.6"S	34°44'56.8"E
			Kiaboega	Field 2	0°38'13.9"S	34°44'16.4"E
			Bonyagatenyi	Field 3	0°39'35.4"S	34°45'16.4"E
			Nyakobaria	Field 4	0°39'33.8"S	34°45'11.5"E
			Mwamasarore	Field 5	0°35'50.8"S	34°42'58.4"E
			Mwamasarore	Field 6	0°36'01.0"S	34°42'45.0"E
			Mwabagaka	Field 7	0°36'04.2"S	34°42'46.2"E
			Mwabagaka	Field 8	0°36'09.6"S	34°42'49.0"E
			Mwamoja	Field 9	0°36'15.5"S	34°43'05.9"E
			Mwamoja	Field 10	0°36'20.7"S	34°43'06.5"E
Western	Busia	Matayos	Namikoe	Field 1	0°21'31.2"N	34°10'15.7"E
			Buroboi A	Field 2	0°21'32.7"N	34°10'17.6"E
			Buroboi B	Field 3	0°21'38.2"N	34°10'08.8"E
			Nabisiongo	Field 4	0°22'21.4"N	34°09'24.1"E
			Emaseno	Field 5	0°25'21.6"N	34°08'46.0"E
			Emaseno	Field 6	0°25'43.2"N	34°08'50.2"E
			Emaseno	Field 7	0°25'50.8"N	34°08'55.6"E
			Emaseno	Field 8	0°26'37.8"N	34°08'38.5"E
			Buruba	Field 9	0°26'36.8"N	34°06'44.3"E
			Buruba	Field 10	0°26'45.2"N	34°06'42.9"E
	Teso	Teso South	Angorom	Field 1	0°29'53.9"N	34°07'41.7"E
			Andungos	Field 2	0°30'21.6"N	34°08'28.3"E
			Andungos	Field 3	0°30'37.8"N	34°08'48.0"E
			Andungos	Field 4	0°30'46.3"N	34°08'57.9"E
			Andukumut	Field 5	0°30'51.3"N	34°08'54.6"E
			Andukumut	Field 6	0°30'49.7"N	34°09'02.6"E
			Alomodoi	Field 7	0°30'52.4"N	34°09'05.5"E
			Alomodoi	Field 8	0°30'57.9"N	34°09'00.7"E
			Andukumut	Field 9	0°30'57.9"N	34°08'54.6"E
			Andukumut	Field 10	0°31'03.1"N	34°08'48.9"E
Eastern	Embu	Manyatta	Kangaru	Field 1	0°30'24.5"S	37°27'23.3"E
			Njukiri	Field 2	0°31'09.4"S	37°26'55.7"E
			Njukiri	Field 3	0°31'05.1"S	37°26'55.3"E
			Njukiri	Field 4	0°30'45.2"S	37°26'53.6"E
			Mariamairi	Field 5	0°30'07.9"S	37°26'35.8"E
			Mariamairi	Field 6	0°30'03.4"S	37°26'50.8"E
			Githungururu	Field 7	0°29'27.7"S	37°27'14.1"E
			Kangaru (KALRO, Embu)	Field 8	0°30'21.0"S	37°27'26.6"E
			Iveche	Field 9	0°30'54.1"S	37°27'59.0"E
			Iveche	Field 10	0°31'14.0"S	37°28'18.1"E
	Makueni	Nzaui	Kiinze	Field 1	1°56'54.9"S	37°31'52.0"E
			Kinui	Field 2	1°56'35.3"S	37°32'06.1"E
			Kikuu	Field 3	1°57'22.6"S	37°33'58.9"E
			Kikuu	Field 4	1°57'22.0"S	37°33'58.9"E
			Kalima	Field 5	1°58'41.8"S	37°35'43.2"E
			Kalima	Field 6	1°59'41.7"S	37°35'56.0"E
			Inyeke	Field 7	1°59'48.0"S	37°35'54.0"E
			Inyeke	Field 8	1°59'54.8"S	37°36'16.6"E
			Kyanguu	Field 9	1°58'12.0"S	37°34'39.6"E
			Kyanguu	Field 10	1°58'12.1"S	37°34'41.4"E

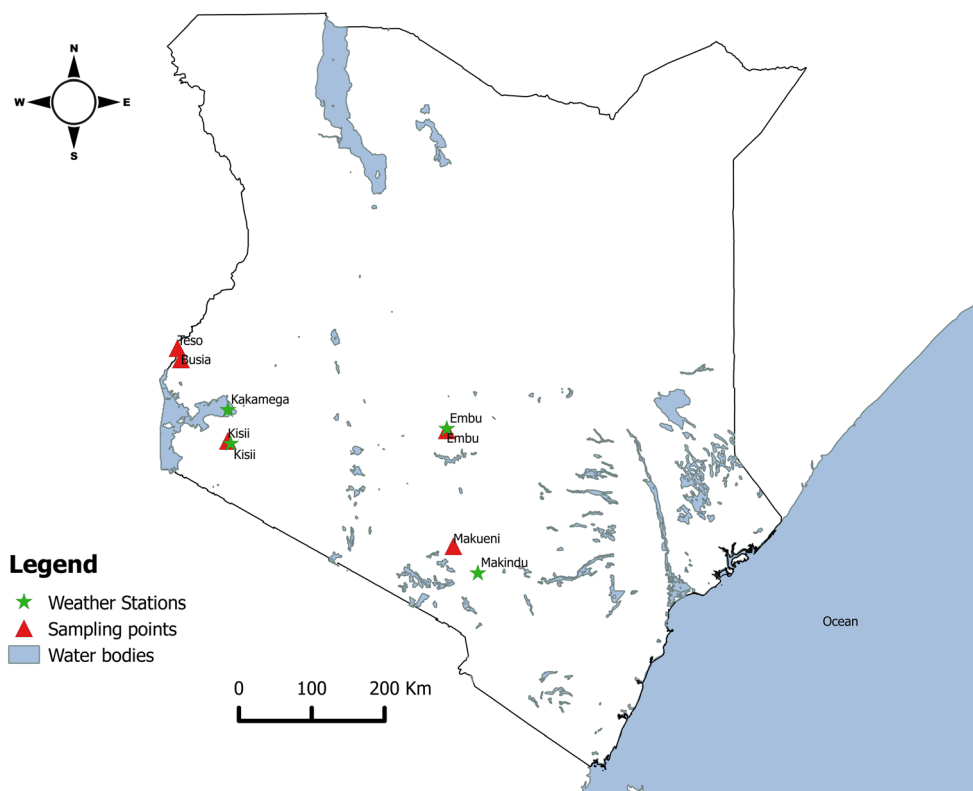
November (SON) and December, January, February (DJF). A positive and negative Kendall tau coefficient ($P < 0.05$) indicates an increasing and decreasing trend respectively.

Results

Thirteen PPN genera were identified across the five counties with a significant difference in the abundance of *Meloidogyne* ($F = 4.480_{[4, 48]}$; $P = 0.004$). Makueni county had the highest

number (11) of nematode genera. Kisii county had the highest number of *Meloidogyne* population and the least was in Teso county (Table 3). Some nematode genera were exclusively observed in a single county. These are *Criconemella* (Makueni county), *Hoplolaimus* (Teso county) and *Trichodorus* (Makueni county). *Helicotylenchus*, *Meloidogyne*, *Pratylenchus*, *Rotylenchulus*, *Rotylenchus* and *Tylenchorhynchus* were observed in all the Counties. The nematode genera, *Filenchus*, *Scutellonema* and *Tylenchus* were recorded in 80% of the sampled fields.

Fig. 1 Map of Kenya showing the soil sampling points and weather stations



Relative prominence (RP) values (Table 4) which indicate the frequency of occurrence of nematode genera compared to that of all genera were different in the five counties. The most prevalent genera (RP >10%) across all Counties were *Meloidogyne*, *Pratylenchus* and *Rotylenchus*. *Paratylenchus* was not recorded in Embu and Makueni counties. The nematode genera *Tylenchus* and *Filenchus* had high RP values in

Makueni county. The highest RP values for *Pratylenchus* (16.52%) and *Rotylenchus* (13.4%) were recorded in Embu and Busia counties respectively (Table 4).

The PPN population structure in sweet potato fields in 28 villages of Busia, Embu, Kisii, Makueni and Teso counties was inferred using a heat map (Fig. 2). There was a clear grouping of the villages into two major clusters. Each cluster comprised of

Table 2 Characteristics of weather stations in Kisii, Busia, Teso, Embu and Makueni counties

Soil sampling site	Weather station	Latitude	Longitude	Altitude asl (m)	Type of record	Record period
Busia Teso	Kakamega	0°16'S	34°45'E	1585	Rainfall	1960–2014
					Maximum temperature	1980–2014
					Minimum temperature	1980–2014
Kisii	Kisii	0°41'S	34°47'E	1761	Rainfall	1964–2013
					Maximum temperature	1976–2013
					Minimum temperature	1976–2013
Embu	Embu	0°30'S	37°27'E	1493	Rainfall	1976–2014
					Maximum temperature	1976–2012
					Minimum temperature	1976–2014
Makueni	Makindu	2°17'S	37°50'E	1000	Rainfall	1960–2013
					Maximum temperature	1974–2014
					Minimum temperature	1974–2014

Table 3 Nematode abundance in 200 cm³ of soil from sweet potato fields in Busia, Embu, Kisii, Makueni and Teso counties

	Busia	Embu	Kisii	Makueni	Teso
<i>Criconemella</i>	0	0	0	55 ± 3.57	0
<i>Filenchus</i>	0	39 ± 0.26	72 ± 0.48	99 ± 6.76	36 ± 0.23
<i>Helicotylenchus</i>	44 ± 2.09	48 ± 1.24	71 ± 0.26	60 ± 1.0	43 ± 0.35
<i>Hoplolaimus</i>	0	0	0	0	46 ± 0.26
<i>Meloidogyne</i>	81 ± 0.55	73 ± 0.51	124 ± 0.29	61 ± 0.55	53 ± 0.32
<i>Paratylenchus</i>	52 ± 0.26	0	44 ± 1.14	0	50 ± 0.70
<i>Pratylenchus</i>	57 ± 0.78	73 ± 2.39	73 ± 1.04	44 ± 0.48	57 ± 0.55
<i>Rotylenchulus</i>	124 ± 0.26	46 ± 0.26	46 ± 0.51	50 ± 2.47	80 ± 1.34
<i>Rotylenchus</i>	57 ± 0.7	73 ± 0.38	60 ± 0.35	43 ± 0.58	59 ± 0.91
<i>Scutellonema</i>	0	42 ± 0.1	39 ± 0.26	46 ± 0.26	41 ± 0.78
<i>Trichodorus</i>	0	0	0	59 ± 0.26	0
<i>Tylenchorhynchus</i>	55 ± 0.15	39 ± 0.82	58 ± 1.14	33 ± 0.26	42 ± 0.74
<i>Tylenchus</i>	53 ± 2.98	55 ± 1.34	26 ± 0.26	112 ± 0.55	0

Data represents back transformed means ± SE

villages from all the five counties. The distribution and abundance of nematode genera depicted in the heat map showed that *Meloidogyne*, *Rotylenchus* and *Pratylenchus* were abundant in similar sites to those identified through the relative prominence analysis. Sweet potato fields in Nyabungututu, Nyakobaria (Kisii county), Buroboi A, Buroboi B, Nabisiongo, Namikoe (Busia county), Iveche (Embu county), Kinui, Kalima, Kiinze (Makueni county) and Angorom (Teso county) villages were clustered together. The soil samples from these villages did not have *Rotylenchulus*, *Hoplolaimus* or *Scutellonema* populations. In the same cluster, Kinui and Kiinze villages (Makueni county) were the only areas out of the five counties where the nematode genera *Trichodorus* and *Criconemella* were recorded. The highest populations of *Meloidogyne* and *Rotylenchus* were observed in Emaseno village which was part of the second major cluster. Njukiri village was also part of this cluster and it had the highest number of *Pratylenchus*. The nematode genera were also grouped into two main clusters with the smallest cluster consisting of *Trichodorus*, *Criconemella* and *Tylenchus* which were absent from most counties.

Across the five counties, significant differences in soil physical and chemical properties were noted except for copper and potassium (Table 5). In the CCA analysis (Fig. 3) on the relationship between soil properties and PPN abundance, the first two axes accounted for 75.6% of the variance. There was a significant ($P < 0.05$) relationship between PPN abundance and sodium, calcium and iron. The nematode genera *Criconemella* and *Trichodorus* which were observed in Makueni county showed a non-significant correlation with sand (Sd).

During the sampling period (April, 2015) the mean monthly rainfall was 368.5 mm, 158.4 mm, 139.2 mm, 71.4 mm and 368.5 mm in Busia, Embu, Kisii, Makueni and Teso counties

respectively. Maximum temperature in Busia, Embu, Kisii, Makueni and Teso counties was 28 °C, 25 °C, 24.5 °C, 30.7 °C and 28 °C respectively while the minimum temperature was 13 °C, 11.7 °C, 15.7 °C, 17.7 °C and 13 °C respectively. There was a significant difference ($P < 0.05$) in rainfall, maximum and minimum temperature across the five counties. Makueni county had the lowest amount of rainfall and the highest maximum and minimum temperature.

Canonical correspondence analysis was used to evaluate the relationship between nematode genera abundance and rainfall, maximum and minimum temperature. The first axis accounted for 53.2% of the variance and the second axis accounted for 15.8% of the variance. Permutation tests for climatic variables revealed that the relationship between rainfall and nematode genera was significant ($P < 0.05$) while maximum and minimum temperatures were not significant ($P = 0.61$ and $P = 0.63$ respectively). Rainfall was highly correlated with CCA1 (Fig. 4). The nematode genera *Aphelenchoides* (Aphd), *Criconemella* (Cric), *Filenchus* (Filen), *Scutellonema* (Scut), *Trichodorus* (Tric) and *Tylenchus* (Tyle) were associated with maximum and minimum temperature but the relationship was not statistically significant.

There was an annual increase in rainfall across all the Counties but the increase was not significant (Table 6). For each respective record period of long term temperature data across the five counties, a significant increase in maximum temperature was observed annually. During MAM season, a significant rise in maximum temperature was recorded in all the Counties. Kakamega, Kisii and Makueni counties had a significant increase in maximum temperature during the JJA and DJF seasons. A significant increase in annual minimum

Table 4 Absolute frequency and prominence values of plant parasitic nematodes in Busia, Embu, Kisii, Makueni and Teso Counties

County	Nematode genus	Number of genera	^a Absolute frequency (%)	^b Prominence value	^c Relative prominence value (%)
Busia	<i>Helicotylenchus</i>	8	30	120.5	8.23
	<i>Meloidogyne</i>		100	405	27.67
	<i>Paratylenchus</i>		10	82.2	5.62
	<i>Pratylenchus</i>		40	180.2	12.31
	<i>Rotylenchulus</i>		10	196.1	13.4
	<i>Rotylenchus</i>		70	238.4	16.29
	<i>Tylenchorhynchus</i>		20	123	8.4
	<i>Tylenchus</i>		20	118.5	8.09
Embu	<i>Filenchus</i>	9	10	61.7	3.95
	<i>Helicotylenchus</i>		30	131.5	8.42
	<i>Meloidogyne</i>		100	365	23.37
	<i>Paratylenchus</i>		50	258.1	16.52
	<i>Rotylenchulus</i>		10	72.7	4.65
	<i>Rotylenchus</i>		60	282.7	18.1
	<i>Scutellonema</i>		40	132.8	8.5
	<i>Tylenchorhynchus</i>		30	106.8	6.84
	<i>Tylenchus</i>		30	150.6	9.64
Kisii	<i>Filenchus</i>	10	40	227.7	11.43
	<i>Helicotylenchus</i>		30	194.4	9.76
	<i>Meloidogyne</i>		100	620	31.14
	<i>Paratylenchus</i>		20	98.4	4.94
	<i>Pratylenchus</i>		40	230.8	11.59
	<i>Rotylenchulus</i>		30	126	6.33
	<i>Rotylenchus</i>		60	232.4	11.67
	<i>Scutellonema</i>		10	61.7	3.1
	<i>Tylenchorhynchus</i>		30	158.8	7.97
	<i>Tylenchus</i>		10	41.1	2.06
Makueni	<i>Criconemella</i>	11	10	87	4.84
	<i>Filenchus</i>		20	221.4	12.33
	<i>Helicotylechus</i>		20	134.2	7.47
	<i>Meloidogyne</i>		100	305	16.98
	<i>Pratylenchus</i>		70	184.1	10.25
	<i>Rotylenchulus</i>		20	111.8	6.23
	<i>Rotylenchus</i>		70	179.9	10.02
	<i>Scutellonema</i>		10	72.7	4.05
	<i>Trichodorus</i>		10	93.3	5.2
	<i>Tylenchorhynchus</i>		10	52.2	2.91
	<i>Tylenchus</i>		40	354.2	19.72
	Teso		<i>Filenchus</i>	10	20
<i>Helicotylenchus</i>		40	136		9.46
<i>Hoplolaimus</i>		10	72.7		5.06
<i>Meloidogyne</i>		90	251.4		17.49
<i>Paratylenchus</i>		30	136.9		9.53
<i>Pratylenchus</i>		50	201.5		14.02
<i>Rotylenchulus</i>		10	126.5		8.8
<i>Rotylenchus</i>		40	186.6		12.98
<i>Scutellonema</i>		30	112.3		7.81
<i>Tylenchorhynchus</i>		40	132.8		9.24

Table 4 (continued)

County	Nematode genus	Number of genera	^a Absolute frequency (%)	^b Prominence value	^c Relative prominence value (%)
All counties	<i>Criconemella</i>	13	2	38.9	0.49
	<i>Filenchus</i>		18	521.8	6.57
	<i>Helicotylechus</i>		30	728.5	9.18
	<i>Hoplolaimus</i>		2	32.5	0.41
	<i>Meloidogyne</i>		98	1940.3	24.44
	<i>Paratylenchus</i>		12	252.9	3.19
	<i>Pratylenchus</i>		50	1074.8	13.54
	<i>Rotylenchulus</i>		16	692	8.72
	<i>Rotylenchus</i>		60	1130.9	14.24
	<i>Scutellonema</i>		18	356.4	4.49
	<i>Trichodorus</i>		2	41.7	0.53
	<i>Tylenchorhynchus</i>		26	578.7	7.29
	<i>Tylenchus</i>		20	550.1	6.93

^a Absolute frequency = (Number of samples containing a nematode genus/Number of samples collected) X 100
^b Prominence value = Absolute density X square root (absolute frequency); Absolute density = Mean number of nematodes/100 cm³ soil
^c Relative prominence = (Prominence value of a nematode genus/sum of prominence values for all nematode genera) X 100

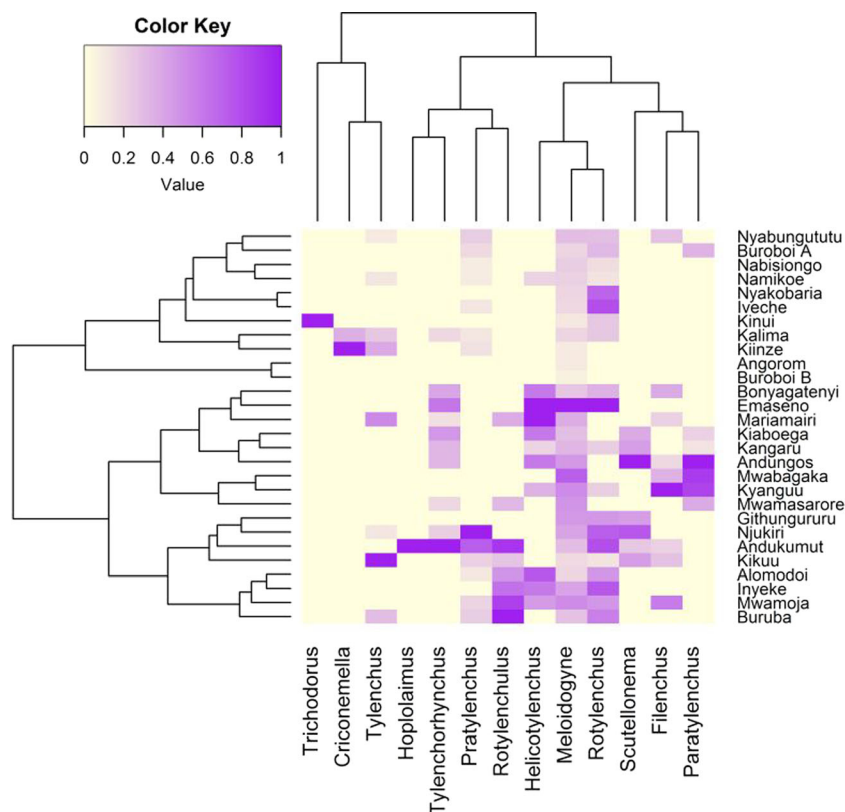


Fig. 2 Heatmap of parasitic nematode genera in sweet potato fields in Nyabungututu, Nyakobaria, Bonyagatenyi, Kiaboega, Mwabagaka, Mwamasarore, Mwamoja (Kisii county), Buroboi A, Buroboi B, Nabisiongo, Namikoe, Emaseno, Buruba (Busia county), Iveche, Mariamairi, Kangaru, Githungururu, Njukiri (Embu county), Kinui, Kikuu, Kalima, Kiinze, Kyanguu, Inyeke (Makueni county), Angorom, Andungos, Andukumut and

Alomodoi villages (Teso county). Ward’s clustering algorithm was applied to the Bray-Curtis dissimilarity matrix of nematode abundance in sweet potato fields in 28 villages. Dendrogram of villages where sweet potato fields were sampled is along the left axis. Upper dendrogram represents the nematode genera. The color key scale represents normalized nematode abundances with intensity of color representing nematode abundance 200 cm⁻³

Table 5 Physical and chemical properties of soil collected from sweet potato fields ($n = 10$) in five counties

	Busia Mean	SE	Embu Mean	SE	Kisii Mean	SE	Makueni Mean	SE	Teso Mean	SE
Calcium me%	2.6 bc	±0.4	5.52 a	±0.58	3.2 b	±1.11	6.5 a	±0.93	1.1 c	±0.13
Clay %	41.8 b	±5.37	74.8 a	±1.24	50 b	±1.26	27.6 c	±1.6	23.2 c	±2.85
Copper ppm	7.3a	±0.96	6.4a	±2.11	7.4a	±2.17	4a	±0.37	3.2a	±0.49
Iron ppm	153.6 ab	±26.61	28.5 c	±1.39	91.5 abc	±10.16	59.2 bc	±9.28	188.2 a	±76.35
Magnesium me%	2.2 a	±0.31	2.2 a	±0.01	1.1 b	±0.21	2 a	±0.25	1.1 b	±0.21
Manganese me%	0.8 a	±0.01	0.6 b	±0.13	0.8 ab	±0.01	0.3 c	±0.01	0.3 c	±0.01
Phosphorous ppm	40.9 a	±11.02	16 b	±4.14	21.6 b	±2.01	10 b	±1.58	28 ab	±8.07
Potassium me%	0.4a	±0.22	1a	±0.01	1a	±0.52	1a	±0.01	0.2a	±0.13
Sand %	37.2 b	±5.99	7.6 c	±1.15	31.6 b	±2.71	62.8 a	±2.29	53.6 a	±3.51
Silt %	21 ab	±1.37	17.6 b	±0.78	18.4 b	±1.86	9.6 c	±1.07	23.2 a	±1.31
Sodium me%	0.3 b	±0.01	0.5 a	±0.16	0.3 b	±0.13	0.6 a	±0.16	0.1 b	±0.01
Soil pH	6.7 b	±0.3	5.9 c	±0.01	6 c	±0.39	7.7 a	±0.16	5.8 c	±0.21
Total N %	0.08 c	±0.01	0.3 a	±0.01	0.1 cd	±0.01	0.1 b	±0.01	0.1 d	±0.01
Total Organic C %	0.8 c	±0.15	2.5 a	±0.16	0.7 cd	±0.01	1.3 b	±0.01	0.5 d	±0.16
Zinc ppm	36.7 a	±16.51	31.1 ab	±5.82	24.7 abc	±10.17	1.5 c	±0.16	7.5 bc	±2.1

Mean values ± SE are shown. Means with the same letters across a row are not statistically different (Fischer's LSD, $P \leq 0.05$)

temperature was recorded in all counties. Embu and Kakamega counties had a significant increase in minimum temperature during JJA and SON seasons. There was a significant rise in minimum temperature during all seasons in Kisii county (Table 6).

Discussion

Plant parasitic nematodes belonging to the orders Tylenchida and Dorylaimida were identified in Kenyan sweet potato

growing regions. These nematodes cause global yield losses of >\$120 billion p.a. (Chitwood 2011) and there are challenges in controlling the nematodes through application of sustainable nematode management strategies (Thoden et al. 2011).

Economic losses caused by PPN associated with sweet potato may increase due to ineffective management and increased damage resulting from their interaction with fungal, bacterial and viral pathogens (Barker et al. 1994). Nematode genera reported in this study have been previously observed in association with sweet potato (Njuguna and Bridge 1998;

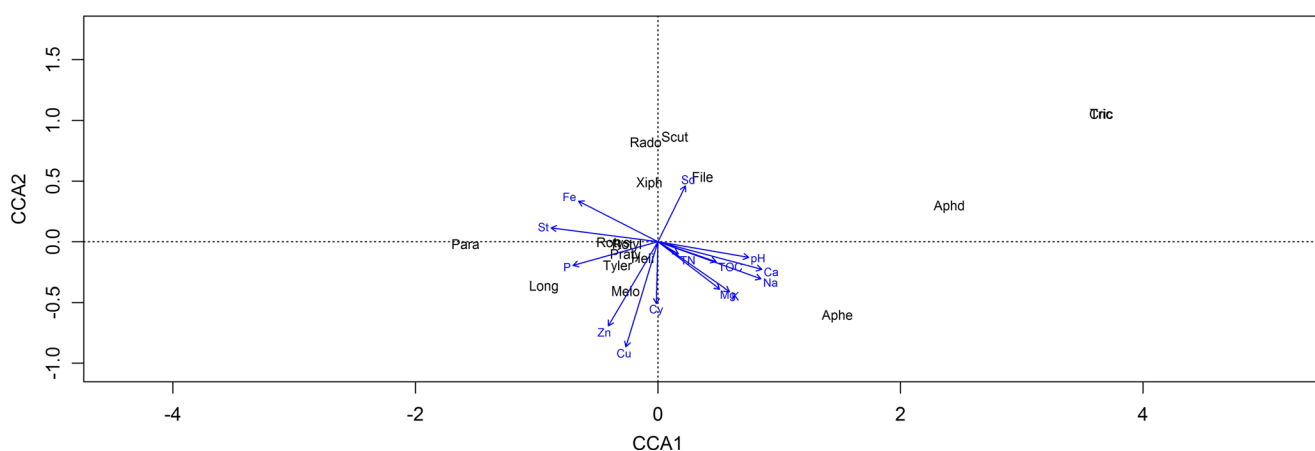


Fig. 3 Canonical correspondence analysis of the relationship between nematode communities and soil properties in Busia, Embu, Kisii, Makueni and Teso counties. The first two axes explain 75.1% of the variance. Arrows represent potassium (K), phosphorous (P), sodium (Na), total nitrogen (TN), pH, total organic carbon (TOC), zinc (Zn), calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), silt (St), sand (Sd) and clay (Cy). The

nematode genera are *Aphelenchoides* (Aphd), *Aphelenchus* (Aphe), *Criconebella* (Cric), *Ditylenchus* (Dity), *Filenchus* (File), *Helicotylenchus* (Heli), *Hoplolaimus* (Hopl), *Longidorus* (Long), *Meloidogyne* (Melo), *Paratylenchus* (Para), *Pratylenchus* (Praty), *Radopholus* (Rado), *Rotylenchulus* (Rotys), *Rotylenchus* (Rotyl), *Scutellonema* (Scut), *Trichodorus* (Tric), *Tylenchorhynchus* (Tyler), *Tylenchus* (Tyle) and *Xiphinema* (Xiph)

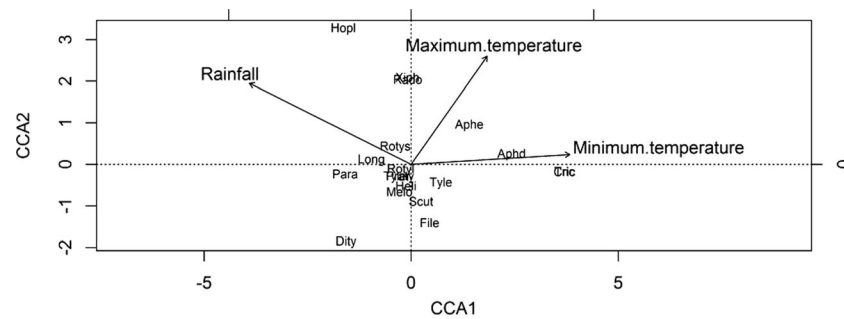


Fig. 4 Canonical correspondence analysis of the relationship between nematode communities and climate variables in Busia, Embu, Kisii, Makueni and Teso counties. The first axis explains 53.2% of the variance while the second axis explains 15.8% of the variance. Arrows represent rainfall, maximum and minimum temperature. The nematode genera are *Aphelenchoides* (Aphd), *Aphelenchus* (Aphe), *Criconebella*

(Cric), *Ditylenchus* (Dity), *Filenchus* (File), *Helicotylenchus* (Heli), *Hoplolaimus* (Hopl), *Longidorus* (Long), *Meloidogyne* (Melo), *Paratylenchus* (Para), *Pratylenchus* (Praty), *Radopholus* (Rado), *Rotylenchulus* (Rotys), *Rotylenchus* (Rotyl), *Scutellonema* (Scut), *Trichodorus* (Tric), *Tylenchorhynchus* (Tyler), *Tylenchus* (Tyle) and *Xiphinema* (Xiph)

Coyne et al. 2003; Marais and Swart 2007; Haougui et al. 2011). *Meloidogyne*, *Pratylenchus* and *Rotylenchus* were the most predominant nematode genera in all counties with an RP value greater than 10%. *Rotylenchus* is associated with 80–100% crop losses (Robinson et al. 1997) and has been reported to infect sweet potato in Uganda (Coyne et al. 2003). *Pratylenchus* and *Meloidogyne* are common endoparasites in most crops in Kenya. The lesion nematode, *Pratylenchus* had

a frequency of occurrence of 64% in soils collected from cabbage farms in Kenya (Waceke 2007) while *Meloidogyne* has been reported in association with beans (Kimenju et al. 1999), coffee (Nzesya et al. 2014), and *Sesbania* (Desaeger and Rao 1999). The PPN *Meloidogyne* is distributed globally and is more damaging in tropical regions (Jones et al. 2013) with the potential to rapidly spread to different geographic locations (Bebber et al. 2014). The juveniles penetrate the roots

Table 6 Kendall Tau coefficients for seasonal and annual rainfall, maximum and minimum temperature time series in four weather stations

	Embu Tau coefficient	<i>P</i> -value	Kakamega Tau coefficient	<i>P</i> -value	Kisii Tau coefficient	<i>P</i> -value	Makindu Tau coefficient	<i>P</i> -value
Rainfall								
MAM	−0.040	0.734	−0.087	0.359	−0.087	0.359	−0.115	0.226
JJA	−0.004	0.980	0.019	0.846	−0.059	0.553	−0.148	0.126
SON	0.041	0.725	0.148	0.115	0.102	0.300	−0.102	0.286
DJF	0.198	0.082	0.002	0.998	0.038	0.070	0.013	0.890
Annual	0.073	0.530	0.037	0.698	0.099	0.315	−0.084	0.378
Maximum temperature								
MAM	0.241	0.040*	0.380	0.002*	0.341	0.004*	0.287	0.009*
JJA	0.102	0.391	0.476	>0.0001*	0.405	0.001*	0.421	>0.0001*
SON	0.273	0.020*	0.373	0.002*	0.173	0.147	0.441	>0.0001*
DJF	0.276	0.019*	0.319	0.008*	0.324	0.006*	0.238	0.031*
Annual	0.311	0.008*	0.519	>0.0001*	0.489	>0.0001*	0.451	>0.0001*
Minimum temperature								
MAM	0.280	0.014*	−0.062	0.614	0.341	0.004*	0.300	0.007*
JJA	0.266	0.019*	0.415	0.001*	0.523	>0.0001*	0.208	0.061
SON	0.448	>0.0001*	0.405	0.001*	0.422	>0.0001*	0.354	0.001*
DJF	0.351	0.0019*	0.141	0.248	0.395	0.0008*	0.254	0.021*
Annual	0.431	>0.0001*	0.305	0.012*	0.496	>0.0001*	0.385	>0.0001*

*Represents statistically significant Tau coefficients ($P < 0.05$). Positive and negative values indicate increasing and decreasing trends respectively. The record period for Embu, Kakamega, Kisii and Makindu weather stations is 1976–2014; 1960–2014; 1964–2013 and 1960–2013 respectively. Climate data for Busia and Teso counties was obtained from Kakamega weather station while that for Kisii, Embu and Makueni counties was obtained from Kisii, Embu and Makindu weather stations respectively. The seasons represented are March, April, May (MAM), June, July, August (JJA), September, October, November (SON) and December, January, February (DJF)

and over time galls are formed on the plant roots and this reduces the uptake of water and nutrients leading to stunted growth and low yields. Kisii county had the highest number of *Meloidogyne* populations. Planting susceptible sweet potato genotypes in this county may result in low yields. Reproduction of *Meloidogyne* on sweet potato is high during the initial growth stages due to availability of penetration sites. For those roots that reach maturity, cracks occur on the surface reducing their quality and market value (Lawrence et al. 1986). Unlike *Meloidogyne* which is a sedentary endoparasite, *Pratylenchus* is a migratory endoparasite and is the third most important PPN worldwide. This endoparasite causes stunting in plants as a result of reduced root growth (Jones et al. 2013).

The reniform nematode, *Rotylenchulus* was recorded in all counties with Busia having the highest PV value (13.4%). Development of *Rotylenchulus* on sweet potato is different from that of *Meloidogyne* but causes similar root cracking. This species causes yield reduction through a “pruning effect” on roots (Clark and Wright 1983). Understanding the interaction between nematode species is key to effective management, for example, reproduction of *Rotylenchulus* is inhibited by the presence of *Meloidogyne* during concomitant infections on sweet potato (Thomas and Clark 1983). Soil properties may also affect the competitive balance of these nematodes (Godefroid et al. 2013). In the heatmap analysis, *Criconemella* was recorded in Kinui and Kalima villages of Makueni county where the monthly rainfall was lower (71.4 mm) than in the other four counties. The low rainfall may be one of the factors contributing to the presence of this genus in Makueni county. The observed correlation of PPN abundance with Sodium, Iron and Calcium has been recorded in other studies (Ardakani et al. 2014; Fiscus and Neher 2002; Yavuzaslanoglu et al. 2012). Understanding the effect of soil properties on PPN communities in sweet potato agroecosystems is an important step in their management since the relationship between soil properties and PPN assemblages is complex and it is influenced by climate (Nielsen et al. 2014).

Nematode abundance and composition is also significantly influenced by rainfall and temperature. In the current study, rainfall was significantly associated with the abundance of nematodes during the sampling period but temperature did not affect the abundance of nematodes. The effect of temperature on nematode abundance may have been masked by other environmental factors. The effect of rainfall on nematode abundance may become more pronounced with the predicted extreme precipitation and differences between wet and dry seasons (IPCC 2013). On a global scale, the abundance of PPN increases with a rise in mean annual temperature (Nielsen et al. 2014). Analysis of long term temperature data in the regions where soil samples were collected showed that maximum and minimum temperature increased annually in all the

five counties. Annual increase in maximum and minimum temperature in Makueni, Kakamega and Kisii has been previously reported (Mugalavai and Kipkorir 2013; Omoyo et al. 2015) with Kenya experiencing an increase in temperature by 1 °C in the last 2 decades. Maximum and minimum temperature are also expected to increase by 1.8–4.3 °C in the 21st century (Hoang et al. 2014).

If the trend in increasing temperature continues it may affect the PPN assemblages in sweet potato fields. Temperatures greater than 25 °C cause an increase in the rate of development and reproduction of *Meloidogyne* (Bird 1972) and *Pratylenchus* (Duyck et al. 2012). *Rotylenchus* is also well adapted to warm climate and it is capable of feeding at temperatures between 0.5 and 42.4 °C (Boag 1980). Furthermore, warming may lead to an increase in fungal pathogens (Pritchard 2011) which would further decrease sweet potato yields due to formation of disease complexes between fungi and nematodes. Low rainfall results in an increase in abundance of *Pratylenchus* and *Rotylenchulus* (Boag 1980). In New Zealand, climate warming is considered a potential risk to crop production due to the possible increase in abundance of *Meloidogyne* spp. (Watson and Pottinger 1990). A shift in virus vector nematodes due to global warming was predicted in Great Britain (Boag et al. 1991) and an increase in infestation of *Meloidogyne* in Brazil coffee agroecosystems was also attributed to warming (Ghini et al. 2008). Shifts in geographic distribution of PPN associated with sweet potato due to an increase in temperature may take a long time (Boag et al. 1991; Neilson and Boag 1996) but movement of PPN between fields may be accelerated by the exchange of planting materials between farmers.

Based on the current study, Kenyan sweet potato fields have a high diversity of economically damaging PPN. The trend in rainfall and temperature increase/decrease in these regions is also changing and this may significantly influence PPN abundance and composition (Nielsen et al. 2014). The effect of changes in temperature and moisture on PPN in sweet potato agro-ecosystems may result from several direct and indirect factors including modification of plant community and soil properties (Colagiero and Ciancio 2011; Kardol et al. 2011; Pritchard 2011). In addition, an interplay of various processes linked to host presence, abundance and susceptibility may also affect the distribution of sweet potato PPN. The potential impact of changes in temperature and moisture on distribution and abundance of PPN in Kenyan sweet potato agro-ecosystems is not easy to predict. The nematode abundance reported in this study may also vary depending on the extraction method used (Den Nijs and Van Den Berg (2013). However, the baseline data in this study provides a starting point from which appropriate nematode management strategies can be put in place in order to mitigate yield losses that may result from PPN.

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