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RESPONSE OF SPK 004 TO *MELOIDOGYNE* SPECIES INFESTATION AND IMPACT OF SWEET POTATO MANAGEMENT PRACTICES ON NEMATOFAUNA IN MWEA, KENYA

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other University

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DEDICATION

This work is dedicated to my lovely family and my supervisors for their love, support, and encouragement.

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LIST OF ABBREVIATIONS AND ACRONYMS

ANOVA	Analysis of variance
Baf	Bacterivore footprint
BI	Basal Index
CI	Channel Index
CIDP	County Integrated Development Plan
Cf	Composite footprint
CM	Cow Manure
C/N	Carbon/Nitrogen
Cp	Colonizer persister
CT	Control
DAP	Days After Planting
EA	East Africa
Ef	Enrichment footprint
EI	Enrichment Index
FAOSTAT	Food and Agricultural Organization Corporate Statistical Database
FLN	Free-Living Nematodes
Fuf	Fungivore footprint
GM	Goat Manure
KALRO	Kenya Agricultural and Livestock Research Organization
KMD	Kenya Meteorological Department
LM	Low Midland
LR	Long Rains season
MG	Marigold
MI	Maturity index
MS	Maize Sweet-Potato intercrop
Omf	Omnivore footprint
Ppf	Herbivore footprint
PPI	Plant Parasitic Index
PPN	Plant Parasitic Nematodes
PRC	Principal Response Curve

Prf	Predator footprint
RCBD	Randomized Complete Block Design
RKN	Root-knot nematodes
Sf	Structure footprint
SI	Structure Index
SPCSV	Sweet potato Chlorotic Stunt Virus
SPFMV	Sweet potato Feathery Motile Virus
SR	Short Rains season
TD	*Tithonia diversifolia*
UN	United Nations

GENERAL ABSTRACT

Sweet potato (*Ipomoea batatas* L.) is an important food crop consumed throughout Africa. However, sweet potato yields are greatly reduced by pests including plant parasitic nematodes. Management of nematodes in sweet potato fields in Kenya has mainly been through the use of nematicides and crop rotation which have limitations. The use of resistant sweet potato cultivars along with other low-cost organic amendments is the most economical, effective, and environmentally safe method of managing root-knot nematodes (RKN) in sweet potato fields. This study sought to evaluate the impact of sweet potato management practices on the population dynamics and diversity of plant parasitic (PPN) and free-living (FLN) nematodes. Field performance of the sweet potato cultivar, SPK 004, which was previously selected as RKN resistant under greenhouse conditions was also assessed. In determining the effect of low-cost management strategies on PPN and FLN, field experiments were established in a randomized complete block design involving four treatments and un-amended controls during long rains (March – July 2018) and short rains (October – February 2019). Soil samples were collected monthly for four months. Nematodes were then extracted and identified to the genus level. Forty-seven nematode genera belonging to five trophic groups were identified. Goat manure had the most pronounced effects on PPN of economic importance in sweet potato. All treatments revealed a low diversity of predatory nematodes. There were differences in metabolic footprints, ecological and functional indices during the LR, and SR. Plots amended with cow manure had significantly high predator and omnivore footprints during long and short rains seasons, respectively. Functional metabolic footprints categorized all plots as degraded in both seasons except in maize - sweet potato intercrop which was structured in short rains season. However, plots amended with goat manure bordered a structured ecosystem in LR while cow manure plots bordered a structured ecosystem in both seasons. A high diversity of free-living nematodes was observed in this study, with all treatments having a significantly high density of bacterivorous nematodes. Goat manure treatment was more effective in increasing the populations of free-living nematodes. To evaluate the field performance of SPK 004 in response to *Meloidogyne* species, trials were conducted in Mwea, Kenya for two seasons. Experimental plots were laid out in a randomized complete block design involving two treatments; plots planted with SPK 004 and plots planted with SPK 004 and treated with a nematicide. Soil samples were collected before planting and during harvest to determine the initial and final RKN population. Root samples obtained at harvest were rated visually for resistance using a galling index. Data were subjected to analysis of variance to determine differences in *Meloidogyne* populations, dry matter content, and yields between the treatments. There were no significant differences in SPK 004 resistance between the two treatments. However, plots planted with SPK 004 and treated with nematicide recorded significantly higher nematode populations in the short rains season. Findings from this study confirmed greenhouse results, where this cultivar was found to be very resistant to *Meloidogyne incognita*. This resistant cultivar may be used in nematode infested fields for the management of RKN. Goat manure may be incorporated as a relatively low-cost nematode management strategy and also as a stimulant of beneficial free-living nematodes.

CHAPTER ONE

INTRODUCTION

1.1 Background information

Sweet potato (*Ipomoea batatas* L.) is an important crop grown in the tropics and sub-tropics around the world (Oliviera Lima *et al*., 2016). In sub-Saharan Africa (SSA), it is the third most important tuber crop after yam and cassava (Yusuf and Wuyah, 2015). Sweet potato plays a key role in food security due to its ability to tolerate drought and it performs well under unfavorable conditions with little or no management inputs (Woolfe, 1992). In Kenya, sweet potato is mainly cultivated by smallholder farmers in Central, Rift Valley, Nyanza, Western and Coast Provinces with intensive production being concentrated in Nyanza and Western regions (Kaguongo *et al*., 2012). The entire sweet potato plant has varied uses such as human food, feed for livestock, and as industrial raw material (Githunguri and Migwa, 2007; Claessens *et al*., 2008; Duvernay *et al*., 2013). However, in Kenya, sweet potato yields have steadily declined from 125,050 hg ha^{-1} in 2014 to 94,220 hg ha^{-1} in 2017 (FAOSTAT, 2019). The decline in sweet potato yields is attributed to various biotic constraints among them nematodes and diseases (Kivuva *et al*., 2014; Echodu *et al*., 2018).

Nematodes are distributed in all environments as both parasites and free-living organisms and they influence crop production in different ways (Coyne *et al*., 2014). Soil temperature, moisture, food source, and host availability influence their growth, reproduction and survival (Pokharel, 2011). Free-living nematodes are beneficial nematodes that play key roles in the soil such as decomposition, mineralization of organic materials and regulation of pests including plant parasitic nematodes (Xiao *et al*., 2010; Neher *et al*., 2012; Ferris *et al*., 2012a). In addition, they are useful bio-indicators of soil health status in agro-ecosystems given their role in decomposition and regulation of microbial communities (Neher, 2001). Free-living nematodes occupy various trophic levels and are classified as bacterivores, fungivores, omnivores, and predators based on their feeding habits (Yeates *et al*., 1993). Bacterivores and fungivores aid in decomposition processes while omnivores and predatory nematodes feed on different food types and are indirectly involved in decomposition and pest regulation services (Hoorman, 2011).

Plant-parasitic nematodes (PPN) on the other hand negatively affect crop productivity. Concomitant infection of plants with nematodes and other pathogens constitute an important crop production constraint (Talwana *et al*., 2015). Among the top 10 PPN of economic importance, root-knot nematodes (RKN; *Meloidogyne* species) are classified as the most damaging due to their extensive host range and their rapid spread and colonization ability (Jones *et al*., 2013; Bebber *et al*., 2014). Of the four commonly occurring *Meloidogyne* species, *Meloidogyne incognita* is the most common species associated with sweet potato due to it being a suitable host (Jatala, 1991; Suzuki *et al*., 2012). *Meloidogyne* species are estimated to cause yield losses of up to 47.7% in sweet potato (Gapasin and Valdez, 1979). Other than RKN, sweet potato is also attacked by other PPN such as *Rotylenchulus*, *Pratylenchus*, *Ditylenchus*, *Scutellonema,* and *Paratrichodorus* (Olabiyi *et al*., 2016; Niere and Karuri, 2018). Typical symptoms of sweet potato infected by parasitic nematodes include lesions, root cracks, wilting, necrosis, and galls (Coyne *et al*., 2014). Cracking reduces the quality and marketability of the storage roots and also provide entry sites for other soil pathogens (Lawrence *et al*., 1986; Cervantes-Flores *et al*., 2008). Formation of root galls alters uptake, transport, and translocation of water, photosynthates and minerals (Williamson and Hussey, 1996). Worldwide, PPN causes an annual estimated yield loss of up to US $118 billion in many crops (Atkinson *et al*., 2011).

Management of PPN is mainly through the use of nematicides and soil fumigants. Despite these chemicals being fast-acting and effective (Adegbite and Agbaje, 2007; Dubey and Trivedi, 2011), their use is limited due to their negative effects on the environment, non-target organisms, human and animal health (Udo and Ugwuoke, 2010). Other nematode management strategies include crop rotation, cover cropping, soil solarization, and use of organic and inorganic amendments which have their own limitation (Mcsorley, 2011; Hajji and Horrigue-Raouni, 2012; Renc'o, 2013). For instance, crop rotation is complex in its design and implementation, especially where many nematode species are present (Briar *et al*., 2016). Soil solarization is expensive and hence inapplicable in large scale farming (Briar *et al*., 2016). The use of organic amendments presents a promising option which not only improves plant growth and increases yields but also controls soil-borne pests and diseases, including parasitic nematodes (Akhtar and Malik, 2000; Oka, 2010; Renc'o *et al*., 2011). Commonly used organic amendments with suppressive effects on PPN include animal manure, green manure and composted materials (Kimenju *et al*., 2008; Rivera and Aballay, 2008; Hu and Qi, 2010; Renc'o *et al*., 2011; Renc'o, 2013; Amulu and Adekunle, 2015; Osunlola and Fawole, 2015). These methods not only suppress plant parasitic nematodes but also stimulate free-living nematodes due to the addition of nutrients to the soil (Thoden *et al*., 2011). The effectiveness of organic amendments on PPN infecting sweet potato in Kenya has not been evaluated. The use of resistant sweet potato cultivars along with other low-cost organic nematode management strategies will be the most effective and environmentally safe method of suppressing RKN and other PPN in sweet potato fields.

This study, therefore, sought to assess the field performance of SPK 004 which is a local Kenyan sweet potato cultivar previously selected as RKN resistant under greenhouse conditions. It also aimed at determining the effect of intercropping sweet potato with maize, application of *T. diversifolia,* cow and goat manure on the abundance and diversity of both plant-parasitic and free-living nematodes, and how these amendments affected nematode metabolic footprints, ecological and functional indices.

1.2 Statement of the problem

Sweet potato plays a key role in food security (Woolfe, 1992). However, increased incidences of plant parasitic nematodes and other soil-borne pathogens have resulted in a decline in its production. Plant parasitic nematodes reduce crop yields by affecting both above and below-ground plant parts. Typical symptoms include galls, stunted growth, chlorosis and cracking of the roots among others (Coyne *et al*., 2014). Stunted growth, chlorosis and poor yields are as a result of disruption of water transport and photosynthates by nematodes. This has considerable effects on crop productivity. Annually, nematodes have been estimated to cause yield losses of US $118 billion worldwide (Atkinson *et al*., 2011). Thus, there is a need to adopt farming methods that will help in the management of plant parasitic nematodes. The use of resistant cultivars has been demonstrated to be effective and economical in managing nematodes especially root-knot nematodes, resulting in better yields and good quality tubers that increase marketability. However, knowledge of suitable cultivars, their availability to farmers, and even their performance in field conditions is limited. For instance, SPK 004, a local Kenyan sweet potato cultivar has been revealed to be resistant to *Meloidogyne incognita* under greenhouse conditions (Karuri *et al*., 2017). On the other hand, information on its field performance remains elusive.

1.3 Justification

Kenya's population has increased from 28.7 million inhabitants in 1999 to 49.7 million inhabitants in 2017 and is projected to be 67 million by 2030 (UN, 2017). Unpredictable climatic conditions and crop infestation by plant parasitic nematodes have resulted in a decline in food production. Therefore, there is an urgent need to increase food production by growing crops that show resistance to pests and diseases. Sweet potato is an ideal crop that not only plays a key role as a food security crop but also as a commercial and subsistence crop. However, sweet potato yields are greatly reduced due to infection by root-knot nematodes, which are widely distributed in Kenyan agro-ecosystems (Kimenju *et al*., 2009). Root-knot nematodes affect the quality of marketable roots and also predisposes the crop to other disease-causing organisms in the soil such as fungi and bacteria (Cervantes-Flores *et al*., 2008). Resource-constrained farmers in developing countries suffer yield losses of up to 85% due to *Meloidogyne* spp. (Coyne *et al*., 2014). The use of resistant sweet potato varieties will be the most economical, effective, and environmentally safe method of managing RKN in Kenyan sweet potato fields. Apart from RKN, other parasitic nematodes affect sweet potato productivity either directly or synergistically with other pathogenic fungi or bacteria, hence the need to control these nematodes. Most nematode management strategies increase the cost of production and have negative effects on environmental and human health. The use of low-cost organic nematode management strategies will be the most economical and environmentally safe method of managing PPN in sweet potato.

1.4 Research questions

1. What is the response of the sweet potato cultivar SPK 004 to infection by *Meloidogyne* species under field conditions?
2. How do different farming practices affect the population dynamics and diversity of parasitic nematodes during different growth stages of sweet potato?
3. How do different farming practices affect the population dynamics and diversity of free-living nematodes during different growth stages of sweet potato?

1.5 Objectives of the study

1.5.1 General objective

To evaluate the impact of sweet potato management practices on nematode communities and the field performance of SPK 004 in response to *Meloidogyne* species infestation.

1.5.2 Specific objectives

1. To determine the response of the sweet potato cultivar, SPK 004 to *Meloidogyne* species under field conditions
2. To assess the impact of different farming practices on population dynamics and diversity of plant parasitic nematodes in sweet potato.
3. To determine the population dynamics and diversity of free-living nematodes in sweet potato under different farming practices.

CHAPTER TWO

LITERATURE REVIEW

2.1 Sweet potato production and importance

Sweet potato (*Ipomoea batatas* L.*)* is among the world's important tuber crops widely cultivated in the tropic and sub-tropic regions (Lima *et al*., 2016). In sub-Saharan Africa, it is the third most important root and tuber crop after cassava (*Manihot esculenta*) and yam (*Dioscorea* species) (Yusuf and Wuyah, 2015). It is also the seventh most important crop on fresh weight basis after wheat, rice, maize, potato, barley, and cassava (Piedra-Buena *et al*., 2011). It plays a critical role as a source of food as it yields more reliably within a relatively short period than many other crops (Wabwile *et al*., 2016). This traditional crop has a short growing period and is thus able to fit in any cropping system. Its productivity is high per unit area compared to other crops as it performs well in less fertile soils with few agricultural inputs and is also drought insensitive. These characteristics make it an ideal crop for securing food to millions of people with low income (Woolfe, 1992).

Sweet potato has three main growth stages which include the initial, intermediate, and final phases. These phases vary with time and are also influenced by the variety (Woolfe, 1992). The initial phase occurs between zero to four weeks and in this stage, the rapid growth of adventitious/young roots and slow growth of vines occur. Intermediate phase occurs between the fourth to the eighth week and this involves rapid growth of vines, increase in leaf area and initial development of storage roots while in the final phase which occurs between seven to fifteen weeks, growth of vines ceases, leaf area reduces due to falling and yellowing and bulking of storage roots rapidly occurs (Woolfe, 1992; Stathers *et al*., 2013).

Sweet potato has various uses. The crushed tuber is used for making pastry, bread, and baby weaning foods (Kidmose *et al*., 2007). It is also a source of raw materials for industries where it is used to produce fermented products such as wine and ethanol (Duvernay *et al*., 2013). All plant parts are used as livestock feeds and the storage roots are sold for income generation (Githunguri and Migwa, 2007; Claessens *et al*., 2009). In

Kenya, sweet potato farmers in collaboration with value addition companies process the sweet potato for local and export markets (Kivuva *et al*., 2014). In addition, to the cultivation of white-fleshed varieties, farmers also cultivate orange and yellow-fleshed varieties which are rich in beta-carotene, a precursor for vitamin A. These are important in alleviating vitamin A deficiency especially in low-income countries and in particular among children and pregnant mothers (Hagenimana *et al*., 2000; Hagenimana *et al*., 2001; Hotz *et al*., 2012). Despite its versatility as a food security crop and numerous benefits, sweet potato production has declined from 125,050 hg/ ha in 2014 to 94,220 hg/ ha in 2017 in Kenya (FAOSTAT, 2019).

2.2 Sweet potato production constraints

Sweet potato production is constrained by different biotic and abiotic factors among them nematodes, weevils, aphids, and diseases caused by viruses, fungi, and bacteria (Nedunchezhiyan *et al*., 2012; Kivuva *et al*., 2014; Johnson and Gurr, 2016). Sweet potato weevils especially *Cylas formicarius* are among the production constraints which have been reported to cause yield losses of up to 45% (Lagnaoui *et al*., 2000). Viruses especially complex ones such as Sweet Potato Feathery Mottle Virus (SPFMV) and Sweet Potato Chlorotic Stunt Virus (SPCSV) constitute an important production constraint estimated to cause yield losses in the range of between 80 - 90% (Mukasa *et al*., 2006). Virus and weevil attacks predispose the tubers to other soil pathogens and diseases resulting in up to 100% losses (Kivuva *et al*., 2014). Nematodes are also attributed to causing significant yield reduction in sweet potato especially the root-knot nematodes (*Meloidogyne* species).

2.2.1 Plant parasitic nematodes associated with sweet potato

Plant parasitic nematodes are among the major biotic constraints in most crops. Worldwide they account for yield losses of up to US$ 118 billion (Atkinson *et al*., 2011). Among the parasitic nematodes associated with sweet potato are root-knot nematodes; *Meloidogyne* spp.) (Olabiyi *et al*., 2016; Niere and Karuri, 2018). These species are the most damaging among the top ten economically important plant-parasitic nematodes, and are distributed in Kenyan fields (Maina *et al*., 2011; Jones *et al*., 2013). *Meloidogyne incognita* is the most damaging species associated with sweet potato (Jatala and Russell, 1972; Suzuki *et al*., 2012). Other species attacking sweet potato include *M. arenaria, M. javanica,* and *M. hapla* (Lima *et al*., 2016). Typical symptoms of sweet potato attacked by *Meloidogyne* species include root galling, necrosis, and cracking. Root galls interfere with uptake and transport of water and photosynthates to different parts of the plant. As a result, above-ground symptoms of nutrient deficiency such as chlorosis, reduced shoot weight, and stunted growth occur (Williamson and Hussey, 1996). Longitudinal cracking of the roots and necrosis reduces the quality and marketability of storage roots (Lawrence *et al*., 1986; Siji, 2012). Root cracks also provide penetration and establishment of soil pathogens such as fungi which cause subsequent rotting (Lawrence *et al*., 1986). Specifically in sweet potato, *Meloidogyne* species are estimated to cause yield losses of up to 47.7% (Gapasin and Valdez, 1979). Thus, if no necessary measures are taken to control their spread and distribution in sweet potato fields, farmers will continue encountering serious losses.

Other parasitic nematodes associated with sweet potato include *Rotylenchulus, Pratylenchus, Ditylenchus, Paratrichodorus, Trichodorus, Longidorus*, *Helicotylenchus, Scutellonema, Hoplolaimus, Criconemella*, *Hemicycliophora*, *Hemicriconemoides* and *Xiphinema* species (Haougui *et al*., 2011; Karuri *et al*., 2017; Niere and Karuri, 2018). These nematodes occur alone or in association with other species causing serious infections. For example, *Rotylenchulus* and *Meloidogyne* species may occur alone or together causing concomitant infections (Thomas and Clark, 1983a; 1983b; Agu, 2006). Others like *Xiphinema*, *Longidorus,* and *Trichodorus* species act as vectors for transmitting viruses (Macfarlane, 2003; MacFarlane and Robinson, 2004). Different parasitic nematodes also affect sweet potato at distinct growth stages. For instance, *Rotylenchulus reniformis* attacks sweet potato during the first two stages and reduces the root system through a “pruning” effect (Clark and Wright, 1983) while *Meloidogyne incognita* affects the second and third growth stages (Lawrence, 1984; Agu, 2004). Thus, it is important to control these nematodes to mitigate or curb the losses incurred through infections.

2.3 Management of plant parasitic nematodes

2.3.1 Plant resistance in the management of root-knot nematodes (RKN)

Management of RKN in sweet potato has mainly been through chemical nematicides and crop rotation which have limitations. Chemical nematicides have been successfully used but their use is limited due to their negative effects on the environment, non-target organisms, human and animal health (Udo and Ugwuoke, 2010; Renc'o and Kovacik, 2012). Crop rotation has limited utility against nematode species with a wide host range such as *Meloidogyne* species which may parasitize as many as 3000 plant species (Abad *et al*., 2003). Thus the use of resistant cultivars is an ideal method that is cost-effective, safe, and environmentally-friendly (Gregory *et al*., 2017). Resistance refers to the plant's ability to suppress reproduction and nematode development (Mukhtar *et al*., 2014). Resistance to RKN is often controlled by multiple genes (Cervantes-Flores *et al*., 2002).

In a research study conducted by Corbett *et al*., (2011), the Mi-1.2 gene present in tomato was found to confer resistance against several species of RKN (*Meloidogyne* spp.). Completely or highly resistant cultivars allow little or no nematode reproduction. Juveniles in resistant cultivars are either incapable of penetrating the root, fail to develop after penetrating the roots or females fail to reproduce (Komiyama *et al*., 2006; Mukhtar *et al*., 2014). Moderately resistant cultivars allow some nematode reproduction while susceptible ones allow juveniles to penetrate through the roots, mature, and produce many eggs (Mukhtar *et al*., 2014). The use of sweet potato resistant cultivars significantly reduces the production costs and results in good-quality tubers and yields of high commercial value (Suzuki *et al*., 2012; Karuri *et al*., 2017).

Resistance to root-knot nematodes is often determined through assessments of galling severity, root necrosis, number of eggs, and egg masses (Piedra-Buena *et al*., 2011). Key attributes among crop varieties that show resistance of RKN are often manifested through reduction of root galling and necrosis severity, reduction or inhibition of nematode reproduction and establishment of feeding sites (Corbett *et al*., 2011). Galling index is a measure of nematode infection and has been used in the selection of sweet potato and yam cultivars with resistance to *M. incognita* (Cervantes-Flores *et al*., 2008; Mudiope *et al*., 2012). Research studies conducted on sweet potato and okra cultivars inoculated with

M. incognita races 1 and 3 showed that different cultivars have different levels of resistance (Mukhtar *et al*., 2014; Bernard *et al*., 2017; Karuri *et al*., 2017). Highly resistant cultivars show low root galling and necrosis, a low number of eggs and nematodes, and high fresh root weight. Susceptible cultivars usually have high levels of root galling and necrosis and fresh root weight is very low (Bernard *et al*., 2017). The resistance levels among sweet potato cultivars or their ability to endure infection by pathogens with minor effects on agronomic performances such as yield are due to specific genes (Cervantes-Flores *et al*., 2002).

In Kenya, various sweet potato cultivars are grown and these include Kemb 10, SPK 004, KSP 20, KSP 11, SPK 013, Kemb 23, Ex-Diani, and Mafuta (Karuri *et al*., 2017; Makini *et al*., 2018). Some cultivars tend to perform well in specific regions such as SPK 013 which performs well in the western region while others are suitable in most regions such as SPK 004 and Kemb 10 (Makini *et al*., 2018). Since its release in the year 2000, SPK 004 cultivar has been widely cultivated in Kenya (Mcharo and Ndolo, 2013). The cultivar has desirable attributes such as high sugar content, a large amount of beta-carotene, high dry matter content, high yields, and palatability (Karuri, 2009; Kidmose *et al*., 2007; Mcharo and Ndolo, 2013). SPK 004 is resistant to SPVD and has relatively stable yields in different environments (Karuri *et al*., 2009; Mwololo *et al*., 2009). In a greenhouse experiment conducted to determine the resistance levels among the various sweet potato varieties, SPK 004 was found to be highly resistant to *Meloidogyne incognita* (Karuri *et al*., 2017). Despite SPK 004 cultivar having these desirable traits, information on its performance in terms of RKN resistance and yields in the field is very scanty.

2.3.2 Management of other plant parasitic nematodes

Other than nematicides, plant parasitic nematodes are controlled using various strategies. These strategies include use of crop rotation, cover cropping, soil solarization, organic amendments such as animal manures, green manures and biological control agents (Everts *et al*., 2006; La Mondia, 2006; Hooks, *et al*., 2010; Mcsorley, 2011; Maina *et al*., 2011; Riga, 2011; Osunlola and Fawole, 2015). The use of organic amendments presents an alternative strategy of managing PPN as it results in a reduction of PPN population (Thoden *et al*., 2011). It is also a low-cost alternative for small-holder farmers with limited resources (Renc'o and Kovacik, 2012). Soil organic amendments are relatively cheap and have positive effects on soil quality and growth of plants (Renc'o, 2013). Application of different soil amendments support beneficial free-living nematodes and improve crop yields (Pakeerathan *et al*., 2009; Renc'o *et al*., 2007). Organic amendments reduce root infection by nematodes in various ways such as acting as physical barriers to their movement (Pakeerathan *et al*., 2009).

The different types of organic amendments used to suppress parasitic nematodes population include green plants such as *T. diversifolia*, cover crops, animal manure, compost, and plant residues (Renc'o and Kovacik, 2012). These amendments have varying effects on nematodes as well as the crops. Generally, a reduction in nematodes and an increase in crop yields are reported in various studies following the addition of green plants and organic amendments (Renc'o *et al*., 2011; Thoden *et al*., 2011). A decrease in PPN following application of different organic amendments is associated with the production of nematicidal compounds such as nitrogenous components including ammonia, different secondary metabolites, and organic acids (Thoden *et al*., 2011). Organic acids released during decomposition are toxic to parasitic nematodes. However, the nematicidal activity of the released organic acids depends on the physicochemical parameters of soil such as pH and temperature (Oka, 2010).

2.3.2.1 Use of green manure

Green manure (GM) play beneficial roles such as protecting soil from erosion, increasing nutrients and improving soil physicochemical and biological properties (Jama *et al*., 2000; Mwangi and Mathenge, 2014; Chimouriya *et al*., 2018). Secondary benefits of GM include control of soil pathogens including parasitic nematodes through several mechanisms such as the release of phytochemicals that are toxic to nematodes and stimulation of antagonists (Hooks *et al*., 2010). Among the green manure crops that have been reported to be effective in suppressing PPN include *Brassica*, *Crotalaria juncea*, *Leucaena leucocephala*, and *T. diversifolia* (Mathagu, 2002; Kimenju *et al*., 2008; Riga, 2011: Silpi and Dhillon, 2017).

In Kenya, *T. diversifolia* is used for various purposes such as improving soil fertility and plant growth due to the provision of essential nutrients such as nitrogen (Jama *et al*., 2000; Mwangi and Mathenge, 2014). It is also a suppressant of nematode species when incorporated into the soil (Kimenju *et al.*, 2008; Akinyemi *et al*., 2009; Akpheokhai *et al*., 2012; Odeyemi *et al*., 2014). *T. diversifolia* acts as an antagonistic plant by producing nematicidal compounds such as alkaloids and saponins, which are toxic to nematodes and other crop pests (Kimenju *et al*., 2008; Odeyemi and Adewale, 2011). These compounds suppress galling and nematode reproduction (Akpheokhai *et al*., 2012; Odeyemi *et al*., 2014). Reduction in nematode population and damage improves root health, root anchorage, and uptake of water and nutrients (Akpheokhai *et al*., 2012). Despite *T. diversifolia* green manure being readily available, its potential in managing nematodes in sweet potato fields has not been fully exploited.

2.3.2.2 Use of animal manure

Organic manure not only improves soil properties and overall yields but also reduces losses resulting from pests and diseases (Nahar *et al.*, 2006; Pakeerathan *et al*., 2009; Renc'o and Kovacik, 2012). Organic manure is rich in elements such as nitrogen, calcium, magnesium, phosphorous, and micro-elements such as zinc and copper which are important nutrients for plant growth (Hu and Qi, 2010). At small-scale, this manure is readily available, environmentally friendly, and relatively cheap (Rivera and Aballay, 2008). Frequently used animal manure include that from poultry, cows, goats, horses, and swine and they have been reported to be effective in suppressing PPN (Orisajo *et al*., 2008; Pakeerathan *et al*., 2009; Abolusoro *et al*., 2013; Daramola *et al*., 2013; Tanimola and Akarekor, 2014; Amulu, and Adekunle, 2015; Osunlola and Fawole, 2015).

Efficacy of goat manure in suppressing nematodes has been reported by various authors (Pakeerathan *et al*., 2009; Tanimola and Akarekor, 2014; Osunlola and Fawole, 2015). Suppression of nematode populations by goat dung is due to the resulting changes in soil physical and chemical properties which may alter the relationship between plant and nematodes resulting in the plant being more resistant to nematode development within the roots (Osunlola and Fawole, 2015). Goat manure pellet-like structure increases soil particles' ability to aggregate thereby restricting nematode movement and this, in turn, suppresses the nematode population (Pakeerathan *et al*., 2009). Similarly, the effectiveness of cow manure in managing nematodes has been reported in various studies, as manifested by a reduction in root galling, nematode reproduction and populations (Abolusoro *et al*., 2013; Tanimola and Akarekor, 2014; Amulu and Adekunle, 2015; Galadima *et al*., 2015; Osunlola and Fawole, 2015). A decrease in PPN is associated with the production of nematicidal compounds such as ammonia, different secondary metabolites, and organic acids (Thoden *et al*., 2011). In addition, organic manure stimulates the multiplication of soil microorganisms such as fungi and bacteria, which are parasites of nematodes. Animal manure is also rich in essential macro and micro-elements which are important for the growth and development of plants. The development of a healthy root system may render plants to be more resistant to nematode infection (Oka, 2010; Thoden *et al*., 2011). However, nematicidal activity depends on soil physical and chemical parameters such as pH and temperature (Oka, 2010).

2.3.2.3 Intercropping as a nematode management practice

Intercropping is growing two or more crops in the same field at the same time. The main goal is to increase yields by making use of resources not utilized by a single crop. This method minimizes crop failure, ensures resources are effectively used, and may play a great role in food security (Ouma and Jeruto, 2010). In Kenya, intercropping is widely practiced and legumes are included often to improve the soil’s nitrogen status (Clermont Dauphin, 1995). This cropping system has been used in the management of nematodes with varying responses being reported. Studies conducted to evaluate the effect of intercropping different crops on plant parasitic nematodes have reported a decrease in the population of PPN (Berry *et al*., 2009; Chitamba *et al*., 2014; Ismail and Hassabo, 2014; Linguya *et al*., 2015). However, other studies have reported that intercropping may result in negative effects such as increasing PPN populations, especially where susceptible hosts are intercropped (Berry *et al*., 2009). Reduction in populations of plant-parasitic nematodes may, therefore, depend on host suitability or the companion crops used (Berry *et al*., 2009). The companion crop can either be a suitable or poor host of the nematodes. Poor host crops have a greater impact on reducing nematodes compared to intermediate or good hosts (Chitamba *et al*., 2014). Despite it being relatively cheap and easy to practice, very few studies have focused on the impacts of intercropping sweet potato with other crops as a nematode management strategy.

2.4 Free-living nematodes

Besides PPN, sweet potato is also associated with free-living nematodes. These groups of nematodes form the larger portion of nematodes yet very little attention is paid to them, compared to PPN (Andrássy, 2009). These beneficial organisms occupy different trophic levels and are often grouped based on their feeding habits. They include bacterial feeders, fungal feeders, omnivores, and predatory nematodes (Yeates *et al*., 1993). Their main roles are nutrient mineralization, decomposition of organic matter, biological control of nematodes and they are also indicators of the health status of the ecosystem (Ingham *et al*., 1985; Bongers, 1990; Neher, 2001; Khan and Kim, 2007; Ferris *et al*., 2012). Bacteria feeding nematodes feed on bacteria and are known to contribute between 30% and 50% of nitrogen present in the plant through their activities (Ingham *et al*., 1985). Fungivorous nematodes feed by puncturing the cell wall of fungal hyphae using their stylet (Ingham *et al*., 1985). Predatory nematodes feed on invertebrates such as protozoa, rotifers, and other nematodes. They unsystematically feed on both free-living and plant-parasitic nematodes. Omnivores consume a wide variety of food such as invertebrates, bacteria, plant, and fungi.

2.4.1 Organic amendments and their effect on free-living nematodes

In general, the application of any organic soil amendments has been reported to increase the population of free-living nematodes especially bacterivores and fungivores (Thoden *et al*., 2011). Animal manure and compost increase free-living nematodes (Villenave *et al*., 2003; Forge *et al*., 2005; Nahar *et al*., 2006; Wang *et al*., 2006; Langat *et al*., 2008). The elevated numbers of free-living nematodes especially bacterial and fungal feeding nematodes under organic substrates application is thought to be due to an increase in bacteria and fungi populations that provide excellent food sources (Griffiths *et al*., 1994). Amendments with low carbon: nitrogen (C/N) ratio such as animal manures are good sources of bacteria and thus induce bacteria population while amendments with a high C/N ratio fuels fungal nematode population (Thoden *et al.*, 2011).

An increase in bacterial feeding nematodes in response to the organic amendment application is often observed. However, varying responses are often manifested in relation to the other trophic groups (fungivores, omnivores, and predators). Pan *et al*. (2015), Wang *et al*. (2006) and Villenave *et al.* (2010) reported that the application of organic amendments has significant effects on bacterivores but not on fungivores, omnivores, and predatory nematodes. In fields amended with manure, omnivores have been shown to increase while predatory nematodes remain unaffected (Hu and Cao, 2008; Leroy *et al*. 2009). Maintenance and increase in the populations of free-living nematodes are important owing to their key soil functions such as decomposition, nutrient mineralization, and biological control of PPN (Khan and Kim, 2007; Ferris *et al*., 2012). Application of low-cost amendments as a technique for controlling PPN may affect the structure, population dynamics, and diversity of free-living nematodes. Since free-living nematodes perform key soil functions, it is imperative that the impact of different PPN management strategies on these nematodes is evaluated.

CHAPTER THREE

Response of sweet potato cultivar, SPK 004 to *Meloidogyne* species under field conditions

3.0 Abstract

The root-knot nematodes (RKN), *Meloidogyne* species are devastating sweet potato pests that cause huge yield losses. Various strategies have been used with limited success to manage these damaging nematodes. This study sought to evaluate the field performance of SPK 004, a local Kenyan sweet potato cultivar that has been previously selected as resistant to RKN (*Meloidogyne incognita*) under greenhouse conditions. Field trials were conducted in a field naturally infested by RKN in Mwea, Kenya. Experimental plots were established in a randomized complete block design, where two treatment plots were planted with SPK 004, while other plots were planted with SPK 004 and treated with a nematicide. Soil samples were collected before planting and during harvest to determine the initial and final RKN population. Root-knot nematodes were extracted using the modified Baermann technique before identification to the genus level. Root samples obtained at harvest were rated visually for resistance using galling index (GI) on a scale of 1-5, where 0 = 0 galls and 5 ≥ 100 galls. Dry matter content and marketable yield were also determined. Analysis of variance was used to determine differences in the number of nematodes, yield, and dry matter content between the two treatments. Tukey HSD test was used to separate significantly different treatment means. The GI was used to classify SPK 004 as resistant or susceptible. There was no significant difference in SPK 004 resistance in the two treatments. However, nematicide plots had a higher number of *Meloidogyne* species, higher GI, and low marketable yields. Findings from this study confirmed the greenhouse results, where this cultivar was found to be very resistant to *Meloidogyne incognita*. This nematode-resistant sweet potato cultivar may be used in sweet potato fields infested with high populations of *Meloidogyne* species and in rotation with non-host crops for management of RKN. This will be useful in not only reducing the production costs, overreliance on nematicides, and their associated negative effects but also in increasing the quality and market value of storage roots.

3.1 Introduction

Sweet potato (*Ipomoea batatas*) is an important crop that is widely cultivated in tropical and subtropical regions around the world (Oliviera Lima *et al*., 2016). Its ability to tolerate drought and perform well under unfavorable conditions makes it a preferred food security crop in SSA (Woolfe, 1992; Kaguongo *et al*., 2012; Stathers *et al*., 2013). Sweet potato is used as human food, feed for livestock, and as industrial raw material (Githunguri and Migwa, 2007; Claessens *et al*., 2008; Duvernay *et al*., 2013). Cultivation of orange and yellow sweet potato varieties help in alleviating vitamin A deficiency as they are rich in beta-carotene, a precursor for vitamin A (Hagenimana *et al*., 2000; Hotz *et al*., 2012). Despite its versatility as a food security crop and numerous benefits, sweet potato yields are affected by various biotic factors among them plant-parasitic nematodes. Parasitic nematodes attacking sweet potato include *Meloidogyne* species (root-knot nematodes) and *Rotylenchulus* species (Olabiyi *et al*., 2016; Niere and Karuri, 2018).

Root-knot nematodes are ranked as the most damaging plant-parasitic nematodes with a cosmopolitan distribution (Sasser, 1977; Jones *et al*., 2013). This genus is composed of more than 100 species with *Meloidogyne incognita*, *M. javanica*, *M. arenaria,* and *M. hapla* being considered as the four major species (Moens *et al*., 2009). Sweet potato is mostly damaged by *Meloidogyne incognita* as it provides a suitable host for its growth and development (Jatala and Russell, 1972; Suzuki *et al*., 2012). Typical symptoms of sweet potato attacked by RKN include; root galling, longitudinal cracking, and nutrient deficiency symptoms such as chlorosis and reduced shoot (Lawrence *et al*., 1986; Williamson and Hussey, 1996; Siji, 2012). *Meloidogyne* species are estimated to cause yield losses of up to 47.7% in sweet potato (Gapasin and Valdez, 1979). However, paradoxically much more damage caused by RKN goes unnoticed. Thus, if necessary measures are not taken to control the nematodes in sweet potato fields, farmers will continue encountering serious losses.

Management of RKN in sweet potato has mainly been through chemical nematicides and crop rotation with non-host crops with limited success. For instance, nematicides have been successfully used but their use is limited due to their negative effects on the environment, non-target organisms, human and animal health (Udo and Ugwuoke, 2010).

Crop rotation has limited utility against nematode species with a wide host range such as *Meloidogyne* species which may parasitize as many as 3000 plant species (Abad *et al*., 2003). Thus the use of resistant sweet potato cultivars presents an ideal method of managing *Meloidogyne* species as it is cost-effective, safe, and environmentally safe (Gregory *et al*., 2017). This method not only suppresses parasitic nematodes and reduces production costs, but it also improves the quality and yields of sweet potato (Suzuki *et al*., 2012; Karuri *et al*., 2017). Effectiveness of resistant cultivars in the management of root-knot nematodes in sweet potato fields has not been fully explored. The study, therefore, aimed to evaluate the field performance of SPK 004, a local Kenyan sweet potato cultivar that has been previously selected as RKN resistant under greenhouse conditions.

3.2 Materials and methods

3.2.1 Experimental site

The study was carried out at Nyangati sub-location in Mwea, Kirinyaga County, Kenya. It lies between latitude 0° 37´ 11.1" S and longitude 37º 21' 41.2" E. and it is in the Low Midland (LM) agro-ecological zone, at an altitude of 1,204 m above sea level. The soil in the area is vertisol (black cotton soil) with clay content that is higher than 30% (Jaetzold *et al*., 2009). Soil physicochemical properties of the site are given in Table 3.1. During the study period, the temperature ranged between 12.3°C to 21.6°C while precipitation ranged from 21.6 mm to 619.2 mm (Table 3.2).

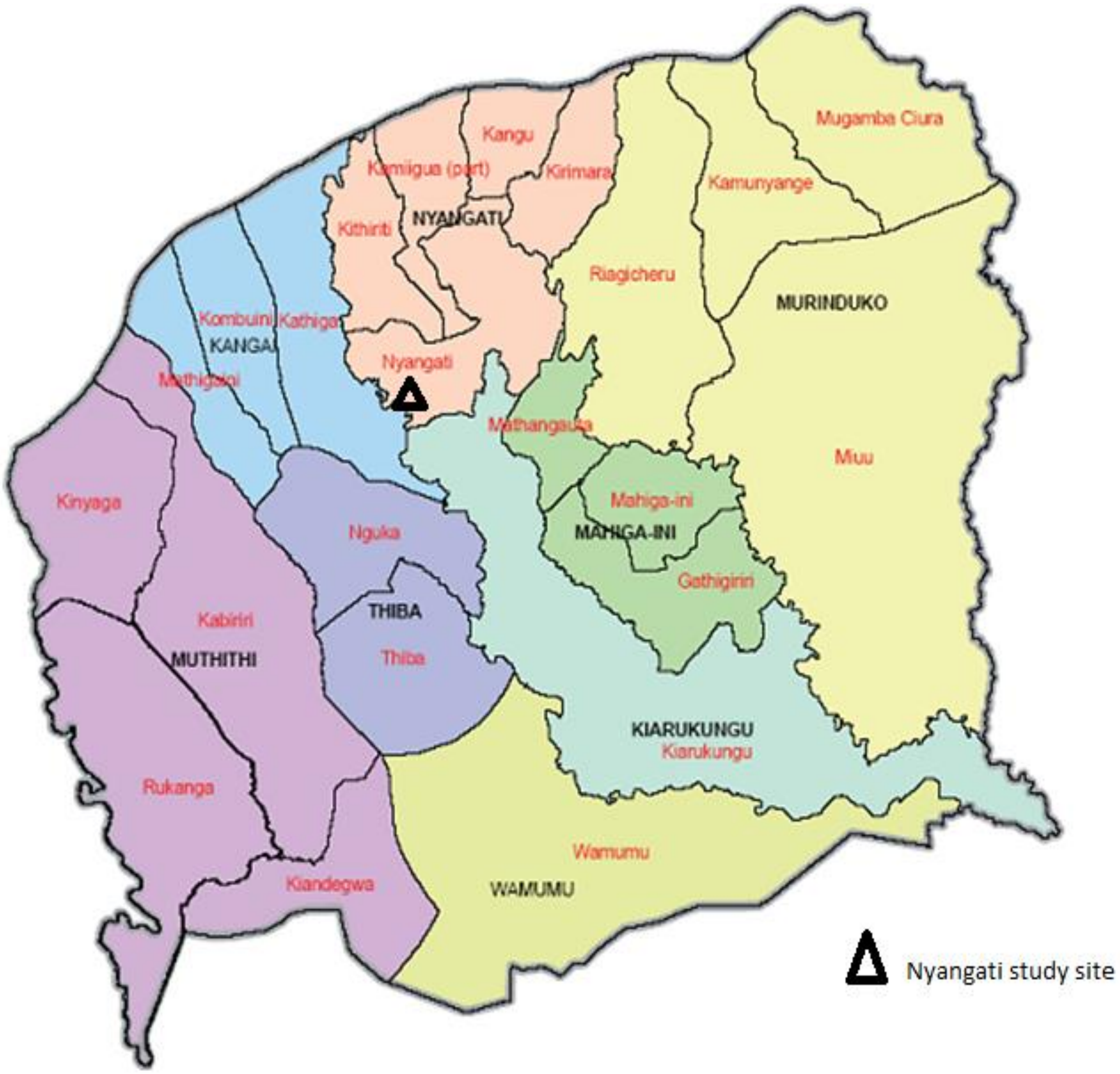

Figure 3.1: Map showing the study area in Nyangati Location, Mwea Constituency (Map obtained from google maps).

3.2.2 Experimental design and planting

The study was conducted during the long rains (March to July 2018) and short rains (October 2018 to February 2019) seasons. The experiment was laid out in a randomized complete block design (RCBD) with four replicates per treatment. The treatment comprised plots planted with SPK 004, and plots planted with SPK 004 and treated with a nematicide (control). Each experimental plot measured 5 m by 5 m and was separated by 1 m buffer zone. Each plot comprised of 12 ridges with 0.6 m spacing. The RKN resistant sweet potato cultivar, SPK 004 was used. The vines were planted on ridges, with a single vine (30 cm long) per hole spaced at 30 cm between the vines and 60 cm between the ridges. Nematicide confidor WG 70^{TM} (nematicide used by farmers in Embu county) was used to treat plots, where the application was done at the soil base in each hole at a rate of 720g kg^{-1} before planting the vines. Weeding was done manually in the first and second months whereas hilling up was done in the third month.

3.2.3 Soil sampling

Soil samples were randomly collected at a depth of 25 cm around the sweet potato roots using a 3.5 cm diameter soil auger. The collection of samples was done at pre-planting and during harvest (0 and 120 days after planting (DAP).Soil samples were collected from five points in each plot using a cross-diagonal sampling pattern (Coyne *et al.*, 2014). After collection, the five soil sub-samples from each plot were mixed thoroughly to homogenize the soil samples and triplicate 250 g of homogenized soil sample per plot was used in nematode extraction. The samples were placed in a well-labeled plastic bag and taken to the university of Embu laboratory for nematode extraction.

3.2.4 Analysis of soil properties and weather data collection

Soil samples were taken to Kenya Agricultural and Livestock Research Organization (Nairobi) for analysis of physicochemical properties. Data on temperature and rainfall during the study period was obtained from the Kenya Meteorological Department.

3.2.5 Collection of plant root samples and determination of dry matter content

During harvest, sweet potato root samples were collected and rated visually for galling severity using a galling index scale of 0-5 where 0= no galls (immune), 1=1-2 galls (highly resistant), 2=3-10 galls (very resistant), 3=11-30 galls (moderately resistant), 4=31-100 galls (slightly resistant) and 5= > freshly harvested 100 galls (susceptible) (Taylor and Sasser, 1978). Root fresh weight was determined. To determine the dry matter content, sixteen pieces of storage roots from each plot were washed, dried, and then peeled. The roots were then sliced into small sections, placed in open trays, and dried at 100°C for three days (until a constant weight was obtained) in an oven. After drying, the samples were weighed immediately to obtain the dry weight. The percentage of dry matter content was calculated as follows;

$$\text{\% Dry matter content} = \text{dry weight/ fresh weight} \times 100 \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

3.2.6 Assessment of sweet potato yield

Marketable and unmarketable yields were determined based on tuber weight. Unmarketable sweet potato tubers, i.e. tubers weighing less than 70 g, deformed, and with cracks as a result of nematodes and other pest damage were sorted out and weighed. Marketable yield was obtained by getting the difference between the harvested yields less the unmarketable yield. The yield obtained from each plot was used to calculate the total yields in tonnes per hectare based on the area of the plot.

3.2.7 Nematode extraction and identification

Root-knot nematodes were extracted using the modified Baermann's technique (Hooper, 1990) from the triplicate 250 g soil samples. The extracted nematodes were heat-killed and fixed in a golden solution (Hooper *et al*., 2005). Subsequently, under a compound microscope, the extracted nematodes were counted and identified to the genus level. Identification was based on their morphological features according to (Bongers, 1988).

3.2.8 Statistical analysis

Treatments effect on RKN population, galling index (GI), percent dry matter content (% DM), total and marketable yields during the two seasons were determined through analysis of variance (ANOVA). Data on RKN population were log-transformed before analysis to standardize the variance. The means were separated using Tukey HSD test. All statistical analyses were performed using R statistical software (R Core Development Team, 2015).

3.3 Results

3.3.1 Soil chemical and physical properties

The soils from study sites exhibited a high percentage of sand (46.67 ± 3.712) and clay (44.0 ± 4.0) and low amounts of silt (9.33 ± 0.667). The soils were slightly acidic with mean pH ± SE, 5.85 ± 0.057. The soils had high amounts of iron and phosphorus and low amounts of sodium and Nitrogen (Table 3.1).

Table 3.1: Soil chemical properties at Nyangati study site

Element	Mean	Standard error
Nitrogen %	0.18	0.003
Calcium me %	2.03	0.05
Phosphorus ppm	16.67	1.667
Potassium me %	0.75	0.096
Calcium me %	6.07	0.788
Magnesium me %	3.63	0.135
Manganese me %	0.97	0.114
Copper ppm	2.95	0.090
Iron ppm	23.50	3.239
Zinc ppm	0.20	0.029
Sodium me %	0.16	0.074

The mean ± Standard error readings are in parts per million (ppm) and mill equivalent (me).

3.3.2. Rainfall and temperature during the study period

Highest amount of rainfall was recorded in April 2018 (619.2 mm) and the least in February 2019 (21.6 mm). August 2018 was the coldest month (12.3^{o}C) and February 2019 the warmest (21.6^{o}C) (Table 3.2).

Table 3.2: Rainfall and temperature data at Nyangati study site.

Month	Rainfall (mm)	Temperature (°C)
March	245	14.6
April	619.2	14.7
May	299.6	14.8
June	78	13.3
July	51.5	12.7
August	18.8	12.3
September	38.5	13.0
October	51.5	14.6
November	100.1	15.5
December	109.2	14.7
January	46.5	13.6
February	21.6	21.6

3.3.3. Performance of sweet potato cultivar SPK 004 under field conditions

During the long rains season, there was no difference between the two treatments in the population density of *Meloidogyne* species, galling index, dry matter content, total yield, and marketable yield. Plots planted with SPK 004 recorded an insignificantly lower number of *Meloidogyne* species and galling index (Figure 3.2; Figure 3.3). These plots also had high dry matter content and marketable yield compared to control (nematicide treated) plots (Table 3.3).

During the short rains season, only *Meloidogyne* population density differed significantly between the two treatments (Figure 3.2; F = 5.052; P = 0.04). Dry matter content, root galls, total and marketable yields did not differ significantly between the two treatments (Table 3.3). Based on the galling index (root galls), the two treatments were very resistant to RKN (*Meloidogyne* species).

Table 3.3: Mean number of *Meloidogyne* species, galling index, dry matter content, total and marketable yield (MY) in SPK 004 plots and SPK 004 plus nematicide (control) plots during long rains and short rains season.

	SPK 004		**Control**			
Long rains season	Mean	SE	Mean	SE	F value	P value
Meloidogyne	49.833a	7.054	58.50a	2.907	1.29	0.283
Galling index	2.667a	0.333	3.00a	0.577	1	0.374
Dry matter content (%)	41.153a	1.347	41.025a	0.115	0.988	0.344
Total yield (t ha^{-1})	8. 264a	0.069	8.333a	0.173	2.5	0.145
MY (t ha^{-1})	3.672a	0.216	3.556a	0.145	0.147	0.721
Short rains season						
Meloidogyne	41.167b	10.3	71.5a	8.721	5.052	0.04*
Galling index	4.00a	0.577	6.00a	1.155	4	0.116
Dry matter content (%)	32.13a	2.097	31.88a	0.1	0.142	0.907
Total yield (t ha^{-1})	6.903a	0.577	6.667a	0.115	0.289	0.603
MY (t ha^{-1})	2.816a	0.276	2.508a	0.115	1.247	0.327

Means and corresponding standard error (SE) within the same row followed by the same letters are not significantly different ($P < 0.05$). SPK 004 and control represent untreated plots planted with SPK 004 and plots planted with SPK 004 and treated with nematicides, respectively. t ha^{-1}= tonnes per hectare,*= $P < 0.05$.

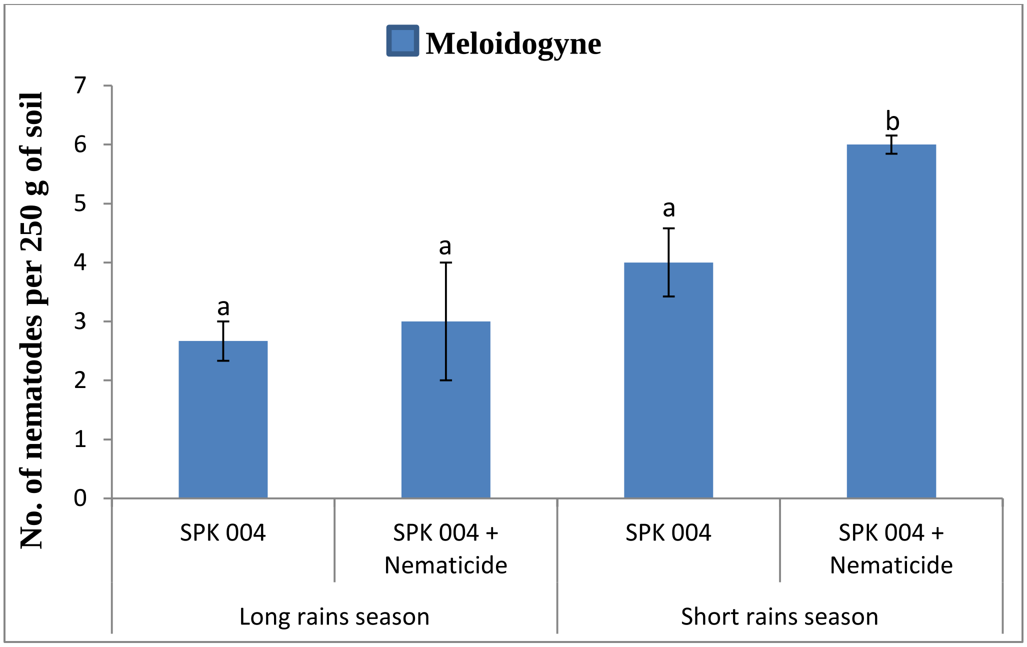

Figure 3.2: Abundance of *Meloidogyne species* in plots planted with SPK 004 and SPK 004 + nematicide plots during long rains and short rains season.

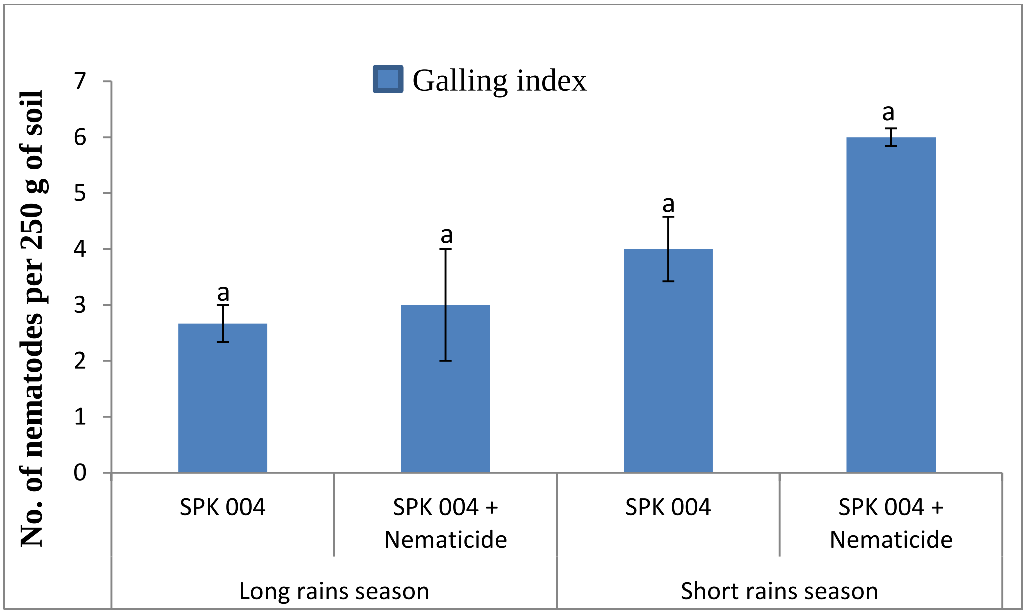

Figure 3.3: Mean number of galls in a plot planted with SPK 004 and SPK 004 + nematicide plots during long rains and short rains season.

3.4 Discussion

The present study aimed at evaluating the field performance of SPK 004 which was previously selected as very resistant to root-knot nematodes under greenhouse conditions

(Karuri *et al*., 2017). The results confirmed that SPK 004 was very resistant to *Meloidogyne* species infection. The level of resistance was comparable between plots that were not treated with nematicides and control plots that had nematicides. Plots planted with SPK 004 had a non-significant low galling index in the two seasons and significantly lower number of *Meloidogyne* species in the short rains season compared to the control. Galling index (GI) is a key feature in measuring nematode infection and was used in this study to measure resistance in combination with the nematode population(Sasser *et al*., 1984). The galling index has been used in the past to select sweet potato and yam varieties with resistance to *Meloidogyne* species (Cervantes-Flores *et al*., 2002; Mudiope *et al*., 2012). Based on the galling index (Taylor and Sasser, 1978), SPK 004 was very resistant to *Meloidogyne* species. It had a mean galling index of 2.667 and 3.00 in the long rains season and 4.00 and 6.00 in the short rains season for SPK 004 and SPK 004 + nematicide plots respectively.

Chemical nematicides have been successfully used to control or suppress root-knot nematode population and root galls (Dubey and Trivedi, 2011; Daramola *et al*., 2013; Tanimola and Akarekor, 2014). This was not the case in the study as SPK 004 treated with nematicide (confidor WG 70) had a higher number of nematodes compared to untreated cultivar in the short rains season. Possible explanations for the increase in the nematode population irrespective of the application of nematicide may be that the nematicide interfered with the resistance level of this cultivar, rendering it susceptible to RKN.

Mechanisms of resistance of sweet potato to *Meloidogyne* species are not fully understood. Both qualitative and quantitative types of inheritance have been proposed for sweet potato resistance to RKN (Ukoskit *et al*., 1997). Molecular and phenotypic data suggest that resistance to *Meloidogyne* species in sweet potato is conferred by several genes (Cervantes-Flores *et al*., 2002). Thus observed resistance may have resulted from the additive effects of the resistance genes (Cervantes-Flores *et al*., 2008). Furthermore, infective juveniles (J2 stage) penetrate both susceptible and resistant cultivars; however, in resistant cultivars, hypersensitive response or necrotic reaction occurs and this prevents nematodes from developing further due to failure of the nematodes to establish feeding sites (Williamson, 1998; Komiyama *et al*., 2006).

Dry matter (DM) is an important characteristic in sweet potato and this is directly linked to consumer's preference (Woolfe, 1992; Mcharo *et al*., 2001). Determination of the dry matter content revealed the two treatments had high dry matter content in the two seasons, which ranged between 31.88 and 42.00%. This percentage is above the critical value of 27% accepted by most consumers (Carey *et al*., 1997). Similar percentage range of DM has previously been reported in various regions in East Africa (Mwanga *et al*., 2007a; 2007b; Karuri, 2009; Mcharo and Ndolo, 2013). High dry matter content in SPK 004 is an added advantage as Kenyan consumers prefer sweet potato genotypes with a high dry matter with mealy texture compared to those with low dry matter (Mcharo and Ndolo, 2013; Ssemakula *et al*., 2014). Seasonal variation in dry matter content observed in the two seasons may be due to a lower amount of rainfall recorded during this season (Table 3.2). Low amount of rainfall recorded in the short rains season may have contributed to a decrease in the overall expansion of the storage roots and this may have resulted in the low DM content (Mcharo and Ndolo, 2013).

Higher yields have been associated with SPK 004 cultivar in various regions of Kenya and Uganda (Mwanga *et al*., 2007; Mcharo and Ndolo, 2013). Similar observations were made in this study. However, lower yields were recorded in this study compared to yields obtained in other parts of Kenya (Mcharo and Ndolo, 2013). This could be attributed to environmental variations in the different regions where the sweet potato was cultivated. Brenneman *et al*. (2017) observed no significant difference between yields of nematicide-treated and untreated soybean resistant cultivars. Reduction in yields may be attributed to root injury due to penetration and feeding by the nematodes. Infection by *Meloidogyne* species leads to the formation of galls in the roots and giant cells that interfere with the translocation of photosynthates and water in the plant (Di Vito *et al*., 2004). Inadequate supply of water, nutrients, and photosynthates lead to poor growth of foliage and roots which in turn lead to a decline in yield production (Khan and Khan, 1997; Hussain *et al*., 2016; Kayani *et al*., 2017). There were seasonal variations in the total and marketable yields (Table 3). Lower yield in the short rains season may probably have been due to low amount of rainfall which may have resulted in limited root expansion (Ekanayake *et al*., 1990; Mcharo and Ndolo, 2013).

Other than the traits observed from our study (RKN resistant, dry matter, and yield), SPK 004 is widely accepted due to high palatability scores (high sugar content and the low fiber content of the roots), ease of cooking and also resistance to sweet potato virus disease (Karuri, 2009; Mcharo and Ndolo, 2013). It also has high amounts of beta-carotene, a precursor for vitamin A, which is important in alleviating vitamin A deficiency among children and pregnant women (Hagenimana *et al*., 2000; Kidmose *et al*., 2007; Hotz *et al*., 2012).

3.5 Conclusion

This study has revealed that SPK 004 is very resistant to *Meloidogyne* infestation. This cultivar can, therefore, be planted in areas with a high *Meloidogyne* species population. This may reduce the production cost as well as increase the overall yields and market value through reduced cracking of the storage roots. However, further studies are needed as the performance of SPK 004 with *Meloidogyne* resistance may vary under different environmental conditions, and also the effect of continually cropping this resistant cultivar.

CHAPTER FOUR

Impact of different farming practices on population dynamics and diversity of plant parasitic nematodes in sweet potato

4.0 Abstract

Sweet potato is an important food security crop but its production is limited by various biotic constraints including plant-parasitic nematodes (PPN). In Kenya, current PPN management practices in sweet potato have several limitations hence the need for alternative low-cost management strategies. This study tested the efficacy of intercropping maize and sweet potato and application of *Tithonia diversifolia* (marigold), cow and goat manure on suppression of PPN, and the effect of the treatments on metabolic footprints, ecological and functional indices. Field experiments were established in a randomized complete block design involving the four treatments and unamended controls. Soil samples were collected after 30 days for four months during long (LR) and short (SR) rains seasons. Furthermore, the nematodes were identified to the genus level. Forty-seven nematode genera belonging to five trophic groups were identified in both seasons. Principal response curves analysis revealed that goat manure had the most pronounced effects on PPN of economic importance in sweet potato. All treatments indicated a low diversity of predatory nematodes. There were differences in metabolic footprints, ecological and functional indices during LR and SR. In cow manure plots, the predator and omnivore footprint were high during the long and short rains season, respectively. Functional metabolic footprints categorized all plots as degraded in both seasons except plots with intercropping maize and sweet potato which were structured in SR. However, goat manure bordered a structured ecosystem in LR while cow manure bordered a structured ecosystem in both seasons. Goat manure may have enhanced the natural ability of soil to regulate PPN affecting sweet potato. A reduction in soil perturbations may be required to improve the structure of soil food webs in sweet potato fields under organic management.

4.1 Introduction

Sweet potato (*Ipomoea batatas*) is a preferred food security crop in sub-Saharan Africa (SSA) because it is drought tolerant, performs well under unfavorable conditions and requires little or no management inputs compared to other crops (Woolfe, 1992; Kaguongo *et al*., 2012; Stathers *et al*., 2013). In Kenya, sweet potato is mainly cultivated by smallholder farmers in Central, Rift Valley, Nyanza, Western and Coast Provinces with intensive production in Nyanza and Western regions (Kaguongo *et al*., 2012). The entire sweet potato plant has varied uses such as human food, feed for livestock, and as industrial raw material (Githunguri and Migwa, 2007; Claessens *et al*., 2008; Duvernay *et al*., 2013). Sweet potato yields in Kenya have steadily declined from 125,050 hg ha^{-}1 in 2014 to 94,220 hg ha^{-}1 in 2017 (FAOSTAT, 2019). Production is limited by various biotic constraints including weevils, aphids, nematodes, and diseases (Kivuva *et al*., 2014; Echodu *et al.*, 2018). Plant parasitic nematodes (PPN) negatively affect crop productivity. Worldwide, PPN causes an annual estimated yield loss of up to $118 billion in many crops (Atkinson *et al*., 2011).

Sweet potato is characterized by three distinct growth phases with variations in the time for each phase based on the cultivar (Woolfe, 1992). Different parasitic nematodes affect sweet potato at particular growth stages. For instance, the reniform nematode, *Rotylenchulus reniformis* attacks sweet potato during the first two stages and reduces the root system through a "pruning" effect (Clark and Wright, 1983) while *Meloidogyne incognita* affects the second and third growth stages (Lawrence, 1984; Agu, 2004). Concomitant infection by multiple PPN species cause varied responses in sweet potato (Thomas and Clark, 1983a; Agu, 2006). Root galls, necrosis, and root cracking are key symptoms of sweet potato infected by parasitic nematodes (Coyne *et al*., 2014). Root galls limit the absorption and transport of nutrients and water while cracking and necrosis reduce the quality and marketability of storage root (Lawrence *et al*., 1986). The infection sites create entry points for secondary pathogens such as fungi and bacteria which further lowers the yields (Cervantes-Flores *et al*., 2008; Nicol *et al*., 2011).

Economically important PPN associated with sweet potato include *Meloidogyne*, *Pratylenchus*, *Rotylenchulus*, and *Ditylenchus* species (Niere and Karuri, 2018). Most

PPN are controlled using nematicides and soil fumigants. Despite these chemicals being fast-acting and effective (Adegbite and Agbaje, 2007; Dubey and Trivedi, 2011; Abbas *et al*., 2015), their use is limited due to their negative effects on the environment, non-target organisms, human and animal health (Udo and Ugwuoke, 2010; Renc'o and Kovacik, 2012). Other nematode management strategies include the use of resistant cultivars, crop rotation, use of cover crops, soil solarization and use of microorganisms which also have their limitations (Mcsorley, 2011; Hajji and Horrigue-Raouni, 2012; Suzuki *et al.*, 2012; Gregory *et al*., 2017). Resistant cultivars are not available for most crops and those that exist are nematode species-specific and hence not suitable for PPN control in agroecosystems with multiple species (Hockland *et al*., 2012; Briar *et al*., 2016). Crop rotation is complex in its design and implementation, especially where many nematode species are present (Briar *et al*., 2016). Soil solarization on the other hand is expensive and hence inapplicable in large scale farming (Briar *et al*., 2016).

The use of organic amendments presents a promising strategy for control soil-borne pests and diseases including parasitic nematodes (Akhtar and Malik, 2000; Oka, 2010; Renc'o *et al*., 2011). Commonly used organic amendments with suppressive effects on PPN include animal manure, green manure, and composted materials (Kimenju *et al*., 2008; Rivera and Aballay, 2008; Hu and Qi, 2010; Renc'o *et al*., 2011; Renc'o, 2013; Amulu and Adekunle, 2015; Osunlola and Fawole, 2015). A decrease in plant-parasitic nematodes which result from the application of different organic amendments is associated with the production of nematicidal compounds such as ammonia, different secondary metabolites, and organic acids (Thoden *et al*., 2011). However, nematicidal activity depends on the physicochemical parameters of soil such as pH and temperature (Oka, 2010). In addition to the toxic effect of these materials on PPN, the natural ability of soil to regulate PPN is increased by the addition of organic matter due to the increase in predatory and omnivorous free-living nematodes and the general improvement of the soil food web (Sánchez-Moreno and Ferris, 2018). Effectiveness of organic amendments as management strategy of PPN infecting sweet potato in Kenya has not been fully elucidated. This study sought to determine the effect of intercropping sweet potato and maize, application of *Tithonia diversifolia,* cow and goat manure on PPN abundance, nematode metabolic footprints, ecological and functional indices.

4.2 Materials and methods

4.2.1 Experimental site

The study was carried out at Nyangati sub-location in Mwea, Kirinyaga County, Kenya. It lies between latitude 0° 37´ 11.1" S and longitude 37º 21' 41.2" E. and is in the Low Midland (LM) agro-ecological zone, at an altitude of 1,204 m above sea level. The soil is vertisol (black cotton soil) with clay content that is higher than 30% (Jaetzold *et al*., 2009).

4.2.2 Experimental design

The study was conducted during the long rains (March to July 2018) and short rains (October 2018 to February 2019) seasons. The treatments comprised of cow manure (CM), goat manure (GM), marigold (MG) and maize-sweet potato intercrop (MS) while unamended plots were used as controls. The experiment was laid out in a randomized complete block design (RCBD) with four replicates per treatment. Each replicate comprised of an experimental plot measuring 5 m by 5 m and separated by 1 m buffer zone. Each plot comprised of 12 ridges with 0.6 m spacing. One-hundred and twenty sweet potato vines (cultivar, Kemb 10) were planted 0.3 m apart along the ridges in each plot. Cow and goat manure were sourced from a single farmer’s animal shed and allowed to decompose for four weeks before use. *Tithonia diversifolia* (commonly known as marigold) collected from a six-month-old hedge were cut into small pieces and then incorporated into the soil as green manure. The maize variety Pioneer PHB 30G19 was used for the maize-sweet potato intercrop treatment. The plots were each treated separately at planting with cow manure, goat manure, and marigold at a rate of 150 tons ha^{-1}. For the maize and sweet potato intercrop, maize seeds were planted in flatbeds at a spacing of 0.6 m by 0.5 m between maize plants and sweet potato vines planted on ridges at a spacing of 0.3 m by 0.6 m between vines. Weeding was done manually using a hoe.

4.2.3 Soil sampling

Soil samples were randomly collected at a depth of 25 cm around the sweet potato roots using 3.5 cm diameter soil auger. Collection of samples was done at plant establishment (pre-planting /0 days), intermediate (30 and 60 days after planting), and final growth stages (90 and 120 days after planting) (Stathers *et al*., 2013). Soil samples were collected from five points in each plot using a cross-diagonal sampling pattern. After collection, the five soil sub-samples from each plot were mixed thoroughly to homogenize the soil samples and triplicate 250 g of homogenized soil sample drawn per plot (Coyne *et al*., 2014). The soil samples were transported to the University of Embu laboratory for nematode extraction.

4.2.4 Nematode extraction and identification

Using the modified Baermann's technique (Hooper, 1990) nematodes were extracted from the triplicate 250 g soil samples. The extracted nematodes were heat-killed and fixed in a golden solution (Hooper *et al*., 2005). Thereafter, nematodes were transferred to a counting dish, counted, and identified to the genus level using morphological characteristics under a compound microscope (Bongers, 1988).

4.2.5 Analysis of soil properties and weather data collection

Soil samples were taken to Kenya Agricultural and Livestock Research Organization (Nairobi) for analysis of physicochemical properties. Data on temperature and rainfall during the study period was obtained from the Kenya Meteorological Department.

4.2.6 Data analysis

Nematode colonizer-persister (cp) values, trophic guilds, maturity index (MI), maturity index of nematodes in cp 2-5 (MI2-5), plant parasitic index (PPI), soil food web indices and metabolic footprints were computed using Nematode Indicators Joint Analysis (NINJA) online program (Sieriebriennikov *et al*., 2014). The maturity index indicates ecosystem condition based on nematode species composition while MI2-5 is identical to MI but excludes the cp-1 enrichment opportunist nematodes (Bongers, 1990). Basal index (BI) indicates soil food webs that are stressed or depleted due to resource limitations. Channel index (CI) reveals the predominant decomposition pathway while PPI shows the level of herbivore pressure. Enrichment index (EI) indicates the response of enrichment opportunistic nematodes to resource entry into the soil food web while structure index (SI) reflects the degree of trophic connectance in the soil food web as indicated by nematodes in the higher trophic groups which may have a regulatory function in the soil food web (Ferris *et al*., 2001).

Nematode metabolic footprints give an estimate of nematode contribution to various ecosystem services and functions based on biomass and metabolic activity of nematode functional guilds. The metabolic footprint of the entire nematode assemblage is represented by the composite footprint (Cf). The bacterivores (Baf), fungivores (Fuf), herbivores (Ppf), omnivores (Omf) and predators (Prf) metabolic footprints reflect carbon and energy flow into the soil food web through their respective channels. Enrichment (Ef) footprint represents functions by nematodes that quickly respond to resources in the ecosystem while structure footprint (Sf) is the footprint of higher tropic group nematodes which may have regulatory functions in the food web (Ferris, 2010).

Treatments effects on nematode abundance, metabolic footprints, ecological and functional indices during the two seasons were determined through analysis of variance (ANOVA) in R statistical software (R Core Development Team, 2015). Data were transformed where necessary before analysis. Where there were significant differences in the means, post hoc analysis tests were performed using package agricolae in R (De Mendiburu, 2015). response curve (PRC) analysis using vegan package in R (Oksanen *et al*., 2010) was used to compare the response of nematode genera to treatments (Van den Brink and Ter Braak, 1998,1999). Treatment effects on specific nematode genera over time were determined using Monte Carlo permutation test. Renyi diversity profiles that show variations in the frequency and diversity of rare and abundant species along a scale parameter were used to compare the diversity of nematode functional groups in various treatments (Tóthmérész, 1998). The diversity profiles were generated using the R statistical package, vegan (Oksanen *et al*., 2010).

4.3 Results

4.3.1 Soil properties and weather data

Soil physical and chemical properties at the study site are as described in section 3.3.1. Whilst data on rainfall and temperature, obtained from Kenya Meteorological Department are outlined in section 3.3.2.

4.3.2 Effects of different treatments on the relative abundance in nematode communities

A total of 47 nematode genera belonging to five trophic groups (bacterivores, herbivores, fungivores, predators and omnivores) were identified in the two cropping seasons (long rains season (LR) and short rains season (SR)); 47 during LR and 46 in SR. Bacterivores and herbivores were the most dominant nematode feeding guilds followed by omnivores while fungivorous and predatory genera were less frequent in the two seasons (Table 4.1 and 4.2). *Aorolaimus*, *Criconemoides*, *Hoplolaimus*, *Mesorhabditis,* and *Dorylaimus* were only observed during LR (Table 4.1) while *Protorhabditis*, *Drilocephalobus*, *Dorylaimellus*, and *Aporcelaimellus* occurred in SR (Table 4.2). There were significant ($P< 0.05$) differences in the abundance of *Aphelenchoides*, *Acrobeloides*, *Cephalobus*, *Eucephalobus*, *Heterocephalobus*, *Helicotylenchus*, *Longidorus*, *Meloidogyne*, *Pratylenchus*, *Rotylenchulus*, *Tylenchus*, *Nygolaimus* and *Prodorylaimus* across treatments in LR (Table 4.1). Similarly, the number of *Filenchus*, *Acrobeloides*, *Cephalobus*, *Heterocephalobus*, *Plectus*, *Protorhabditis*, *Wilsonema*, *Criconemella*, *Pratylenchus*, *Scutellonema*, *Trichodorus*, *Tylenchorhynchus*, *Discolaimus*, *Dorylaimellus, and Labronema* varied during SR (Table 4.2).

Table 4.1: Average number of nematodes in 250g soil collected from CM = cow manure, CT = control, GM = goat manure MG = marigold and MS = maize-sweet potato intercrop treatments during the long rains season.

Nematode genera	**Cp value**	**CM**		**CT**		**GM**		**MG**		**MS**		**F value**	**P value**
Fungivores		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
Aphelenchoides	2	48.1	11.821	93.6	12.137	59.15	14.686	50.7	12.111	52	10.502	4.661	0.002**
Aphelenchus	2	53.95	10.514	59.8	8.351	51.35	9.686	45.5	11.608	43.55	11.676	2.493	0.050
Filenchus	2	16.9	4.818	7.8	2.386	11.7	3.114	12.35	3.331	12.35	3.828	0.645	0.632
Bacterivores													
Acrobeles	2	18.85	4.760	13	1.886	13	3.128	8.45	3.023	17.55	5.680	2.000	0.075
Acrobeloides	2	9.1	4.012	18.2	4.464	3.9	2.130	3.9	1.910	5.85	3.462	5.362	<0.001**
Alaimus	4	0	0.000	0	0.000	0	0.000	0	0.000	0.65	0.650	1	0.413
Aphanolaimus	3	1.95	1.950	0	0.000	1.95	1.423	0.65	0.650	0.65	0.650	0.506	0.732
Cephalobus	2	92.3	10.872	52	8.003	76.05	11.328	66.95	7.736	87.75	12.364	2.631	0.041*
Cervidellus	2	78	9.572	46.8	5.532	70.2	9.865	61.75	12.543	58.5	11.493	1.885	0.122
Chiloplacus	2	3.25	2.082	0	0.000	1.95	1.065	1.3	0.895	0.65	0.650	1.061	0.382
Eucephalobus	2	97.5	11.836	62.4	9.506	96.85	13.084	86.45	14.249	78	12.547	4.288	0.004**
Geomonhystera	2	0.65	0.650	0	0.000	0.65	0.650	1.3	0.895	0	0.000	0.875	0.483
Heterocephalobus	2	65	9.095	39	8.003	63.05	9.949	39.65	6.832	36.4	4.067	3.650	0.009**
Mesorhabditis	1	0	0.000	0	0.000	0	0.000	0	0.000	0.65	0.650	1	0.413
Plectus	2	22.1	5.821	13	3.267	22.75	6.030	13	4.218	13	3.400	0.832	0.509
Prismatolaimus	3	4.55	3.436	7.8	3.579	1.3	0.895	1.3	0.895	1.3	0.895	1.382	0.248
Rhabditis	1	23.4	8.091	15.6	4.772	18.2	5.995	29.9	9.576	9.1	2.513	1.042	0.391
Tylocephalus	1	0	0.000	0	0.000	0	0.000	0	0.000	0.65	0.650	1	0.413
Wilsonema	2	17.55	6.346	13	2.668	11.05	4.350	16.9	7.610	7.8	2.566	1.384	0.248
Herbivores													
Aorolaimus	3	0	0.000	0	0.000	0.65	0.650	0.65	0.650	0	0.000	0.75	0.561
Criconemella	3	2.6	1.193	0	0.000	0	0.000	1.3	1.300	1.3	0.895	2.481	0.051
Criconemoides	3	0	0.000	0	0.000	1.3	0.895	0.65	0.650	0	0.000	1.714	0.155
Ditylenchus	2	29.25	10.152	62.4	16.270	39	14.702	46.8	18.777	32.5	9.687	1.454	0.223
Helicotylenchus	3	9.75	3.758	0	0.000	9.1	4.910	9.1	3.665	12.35	4.371	5.951	<0.001***
Hoplolaimus	3	0.65	0.650	0	0.000	0.65	0.650	0	0.000	0.65	0.650	0.5	0.736
Longidorus	5	2.6	1.521	18.2	5.844	4.55	1.707	0.65	0.650	2.6	1.521	7.982	<0.001***

Meloidogyne	3	22.1	5.343	93.6	18.900	21.45	6.553	22.75	7.419	40.95	8.811	5.277	<0.001***
Paratrichodorus	4	3.25	1.599	2.6	1.193	3.9	1.910	5.2	2.386	5.2	1.978	0.315	0.867
Pratylenchus	3	39	9.525	39	3.267	39	9.801	33.8	5.368	59.8	12.455	3.25	0.016*
Psilenchus	2	3.9	2.130	0	0.000	5.2	1.739	5.2	1.978	9.75	5.240	2.446	0.054
Rotylenchulus	3	53.95	20.146	54.6	3.478	66.95	22.284	50.05	18.986	57.85	15.192	3.871	0.007**
Rotylenchus	3	13	7.777	5.2	2.386	11.05	4.834	11.05	4.350	11.05	4.247	0.746	0.564
Scutellonema	3	46.8	5.451	59.8	5.844	53.95	7.906	74.1	17.897	76.05	15.619	0.508	0.730
Trichodorus	4	6.5	2.212	2.6	1.193	2.6	1.193	4.55	2.363	8.45	3.920	0.689	0.602
Tylenchorhynchus	3	4.55	1.950	5.2	2.386	2.6	1.193	1.95	1.950	3.25	1.599	1.16	0.325
Tylenchulus	3	9.75	3.384	13	4.620	9.1	3.414	6.5	2.212	11.7	3.253	0.401	0.808
Tylenchus	2	27.95	4.647	31.2	5.532	24.05	4.925	17.55	4.032	21.45	5.758	2.659	0.039*
Xiphinema	5	0.65	0.650	0	0.000	0.65	0.650	1.95	1.423	0.65	0.650	0.573	0.683
Predators													
Discolaimus	5	0	0.000	0	0.000	0.65	0.650	1.3	0.895	0	0.000	1.333	0.266
Mononchus	4	0.65	0.650	0	0.000	1.3	0.895	1.95	1.423	0	0.000	1.023	0.401
Nygolaimus	5	62.4	11.840	15.6	4.772	55.9	9.806	46.15	11.138	56.55	11.714	12.512	<0.001**
Seinura	2	0	0.000	0	0.000	0	0.000	1.3	0.895	0.65	0.650	1.333	0.266
Omnivores													
Dorylaimus	4	0	0.000	0	0.000	0.65	0.650	0	0.000	0	0.000	1	0.413
Eudorylaimus	4	9.75	3.384	15.6	4.772	4.55	1.950	5.2	1.978	6.5	2.907	1.155	0.338
Labronema	4	39	7.662	36.4	6.369	43.55	8.291	33.8	9.212	25.35	6.429	1.003	0.411
Mesodorylaimus	4	3.9	1.910	2.6	1.193	1.3	0.895	2.6	1.789	3.25	1.599	0.4802	0.75
Prodorylaimus	4	0.65	0.650	2.6	1.193	0	0.000	0	0.000	0	0.000	15	<0.001***

***= $P < 0.001$, **= $P < 0.01$, *= $P < 0.05$.Cp = colonizer-persister value.

Table 4.2: Average number of nematodes in 250g soil collected from CM = cow manure, CT = control, GM = goat manure MG = marigold and MS = maize-sweet potato intercrop treatment plots during the short rains season.

Nematode genera	Cp value	CM		CT		GM		MG		MS		F value	P value
Fungivores		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
Aphelenchoides	2	50.05	9.723	57.2	6.695	40.95	7.322	63.7	14.998	91.65	19.454	2.221	0.075
Aphelenchus	2	118.3	17.388	143	6.801	139.75	13.166	164.45	23.279	126.1	15.471	0.989	0.419
Filenchus	2	11.05	3.023	7.8	3.579	4.55	1.423	8.45	3.686	1.95	1.065	2.849	0.029*
Bacterivores													
Acrobeles	2	4.55	2.363	0	0.000	1.95	1.423	3.9	1.661	3.25	1.857	1.447	0.227
Acrobeloides	2	11.05	3.563	0	0.000	13.65	6.074	7.15	2.746	5.85	2.400	3.604	0.009**
Alaimus	4	0	0.000	0	0.000	0	0.000	1.3	1.300	0.65	0.650	0.756	0.557
Aphanolaimus	3	2.6	1.521	2.6	1.193	2.6	1.789	4.55	2.544	3.9	2.684	0.173	0.951
Cephalobus	2	154.7	23.368	143	21.089	231.4	48.574	215.15	40.559	140.4	24.240	3.621	0.009**
Cervidellus	2	55.25	12.220	57.2	10.603	71.5	14.717	57.85	10.047	65.65	20.062	0.749	0.562
Chiloplacus	2	2.6	1.521	2.6	1.193	1.3	0.895	0.65	0.650	2.6	1.521	0.891	0.473
Drilocephalobus	2	26.65	8.719	26	3.267	25.35	6.147	20.8	5.690	15.6	4.281	2.005	0.102
Eucephalobus	2	137.89	16.099	137.80	4.464	206.05	28.548	159.25	18.550	146.9	18.144	1.678	0.164
Geomonhystera	2	7.15	3.052	5.2	2.386	9.1	2.845	8.45	3.304	11.05	4.550	1.26	0.293
Heterocephalobus	2	103.35	8.513	65	6.534	146.9	25.431	130	26.990	101.4	18.205	8.623	<0.001***
Plectus	2	18.2	7.913	28.6	4.383	18.2	5.368	15.6	3.843	27.95	8.450	3.944	0.006**
Prismatolaimus	3	14.95	4.032	5.2	2.386	9.75	2.647	9.1	3.281	14.95	5.835	1.928	0.114
Protorhabditis	1	5.2	3.934	0	0.000	0	0.000	20.15	9.547	0	0.000	26.371	<0.001***
Rhabditis	1	98.15	19.883	57.2	6.141	135.2	36.202	123.5	26.700	49.4	7.521	2.121	0.087
Tylocephalus	2	0	0.000	0	0.000	0	0.000	0	0.000	0.65	0.650	1	0.413
Wilsonema	2	23.4	5.217	44.2	7.450	15.6	4.383	17.55	6.346	26	10.417	2.705	0.037*
Herbivores													
Criconemella	3	1.95	1.423	10.4	2.232	9.1	3.414	2.6	1.521	13.65	4.268	8.009	<0.001***
Ditylenchus	2	1.3	0.895	0	0.000	1.95	1.065	1.3	1.300	3.25	1.857	1.467	0.221
Helicotylenchus	3	1.95	1.950	0	0.000	1.3	1.300	1.95	1.423	0	0.000	0.778	0.543
Longidorus	5	0.65	0.650	0	0.000	0	0.000	0	0.000	0.65	0.650	0.75	0.561
Meloidogyne	3	59.15	8.821	59.8	7.207	59.15	6.897	61.1	7.064	69.55	8.760	0.363	0.834
Paratrichodorus	4	2.6	1.521	5.2	2.386	2.6	2.023	3.9	2.845	1.95	1.423	0.574	0.683
Pratylenchus	3	27.95	7.793	39	8.847	31.85	7.514	29.9	5.972	51.35	10.091	3.379	0.013*
Psilenchus	2	2.6	1.193	2.6	1.193	0.65	0.650	2.6	1.521	7.15	2.400	3.308	0.015*

Rotylenchulus	3	153.4	24.368	156	20.051	209.95	66.450	225.55	47.064	130.65	18.517	1	0.212
Rotylenchus	3	22.1	5.667	26	7.545	9.75	2.964	13	3.772	7.8	3.184	1.714	0.156
Scutellonema	3	25.35	5.375	49.4	8.308	22.75	5.068	38.35	4.760	23.4	3.957	4.658	0.002**
Trichodorus	4	4.55	2.872	0	0.000	4.55	1.950	1.95	1.065	9.1	3.142	3.579	0.010*
Tylenchorhynchus	3	1.3	1.300	7.8	3.579	0	0.000	2.6	1.521	0.65	0.650	4.037	0.005**
Tylenchulus	3	10.4	4.175	10.4	2.922	3.9	2.329	9.1	4.818	8.45	3.023	1.385	0.247
Tylenchus	2	56.55	9.538	78	9.046	61.1	8.649	61.1	8.281	72.8	12.166	2.135	0.085
Xiphinema	5	0	0.000	0	0.000	0.65	0.650	1.3	0.895	0	0.000	1.333	0.266
Predators													
Discolaimus	5	3.25	1.599	0	0.000	0	0.000	1.95	1.065	2.6	1.521	2.499	0.050*
Mononchus	4	0	0.000	0	0.000	1.3	1.300	3.25	2.082	0	0.000	2.396	0.058
Nygolaimus	5	83.85	7.973	83.2	4.046	84.5	10.523	74.1	6.937	105.95	11.977	1.628	0.175
Seinura	2	0.65	0.650	0	0.000	0	0.000	0.65	0.650	1.3	1.300	0.509	0.729
Omnivores													
Aporcelaimellus	5	7.15	2.903	2.6	1.193	2.6	1.521	1.95	1.065	1.3	0.895	1.72	0.154
Dorylaimellus	5	20.15	5.291	26	6.256	17.55	4.647	17.55	4.925	13	5.079	3.575	0.018*
Eudorylaimus	4	5.2	2.386	2.6	1.193	7.15	2.207	5.2	2.733	3.9	2.130	1.559	0.194
Labronema	4	17.55	3.436	0	0.000	13.65	3.828	13	2.829	25.35	4.268	10.107	<0.001***
Mesodorylaimus	4	1.95	1.065	2.6	1.193	1.95	1.423	3.25	1.599	1.95	1.423	0.406	0.804
Prodorylaimus	4	0.65	0.650	0	0.000	0	0.000	1.3	0.895	0	0.000	1.333	0.266

***= *P*< 0.001, **= *P*< 0.01, *= *P* < 0.05.Cp = colonizer-persister value.

4.3.3 Effect of different treatments on nematode communities over time

Nematode genera showed varied responses to treatments over time in both seasons. In the long rains season, time accounted for 24.3% of the variance, and treatment (plus the interaction with time) explained 27.7% of the variance. In the short rains season, the highest variance (30.7%) was due to treatment and the interaction with time while 22.98% was due to time. In both seasons, Monte Carlo permutation tests revealed that treatments had significant ($P<0.05$) effects on nematode communities during each month.

During the long rains season, the response curve analysis showed that the abundance of nematode genera changed progressively across the treatments. *Eudorylaimus, Longidorus* and *Tylenchus* were the main genera driving the response curve. Abundance of *Tylenchus, Tylenchulus* and *Meloidogyne* was reduced in all plots between the first and third month after planting sweet potato. These genera were further reduced in the intercropping maize and sweet potato and cow manure plots between the third and fourth months while *Eudorylaimus* and *Longidorus* increased. *Paratrichodorus, Trichodorus* and *Helicotylenchus* were reduced in marigold and goat manure plots between the third and fourth months (Figure 4.1).

In the short rains season, *Labronema, Criconemella* and *Drilocephalobus* were the key drivers of the curve. Between the second and third month in the marigold and cow manure plots, there was a reduction in the number of PPN belonging to the genera *Criconemella, Pratylenchus, Psilenchus, Trichodorus* and an increase in *Labronema*. These plots also had a low abundance of *Rotylenchus, Tylenchorhynchus* and *Paratrichodorus* between the third and fourth months. In the goat manure plots between the second and third month *Rotylenchulus, Tylenchorhynchus* and *Paratrichodorus* were present in low numbers and there was a decline in the abundance of *Criconemella, Pratylenchus, Psilenchus, Trichodorus* and *Ditylenchus* in the third to fourth month (Figure 4.2).

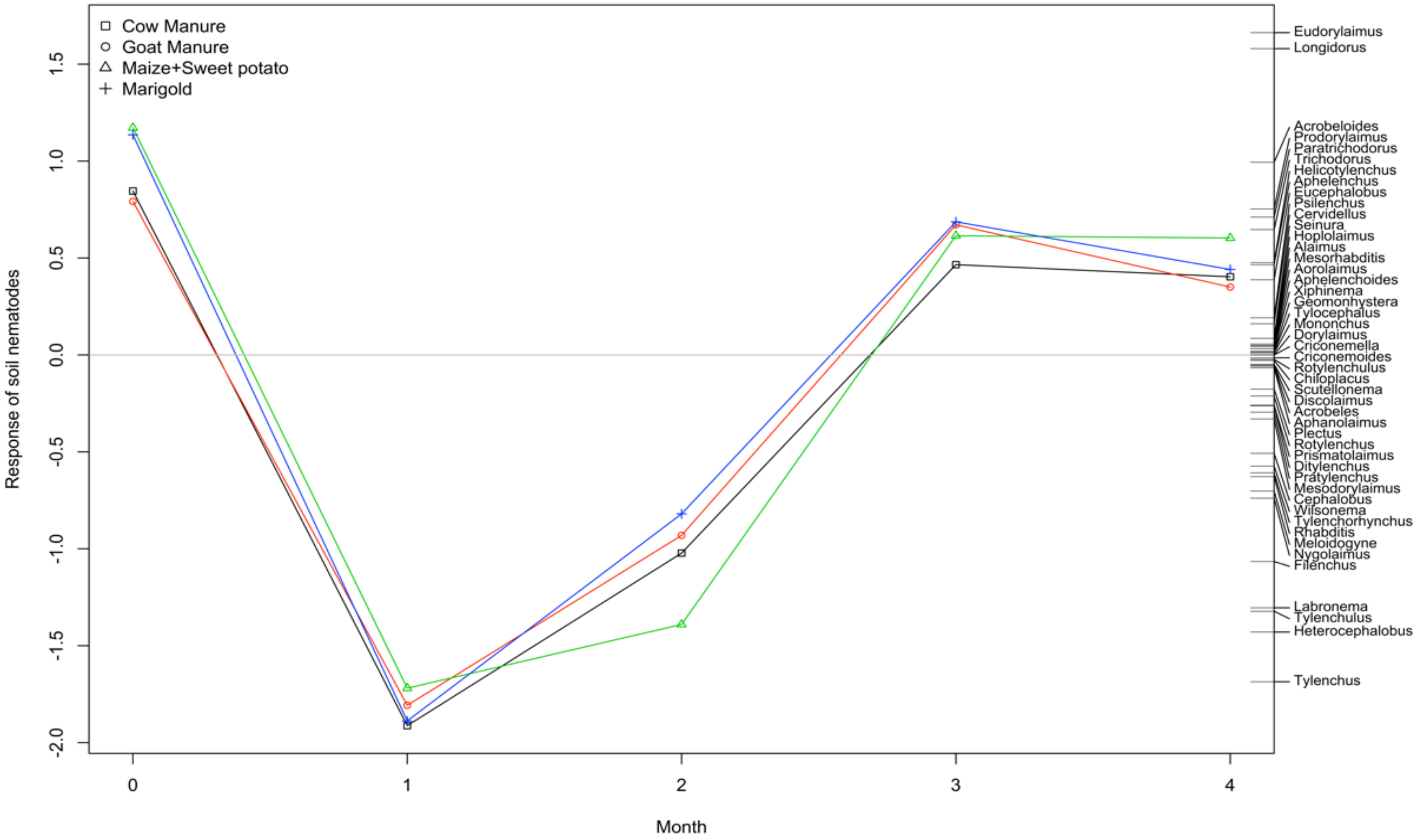

Figure 4.1: Response Curve showing the response of nematode communities to different treatments relative to control overtime during the long rains season. The x-axis represents sampling time in months and the left y-axis shows deviations from the non-amended control (horizontal line at 0.0). The right y-axis represents nematode genera.

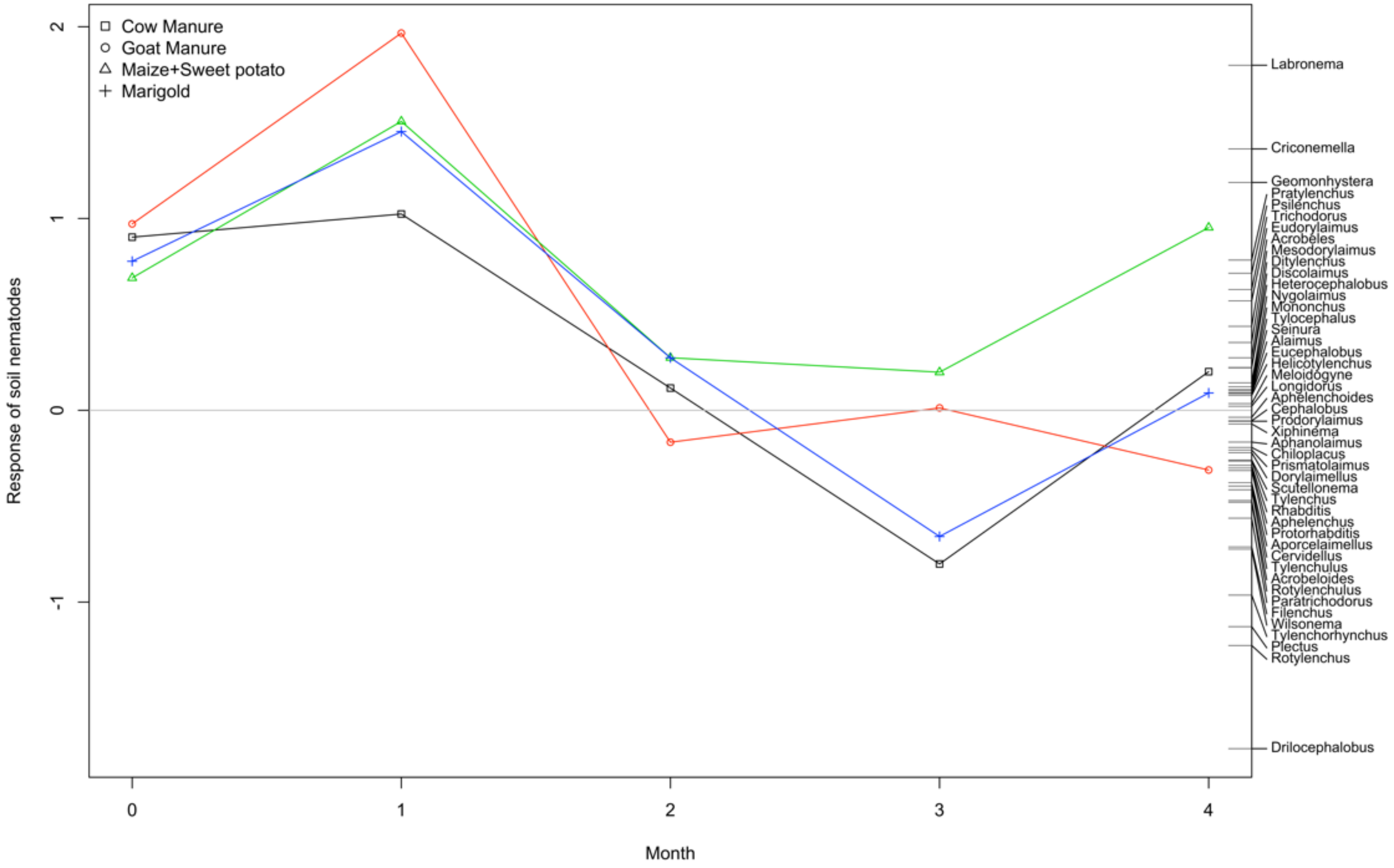

Figure 4.2: Response Curve showing the response of nematode communities to different treatments relative to control overtime during the short rains season. The x-axis represents sampling time in months and the left y-axis shows deviations from the non-amended control (horizontal line at 0.0). The right y-axis represents nematode genera.

4.3.4 Effects of treatments on the diversity of nematode species

Renyi diversity, which is a diversity ordering technique, was used to provide crucial information on nematode diversity with respect to various treatments. In the long and short rains seasons, the diversity profiles of nematode functional groups intersected and they could therefore not be unequivocally ordered due to the differences in diversity of rare and frequent nematode functional groups. During the long rains, the high diversity of predators was recorded in marigold plots while a high frequency of bacterivores was observed in cow manure plots. The control plots exhibited a low diversity of predators and bacterivores (Figure 4.3). In the short rains, control plots had low diversity of all nematode functional groups. A high frequency of bacterivores was recorded in goat manure plots and a high diversity of predators was observed in marigold plots (Figure 4.4).

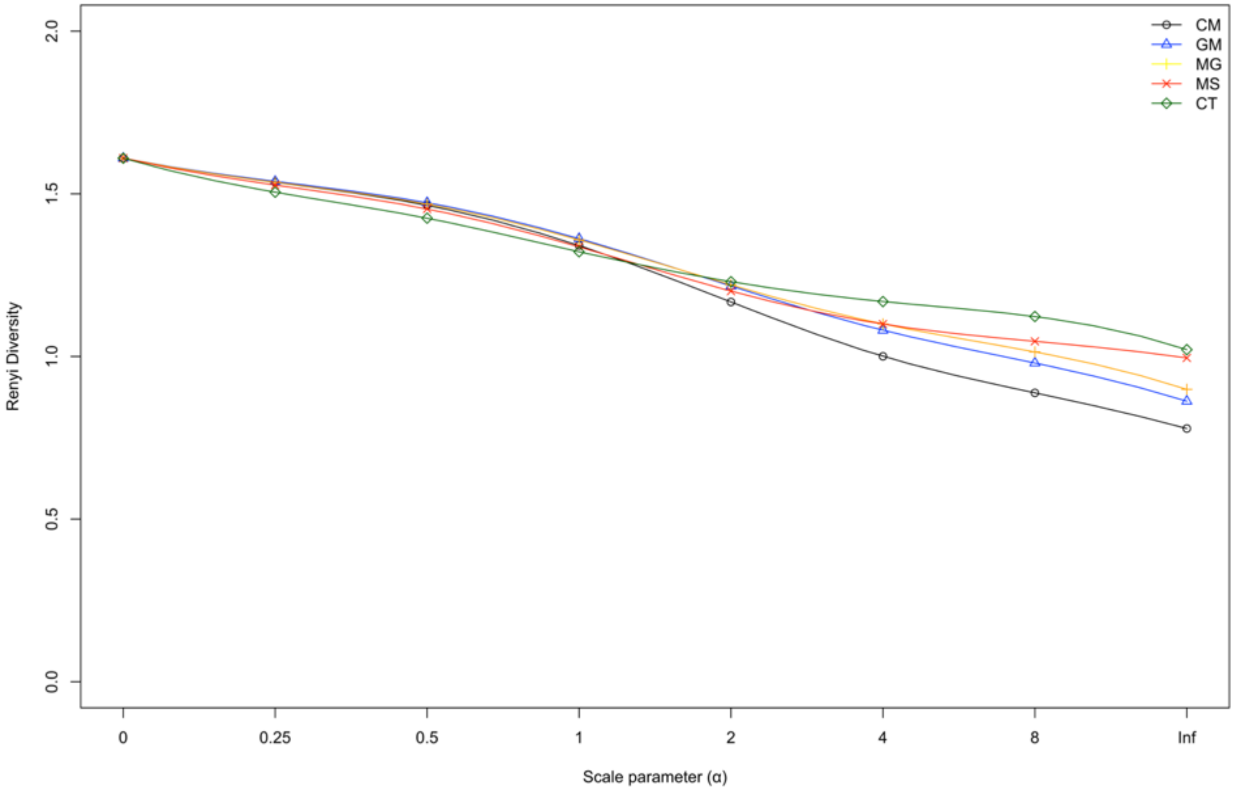

Figure 4.3: Renyi diversity profiles of nematode communities in cow manure (CM), goat manure (GM), marigold (MG), maize-sweet potato intercrop (MS), and control (CT) plots during the long rains. Species richness, Shannon index, the logarithm of the reciprocal Simpson index, and Berger–Parker index are represented by the alpha values 0, 1, 2, and infinity, respectively.

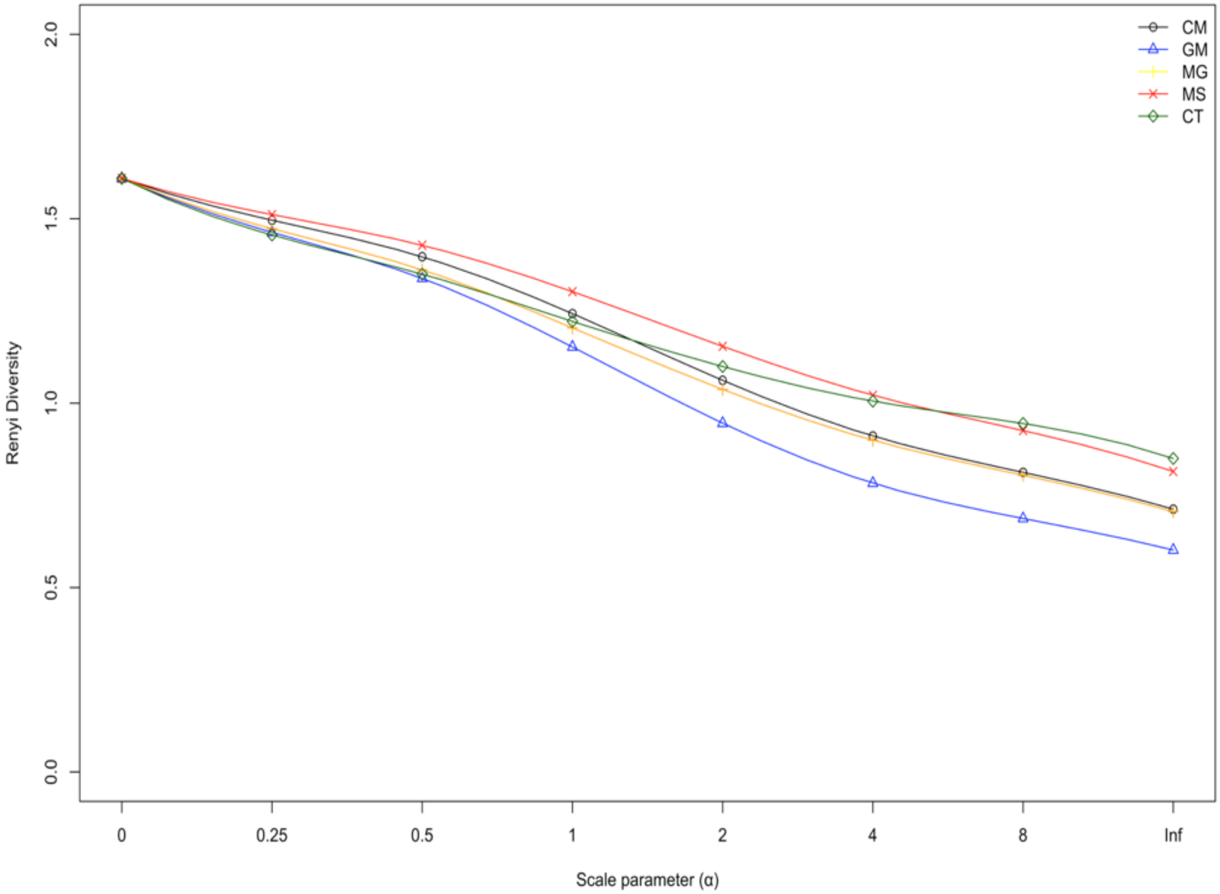

Figure 4.4: Renyi diversity profiles of nematode communities in cow manure (CM), goat manure (GM), marigold (MG), maize-sweet potato intercrop (MS) and control (CT) plots during the short rains. Species richness, Shannon index, the logarithm of the reciprocal Simpson index, and Berger–Parker index are represented by the alpha values 0, 1, 2, and infinity, respectively.

4.3.5 Effects of treatments on ecological, soil food web indices and metabolic footprints

There was a significant variation in the plant parasitic index (PPI), channel index (CI), and enrichment index (EI) across treatments during LR, and in SR all indices were significantly different except PPI and BI (Table 4.3). During LR, intercropping maize and sweet potato plots, high values of maturity index (MI), and basal index (BI) were recorded and high maturity index of 2-5 (MI 2-5) was observed in cow manure plots which also had low enrichment index compared to the control. Goat manure reduced plant parasitic index and increased the structure index while marigold plots had low channel index and basal index. In the short rains season, intercropping maize and sweet potato resulted in high MI, MI 2-5, CI and SI, and a decrease in PPI and EI. Basal index and channel index were low in cow manure plots and goat manure caused a reduction in structure index and maturity index of 2-5. Enrichment index was high in marigold treated plots while the maturity index was low (Table 4.3).

During the long rains season, the treatments significantly influenced composite, herbivore, bacterivore, fungivore, and predator footprints (Table 4.5). Compared to the control, cow manure plots had high bacterivore and predator footprints and a low fungivore footprint. High values of enrichment footprint and structure footprint were observed in marigold and goat manure plots, respectively. Marigold treated plots also had the lowest composite footprint, herbivore footprint, and structure footprint while intercropping maize and sweet potato resulted in a low enrichment footprint. In short rains season, the treatments had significant effects on bacterivore footprint, omnivore footprint, and enrichment footprint. In marigold plots, composite footprint, bacterivore footprint, low fungivore footprint, and enrichment footprint increased relative to the control while the predator footprint decreased. Herbivore footprint, predator footprint, and structure footprint values were high in maize-sweet potato intercrop plots while omnivore footprint was high in cow manure. Cow manure had low herbivore footprint and fungivore footprint and maize-sweet potato intercrop recorded low values of bacterivore footprint and enrichment footprint (Table 4.4).

Graphical representation of the enrichment index and structure index during long rains season revealed a degraded ecosystem (lower left quadrat) in all the plots but cow manure and goat manure plots were bordering a structured ecosystem (Figure 4.5). In short rains season, maize and sweet potato intercropping plots had a structured ecosystem (lower right quadrat) and cow manure plots were on the borderline between a structured and degraded ecosystem. Marigold, goat manure, and control plots were degraded (Figure 4.6).

Table 4.3: Nematode ecological and functional indices in cow manure (CM), goat manure (GM), marigold (MG), maize-sweet potato intercrop (MS), and control (CT) plots during the long and short rains seasons.

Index	CM		CT		GM		MG		MS		F value	P-value
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
Long rains season												
MI	2.42a	0.077	2.32a	0.049	2.43a	0.065	2.35a	0.077	2.43a	0.080	1.04	0.392
MI2-5	2.47a	0.075	2.35a	0.051	2.47a	0.066	2.42a	0.070	2.45a	0.084	0.94	0.445
PPI	2.92b	0.034	3.10a	0.065	2.89b	0.044	2.94b	0.033	2.94b	0.036	5.75	<0.001***
CI	71.38ab	6.720	84.19a	4.575	74.30ab	6.361	65.53b	7.750	79.38ab	5.401	3.10	0.020*
BI	41.79a	3.595	42.57a	2.378	40.80a	3.021	39.56a	2.925	43.46a	3.714	0.33	0.845
EI	27.95b	2.910	35.91a	1.361	28.93ab	2.437	34.56ab	3.184	28.03ab	1.992	2.93	0.026*
SI	48.17a	4.772	41.55a	4.853	48.99a	4.506	43.71a	5.801	45.56a	5.434	1.06	0.384
Short rains season												
MI	2.30ab	0.044	2.28b	0.022	2.20b	0.031	2.18b	0.040	2.43a	0.061	7.43	<0.001***
MI2-5	2.44ab	0.044	2.36b	0.020	2.32b	0.022	2.34b	0.036	2.51a	0.058	4.55	0.002**
PPI	2.94a	0.044	2.95a	0.034	2.97a	0.038	2.94a	0.027	2.90a	0.034	0.90	0.469
CI	39.27b	5.541	50.70ab	2.618	39.52b	5.540	39.62b	6.046	56.59a	4.843	3.28	0.016*
BI	36.43a	2.061	40.94a	0.962	41.39a	1.755	37.79a	1.941	36.52a	2.387	1.87	0.124
EI	41.24ab	2.699	37.19b	1.079	39.39ab	2.752	45.55a	3.261	35.35b	1.831	3.21	0.017*
S1	49.92ab	2.982	45.62ab	1.504	42.40b	1.831	42.91b	2.464	53.09a	3.564	3.63	0.009**

Means ± SE within the same row followed by same the letters are not significantly different. MI= Maturity Index, MI2-5 = Maturity Index of nematodes in cp 2-5, PPI = Plant Parasitic Index, CI = Channel Index, BI = Basal Index, EI = Enrichment Index, and SI = Structure Index. ***= $P< 0.001$, **= $P< 0.01$, *= $P < 0.05$.

Table 4.4: Metabolic footprints in cow manure (CM), goat manure (GM), marigold (MG), maize-sweet potato intercrop (MS) and control (CT) plots during the long and short rains seasons

Footprint	CM		CT		GM		MG		MS		F value	P-value
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
Long rains season												
Cf	5.98b	0.136	6.56a	0.178	5.99b	0.105	5.90b	0.127	6.11b	0.132	5.79	<0.001***
Ppf	4.89b	0.229	6.25a	0.217	4.92b	0.218	4.74b	0.265	5.44b	0.238	9.60	<0.001***
Baf	4.39a	0.146	3.79b	0.194	4.24ab	0.140	4.21ab	0.193	3.91b	0.140	4.42	0.003**
Fuf	2.55b	0.187	3.14a	0.139	2.66ab	0.184	2.61ab	0.201	2.58b	0.165	3.06	0.022*
Prf	3.68a	0.335	1.50b	0.425	3.67a	0.321	3.05a	0.430	3.20a	0.444	13.65	<0.001***
Omf	3.47a	0.381	4.07a	0.143	3.68a	0.335	2.93a	0.429	3.07a	0.369	2.01	0.101
Sf	4.62a	0.209	4.25a	0.170	4.71a	0.165	3.99a	0.365	4.11a	0.348	1.78	0.142
Ef	3.57a	0.282	3.67a	0.204	3.57a	0.235	3.85a	0.241	3.25a	0.202	1.22	0.309
Short rains season												
Cf	6.68a	0.112	6.56a	0.115	6.74a	0.121	6.78a	0.104	6.71a	0.099	1.05	0.386
Ppf	5.99a	0.141	6.02a	0.150	6.07a	0.109	6.09a	0.139	6.13a	0.145	0.23	0.923
Baf	5.30ab	0.174	5.05ab	0.125	5.47a	0.205	5.51a	0.177	4.90b	0.169	4.43	0.003**
Fuf	2.72a	0.148	2.98a	0.064	2.86a	0.098	2.99a	0.144	2.96a	0.120	1.58	0.189
Prf	4.48a	0.122	4.53a	0.054	4.45a	0.122	4.41a	0.099	4.69a	0.116	1.43	0.232
Omf	3.25a	0.307	1.06b	0.319	2.68a	0.371	2.86a	0.300	2.99a	0.404	6.32	<0.001***
Sf	4.84a	0.131	4.64a	0.028	4.75a	0.109	4.71a	0.091	4.99a	0.133	1.80	0.137
Ef	4.98ab	0.213	4.76ab	0.135	5.11ab	0.250	5.17a	0.257	4.51b	0.200	2.69	0.037*

Means± standard error (SE) within the same row followed by same the letters are not significantly different. Cf = composite metabolic footprint, Ppf = herbivore footprint, Baf= bacterivore footprint, Fuf = fungivore footprint, Prf = predator footprint, Omf = omnivore footprint, Sf = structure footprint and Ef = enrichment footprint. ***= $P< 0.001$, **= $P< 0.01$, *= $P < 0.05$

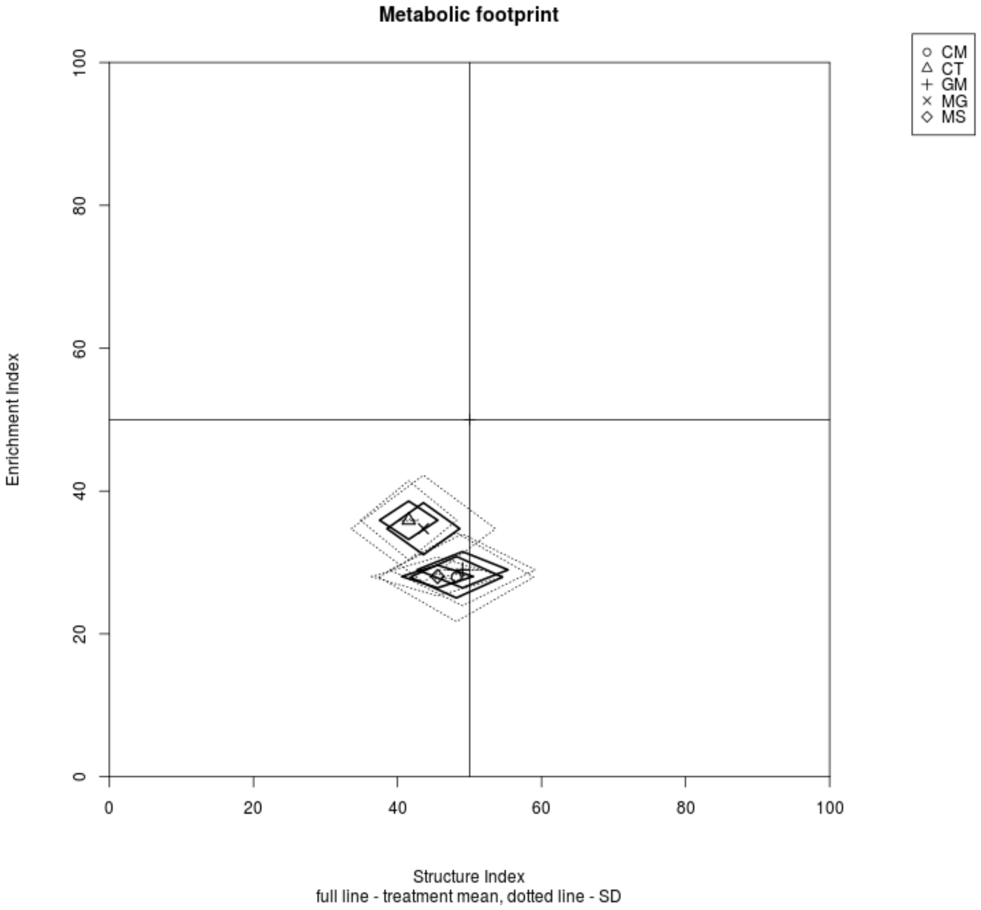

Figure 4.5: Functional metabolic footprint of nematodes in cow manure (CM), goat manure (GM), marigold (MG), maize-sweet potato intercrop (MS), and control (CT) plots during the long rains season.

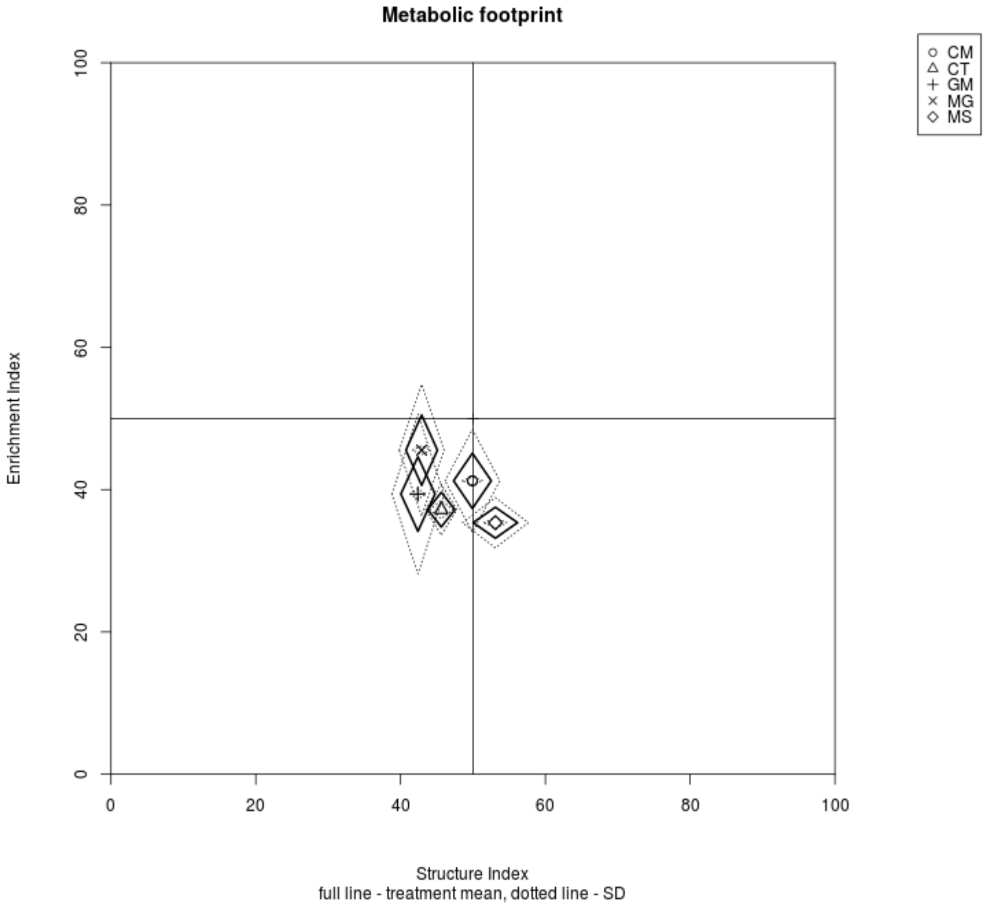

Figure 4.6: Functional metabolic footprint of nematodes in cow manure (CM), goat manure (GM), marigold (MG), maize-sweet potato intercrop (MS), and control (CT) plots during the short rains season.

4.4 Discussion

A high diversity of plant parasitic nematodes and free-living nematodes was observed across treatments during the two seasons. However, there was a difference in the abundance of specific genera in long and short rains seasons. Seasonal variability in nematode genera abundance could be attributed to the differences in temperature and moisture levels that directly and indirectly affect nematode abundance (Sohlenius and Bostrom, 1984; Freckman *et al*., 1987; Hoschitz and Kaufmann, 2004). Huang *et al*. (1984) reported an increase in *Meloidogyne exigua* larvae population during the early weeks of a wet season due to an increase in root growth. Seasonal fluctuations of *Pratylenchus brachyurus* and *Meloidogyne, Helicotylenchus, Cephalobus,* and *Acrobeles* have also been reported (O'Bannon *et al*., 1972; Gomes *et al*., 2003). *Meloidogyne*, *Pratylenchus*, *Rotylenchulus,* and *Ditylenchus* which are the major parasitic nematodes of economic importance (Niere and Karuri, 2018) in sweet potato were recorded in this study. These PPN genera were reported in sweet potato fields in Uganda, Niger, and Kenya (Coyne *et al*., 2003; Haougui *et al.*, 2011; Karuri *et al*., 2017). They attack sweet potato at different growth stages resulting in significant yield losses and a reduction in the quality of marketable roots (Johnson *et al*., 1992; Kistner *et al*., 1993; Hartemink *et al*., 2000).

Population levels of free-living nematodes especially bacterivorous nematodes have been reported to increase following the amendment of soil with different organic substrates (Bulluck *et al*., 2002; Villenave *et al*., 2003; Nahar *et al*., 2006; Langat *et al*., 2008; Pan *et al*., 2015). This was also observed in this study in both seasons. Elevated populations of bacterivorous nematodes may be attributed to increased populations of microorganisms such as bacteria associated with organic amendments which afford excellent energy sources for these nematodes (Bulluck *et al*., 2002).

Treatment effects on nematode genera over time also varied between the two seasons as indicated in the principal response curve analysis. In the long rains season, all treatments reduced the number of *Tylenchus, Tylenchorhynchus* and *Meloidogyne* spp. between the first and third months with cow manure and maize-sweet potato intercropping plots causing a further reduction in these species in the last two months of the growing season. In contrast, during the short rains season, cow manure reduced the number of *Pratylenchus, Criconemella, Trichodorus, Rotylenchus, Tylenchorhynchus,* and *Paratrichodorous* while goat manure reduced *Rotylenchulus, Pratylenchus, Tylenchorhynchus, Paratrichodorous, Criconemella, Trichodorus* and *Ditylenchus* between the second and fourth month.

Reduction of PPN by these amendments at key sweet potato growth stages has the potential to improve yields since most nematode damage by PPN occurs at specific developmental phases (Clark and Wright, 1983; Lawrence, 1984; Agu, 2004). Seasonal changes influence the abundance of nematode genera in fields with organic amendments due to the effect on temperature and moisture on the amendments, soil properties, and nematodes (Jiang *et al*., 2013; Steel *et al*., 2013). The effect of organic amendments on

Criconemella and *Pratylenchus* was different across seasons in a maize field (McSorley and Gallaher, 1996) and in a vineyard, *Rhabditis* spp. and omnivorous nematodes showed varied responses during different seasons (Rahman *et al*., 2014). The reduction in the abundance of some PPN genera by different treatments in this study has also been observed by Kimenju *et al*., (2008), Tanimola and Akarekor, (2014), Osunlola and Fawole, (2015) and Atandi *et al*. (2017). However, Kimpinski *et al*., (2003) reported varying results where no reduction in populations of *Meloidogyne* and *Pratylenchus* was observed with compost and animal manure amendments. Suppressive effects of these materials could be due to the release of nematicidal compounds such as ammonia, modification of soil physicochemical properties, and stimulation of nematode antagonist populations (Oka, 2010; Thoden *et al*., 2011). Marigold and goat manure reduced the population of some PPN in long rains and short rains seasons with GM being most effective against economically important PPN in sweet potato across the two seasons.

Effectiveness of goat manure in reducing PPN in sweet potato, tomato, and okra was reported by Pakeerathan *et al*. (2009), Tanimola and Akarekor, (2014) and Osunlola and Fawole, (2015). The nematicidal potential of goat manure could be attributed to various factors. Goat manure is rich in micronutrients such as nitrogen, potassium and phosphorous, which are essential for plant growth and when applied in sufficient amounts enhance plant growth, in particular, the development of healthy root systems which render plants to be more resistant or tolerant to nematode attack (Pakeerathan *et al*., 2009; Thoden *et al*., 2011). In addition, goat manure is pellet-like and this structure increases the ability of soil particles to aggregate thus restricting nematode movement (Pakeerathan *et al*., 2009). The decomposition of organic matter in goat manure releases nematicidal substances such as ammonia which is very toxic against various parasitic nematodes (Oka, 2010; Thoden *et al*., 2011). On the other hand, marigold inhibits nematode growth and reproduction by producing toxic products (Hooks *et al*., 2010) and stimulating the proliferation of microorganisms that are antagonistic to PPN (Wang *et al*., 2001). Cow manure and marigold also demonstrated their suppressive effects on PPN in other studies under different crops (Kimenju *et al*., 2008; Odeyemi, and Adewale, 2011; Akpheokhai *et al*., 2012; Odeyemi *et al*., 2014; Amulu and Adekunle, 2015; Galadima *et al*., 2015).

Renyi diversity profiles showed low diversity of omnivores and predators in both seasons except in MG where the diversity of predators was high. The low diversity of these nematodes is expected since most of them belong to cp-4 and cp-5 categories which makes them highly sensitive to disturbances including input of organic amendments and also the fact that they need a longer time to re-establish after disturbance, compared to lower cp guilds (fast-growing bacterial and fungal feeding) nematodes (Bongers, 1990). Despite the low diversity, the abundance of some predatory and omnivorous nematodes increased after the application of treatments. This could be attributed to an increase in food sources (amplifiable prey) after the addition of organic resources and the availability of PPN “target prey” (McSorley and Frederick, 1999; Ferris *et al*., 2012b).

Omnivorous and predatory nematodes primarily determine the structure index (SI) (Ferris *et al*., 2001). High SI values are an indicator of a well-structured soil food web that has moderate abilities to suppress parasitic nematodes. This was observed in goat manure plots that had low PPI in the long rains season. Such a stable and complex community is valuable as it may potentially provide a bio-control strategy of regulating or suppressing pests including plant parasitic nematodes (Berkelmans *et al*., 2003). Thus to maintain this pest regulation service, it is important to minimize disturbances brought about by physical and chemical processes such as tillage and fertilizer application which have detrimental effects on higher guild nematodes (Sánchez-Moreno and Ferris, 2018). In this study, lower maturity index values that were observed in marigold plots during the short rains season is collaborated by other studies (Villenave et al., 2003; Forge *et al*., 2005; Hu and Qi, 2010; Li *et al*., 2010). The low values might have resulted from the enrichment effect of the green manure and these values are an indicator of a disturbed ecosystem (Bongers, 1990). Channel index (CI) indicates the predominant organic matter decomposition channel by either bacteria or fungi (Ferris *et al*., 2001). Fluctuations in CI that were observed between the two seasons may have been as a result of a shift from fungal to bacterial decomposition due to the influence of environmental factors on the organic amendments during the two seasons (Steel *et al*., 2013). Low values of the basal index (36.430 - 43.457) were recorded in the two seasons are within the range reported by Sánchez-Moreno and Ferris, (2018). This indicates that amendments did not severely affect the soil food web. High enrichment index values recorded in marigold plots in the short rains are in agreement with findings by Berkelmans *et al*. (2003), Liang *et al*. (2009), Li *et al*. (2010) and Pan *et al*. (2015) and they are characteristics of soil that is dominated by bacteria (Ferris et al., 2001).

Nematofauna functional indices give an insight into the status of an ecosystem but do not provide information on the magnitude of ecosystem functions and services provided by these indicator guilds. Conversely, nematode metabolic footprints proposed by (Ferris, 2010) provide such information as they give an estimate of nematode's contribution to various ecosystem functions and services based on biomass and metabolic activity of nematodes within each functional guild. Enrichment footprint (Ef) indicates carbon and energy flow via r-strategist nematodes (cp-1 bacterivores and cp-2 fungivores) (Ferris, 2010). Higher values of Ef were recorded in marigold plots in SR. This is similar to reports by Fengjuan *et al*. (2017) who observed that Ef was enhanced in plots amended with different organic and inorganic amendments. This, therefore, suggests that marigold treatment might have provided more labile and readily available resources for enrichment opportunists thus significantly increasing their abundance (Ferris, 2010). There was a significant difference in the predator footprint and omnivore footprint in the LR and SR, respectively. In cow manure plots, the Prf and Omf were high during the long and short rains season, respectively while goat manure had a non-significantly high structure footprint in SR. The high values of these footprints, which are indicative of the level of PPN regulation, may have been due to an increase in the availability of prey due to the addition of organic resources (Steel and Ferris, 2016).

The functional metabolic footprint categorized plots with intercropping maize and sweet potato as structured in SR while all the other plots were degraded in both seasons. However, goat manure bordered a structured ecosystem in LR while cow manure bordered a structured ecosystem in both seasons. Degraded plots revealed a depleted food web with insufficient resources to support the nematodes communities while the structured plots are indicative of a more complex ecosystem that has higher trophic groups with high connectance between fungal, omnivore and predatory channels which is beneficial in pest regulation (Ferris *et al*., 2001; Ferris, 2010; Guan *et al*., 2018).

4.5 Conclusion

Economically important PPN were observed in association with sweet potato. Application of organic amendments in sweet potato plots had varying effects on abundance and diversity of parasitic nematodes, metabolic footprints, ecological and functional nematode indices. Seasonal changes in temperature and moisture may have also influenced these observations. Goat manure showed the highest potential in the management of economically important PPN associated with sweet potato during two growing seasons. Soil food web indices revealed a moderate level of disturbance across all treatments. However, based on the functional metabolic footprints, most treatment plots were classified as degraded in both seasons except intercropping maize and sweet potato plots which were structured in SR. Cow manure plots were not severely degraded compared to other treatments in both seasons while goat manure plots were moderately structured in long rains season. The levels of degradation observed in different plots can be reversed into structured ecosystems that provide the soil with the natural ability to regulate pests. This may be achieved by coupling the addition of organic amendments with minimal soil perturbations while considering the effect of climate and soil properties. Organic amendments offer an alternative low-cost nematode management technique that will reduce the cost of sweet potato production for resource-constrained smallholder farmers in Kenya.

CHAPTER FIVE

Population dynamics and diversity of free-living nematodes in sweet potato under different management practices

5.0 Abstract

Sweet potato (*Ipomoea batatas* L.) is an important food crop consumed throughout Africa. This crop is associated with both plant parasitic and free-living nematodes. While plant-parasitic nematodes (PPN) reduce sweet potato productivity, free-living nematodes (FLN) play beneficial roles such as decomposition and nutrient mineralization which are essential in the growth and development of the crop. Farmers use various management practices to control PPN, which in turn may affect other microorganisms in the soil including the beneficial free-living nematodes. Herein, we evaluated the impact of different farming practices on the population dynamics and diversity of free-living nematodes in sweet potato. Field experiments were established in a randomized complete block design involving four treatments and un-amended controls that were replicated four times during long and short rains seasons. Soil samples were collected monthly for four months. Nematodes were then extracted and identified morphologically to the genus level. Thirty-two nematode genera belonging to four trophic groups were identified. Bacterivores were the predominant group while fungivores were the least frequent group in the two seasons. All treatments recorded high densities of bacterivorous nematodes compared to the control. Increased abundance of omnivorous and predacious nematodes was observed across the treatments in the two seasons except in the long rains season where omnivores were high in control. Goat manure was the most effective in stimulating population densities of free-living nematodes. This could be attributed to the nutritious food resources available in this amendment. Thus goat manure may be incorporated in sweet potato fields to ensure that populations of free-living nematodes are maintained or enhanced for continuous provision of the key important soil functions.

5.1 Introduction

Sweet potato is commonly grown by smallholder farmers in sub-Saharan due to its versatility. A majority of these farmers practice subsistence farming whereby low-cost agricultural inputs are utilized. These inputs may bring about changes in the soil food web through their effects on various organisms. Nematodes are key organisms that are found in soil and they perform various functions. In particular, plant-parasitic nematodes (PPN) cause damage to crops while free-living nematodes (FLN) perform key ecological functions in the soil food web. This group of nematodes forms the larger portion of nematodes yet very little attention is paid to them compared with PPN despite their key roles in the soil and plant health (Andrássy, 2009). Free-living nematodes occupy different trophic levels and are often grouped into bacterial feeders, fungal feeders, omnivores, and predatory nematodes based on their feeding habits (Yeates *et al*., 1993). They play eminent roles in the ecosystem which includes; nutrient mineralization, decomposition of organic matter, biological control of parasitic nematodes and also indicate the health status of the ecosystem (Ingham *et al*., 1985; Bongers, 1990; Neher, 2001; Khan and Kim, 2007; Xiao *et al*., 2010; Neher *et al*., 2012; Ferris *et al*., 2012a).

While using various organic amendments to manage plant parasitic nematodes, increase in populations of free-living nematodes have been reported in various research studies (Villenave *et al*., 2003; Forge *et al*., 2005; Nahar *et al*., 2006; Wang *et al*., 2006; Langat *et al*., 2008). The elevated populations of these nematodes especially bacterial and fungal feeding nematodes under organic substrates application is thought to be due to an increase in bacteria and fungi populations that provide excellent food sources (Griffiths *et al*., 1994). However, varying responses are often exhibited by fungivores, omnivores, and predatory nematodes in response to addition of amendments. Significant effects were observed on bacterivores under organic substrate application but not on fungivores, omnivores and predatory nematodes in different studies (Pan *et al*., 2015; Wang *et al*., 2006; Villenave *et al.,* 2010). Manure application increased the number of omnivorous nematodes while predatory nematodes remained unaffected (Hu and Cao, 2008; Leroy *et al*. 2009).

Owing to their key functions in the soil ecosystems (Khan and Kim, 2007; Ferris *et al*., 2012), these nematodes must be maintained or increased. Application of various strategies to control PPN may affect the structure, diversity, and population dynamics of free-living nematodes. Hence this study purposed to assess the effect of intercropping sweet potato and maize, application of *Tithonia diversifolia* green manure, cow and goat manure as PPN management strategies on abundance and diversity of free-living nematodes in sweet potato.

5.2 Materials and methods

5.2.1 Plant material and treatments

Sweet potato vines cuttings (cultivar, Kemb10) measuring 30 cm were planted in plots and treated separately with cattle manure, goat manure, and *T. diversifolia*. An additional treatment that consisted of intercropping maize and sweet potato was also included. Sweet potato vines were planted on ridges and maize on rows. Untreated plots were used as control. Finally, weeding was done as required.

5.2.2 Collection of soil samples

Soil samples were randomly collected at a depth of 25 cm around the sweet potato roots using 3.5 cm diameter soil auger. Collection of samples was done at plant establishment (pre-planting/0 days), intermediate (30 and 60 days after planting), and final growth stages (90 and 120 days after planting) (Stathers *et al*., 2013). Soil samples were collected from five points in each plot using a cross-diagonal sampling pattern. After collection, the five soil sub-samples from each plot were mixed thoroughly to homogenize the soil samples and triplicate 250 g of homogenized soil sample drawn per plot (Coyne *et al*., 2014). The soil samples were transported to the University of Embu laboratory for nematode extraction.

5.2.3 Nematode extraction and identification

Using the modified Baermann's technique (Hooper, 1990) nematodes were extracted from the triplicate 250 g soil samples. The extracted nematodes were heat-killed and fixed in a golden solution (Hooper *et al*., 2005). Thereafter, nematodes were counted and identified morphologically up to the genus level under a compound microscope (Bongers, 1988).

5.2.4 Data analysis

The nematode data were subjected to analysis of variance (ANOVA) to determine treatment effects on free-living nematodes abundance during the two seasons. Before analysis, data were log-transformed where necessary. Differences in means at $P < 0.05$ level were considered statistically significant and were separated using the least significant difference test. All statistical analyses were performed using R statistical software (R Core Development Team, 2015).

5.3 Results

5.3.1 Soil properties and data on rainfall and temperature

Soil physical and chemical parameters and weather data at the site during the study period are tabulated in Table 3.1 and 3.2.

5.3.2 Population dynamics and diversity of free-living nematodes under management practices

A total of 32 nematode genera belonging to four trophic groups (bacterivores, fungivores, predators and omnivores) were identified in the two cropping seasons (long rains season (LR) and short rains season (SR)), 28 nematode genera during LR and 30 nematode genera in SR. Changes in the diversity and genus composition of free-living nematodes were observed in various trophic groups. Bacterivores were the predominant group, followed by omnivores, while fungivores and predatory nematodes were less frequent in the two seasons. *Mesorhabditis* and *Dorylaimus* were only observed during long rains season while *Drilocephalobus*, *Protorhabditis*, *Dorylaimellus*, and *Aporcelaimellus* occurred in SR. Significant differences ($P< 0.05$) in the abundance of *Acrobeloides*, *Cephalobus*, *Eucephalobus*, *Heterocephalobus*, *Aphelenchoides*, *Aphelenchus*, *Nygolaimus*, and *Prodorylaimus* were observed across treatments in LR (Figure 5.1). Similarly, the number of *Acrobeloides*, *Cephalobus*, *Heterocephalobus*, *Plectus*, *Protorhabditis*, *Wilsonema*, *Aphelenchus*, *Filenchus*, *Discolaimus*, *Dorylaimellus*, and *Labronema* varied during SR ($P< 0.05$) (Figure 5.2).

In the long rains season, all treatments recorded a significantly higher number of bacteria feeding nematodes compared to control. Fungivores occurred in lower numbers across the treatments compared to the control plots. Predators occurred in low numbers; however, treated plots recorded a higher number of these nematodes compared to the control plots. A low number of omnivorous nematodes were recorded across the treatments compared to control (Figure 5.3). In the short rains seasons, similar observations were made about bacterivores. However, most treatments increased the number of fungivores, predators, and omnivores (Figure 5.4). Among the treatments, cow manure and goat manure significantly increased the number of free-living nematodes especially bacterivores in the LR and SR seasons.

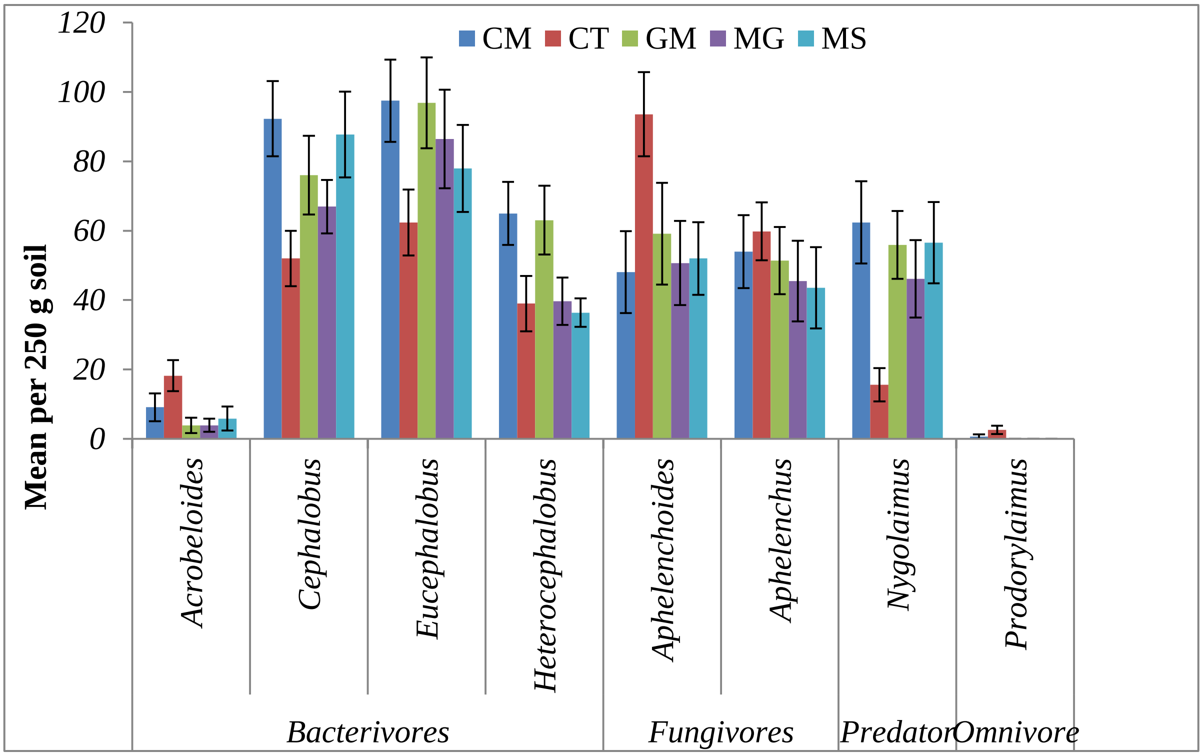

Figure 5.1: Mean abundance of significant nematode genera in CM- cow manure, CT- control GM-goat manure, MG- marigold, and MS- maize intercropped with sweet potato treatments during the long rains season.

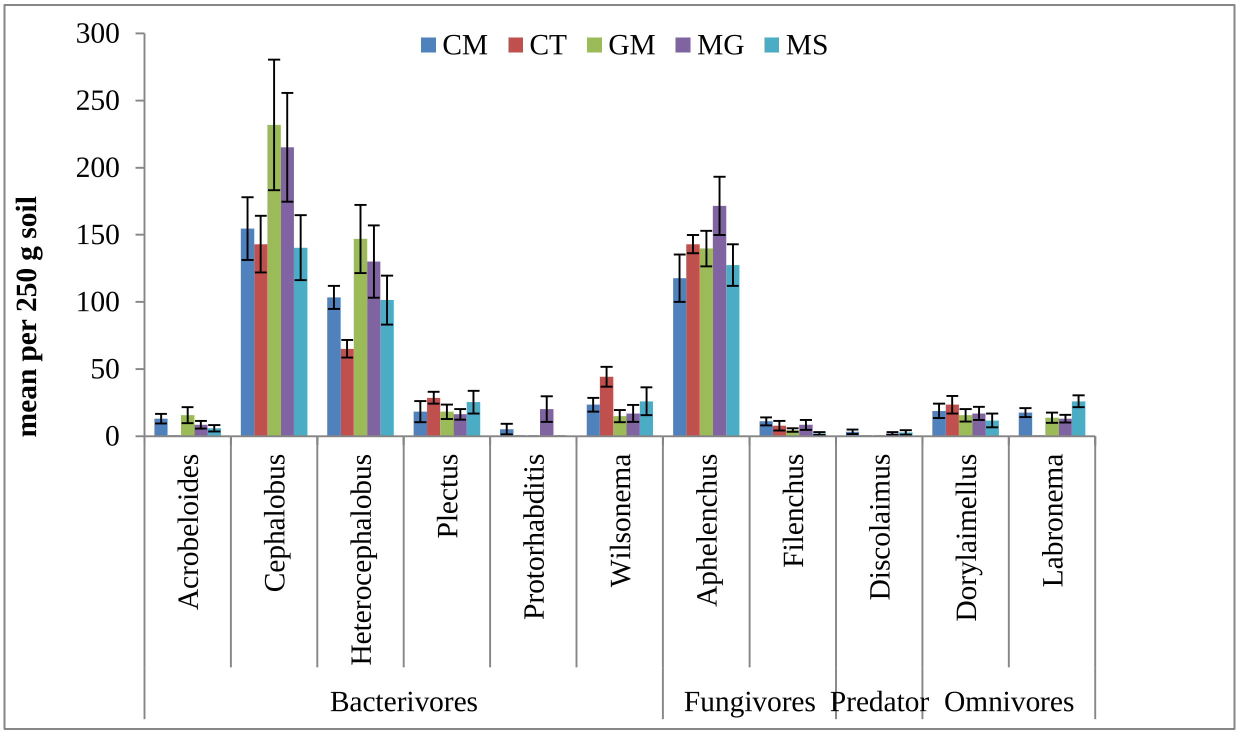

Figure 5.2: Mean abundance of significant nematode genera in CM- cow manure, CT-control GM-goat manure, MG- marigold, and MS- maize intercropped with sweet potato treatments during the short rains season.

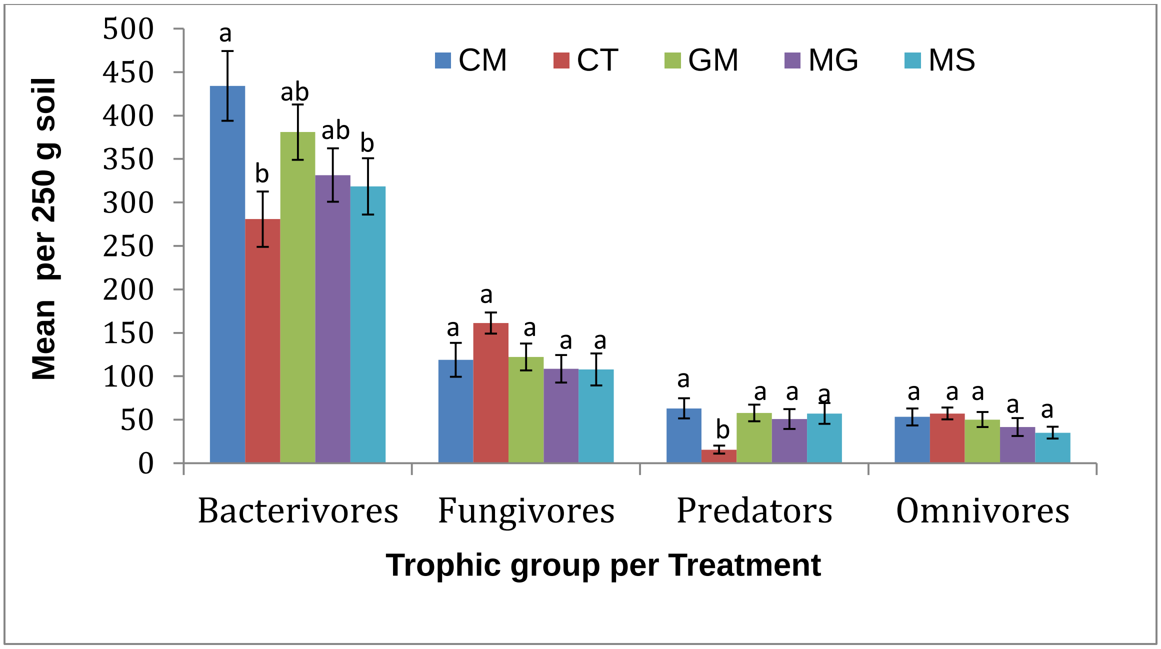

Figure 5.3: Average numbers of free-living nematodes groups in CM – cow manure, CT-control, GM - goat manure, MG - marigold, MS - maize-sweet potato intercrop plots in the long rains season.

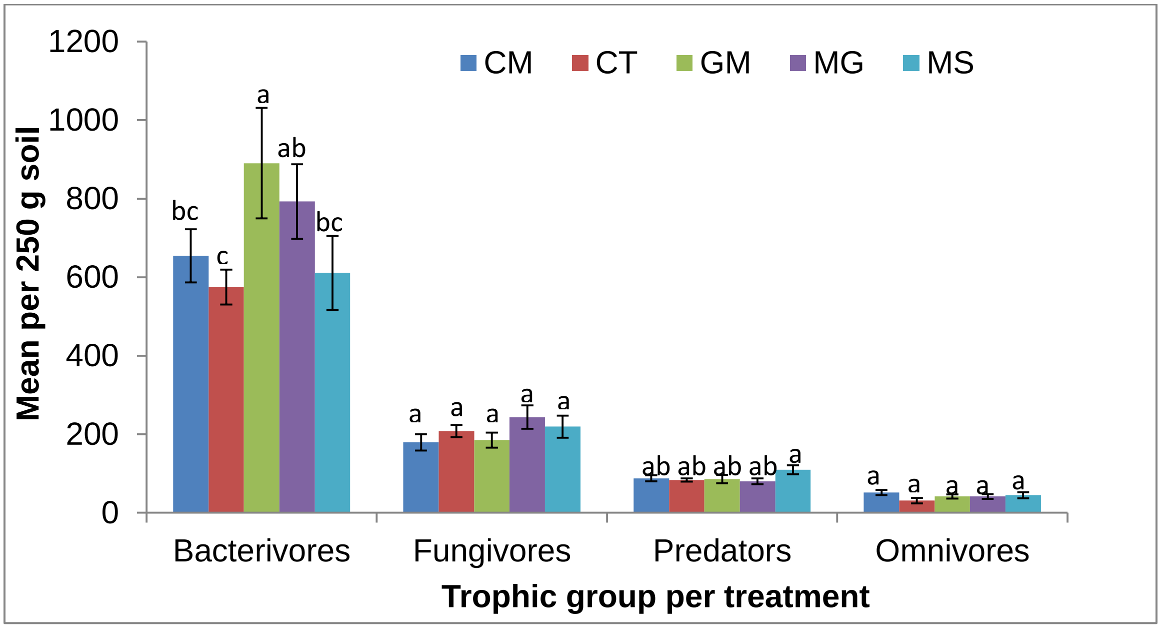

Figure 5.4: Average numbers of free-living nematodes groups in CM – cow manure, CT-control, GM - goat manure, MG - marigold, MS - maize-sweet potato intercrop plots in the short rains season.

5.4 Discussion

A high diversity of free-living nematodes was observed across the treatments during the two seasons. However, specific nematode taxa responded differently to the treatments. Population levels of free-living nematodes especially bacterivorous nematodes have been reported to increase following the amendment of soil with different organic substrates (Bulluck *et al*., 2002; Villenave *et al*., 2003; Nahar *et al*., 2006; Pan *et al*., 2015). This was also observed in this study in both seasons. An increase in the relative abundance of bacteria feeding nematodes may be attributed to increased populations of bacteria associated with applied organic amendments which afford excellent energy sources for these nematodes (Griffiths *et al*., 1994; Bulluck *et al*., 2002). Fungal feeding nematodes exhibited variable responses to the treatments where during the long rains seasons, untreated plots recorded a significantly higher number of fungivores. This might be because fungivores tend to occur in high numbers in undisturbed/stable environments. However, increase in the abundance of fungivores in some treatments (marigold and intercropping plots) in the short rains season could presumably be due to availability of food provided by these amendments (marigold) (Griffiths *et al*., 1994; Bulluck *et al*., 2002).This was in agreement with the findings of Bulluck *et al*., (2002), Hu and Qi, (2010) and Nahar *et al*., (2006) under various animal manure.

Relatively low abundance of predators and omnivores observed in this study have been reported in other studies under the influence of different amendments (Neher, 1999; Atandi, 2018). The majority of nematode genera in these two groups were in c-p 4 and c-p5categories except *Seinura* (c-p 2). These nematodes are highly sensitive to disturbances including input of amendments and rapidly respond to the disturbance through population decline. They also require more time to re-establish after disturbance compared to lower c-p guilds (fast-growing bacterial and fungal feeding nematodes) which probably led to this observation (Bongers, 1990). This may also probably explain the high number of omnivores recorded in the untreated control plots in the long rains season. Likewise, higher densities of omnivorous nematodes have been reported in untreated control plots compared to fertilized and grassland plots amended with manure (Forge *et al*., 2005). Irrespective of the relatively low number, treatments increased the number of predators and omnivores in the two seasons except for omnivores in the long rains season, which were high in the control plots. This probably indicated that input of amendments may not necessarily have negative effects on nematodes in the high-order trophic groups and may enhance the availability of food to these nematodes.

Previous research studies have reported varying responses concerning these two groups of nematodes. An increase in omnivorous nematodes under different organic treatments was reported in various studies (Birkhofer *et al*., 2008; Hu and Cao, 2008; Hu and Qi, 2010a). This was contrary to findings in the long rains seasons. However, their findings on predatory nematodes concurred with observations in this study during the two seasons. An increase in population densities of predacious nematodes observed in our study has been reported in soils treated with manure (Forge *et al*., 2005). Enhancement of predacious and omnivorous nematodes is beneficial as it may suppress plant-feeding nematodes through predation and may also contribute to increased nutrient mineralization (Berkelmans *et al*., 2003; Hu and Cao, 2008). In addition to the above explanations, an effect on temperature and moisture on the amendments and soil properties may have influenced the abundance and diversity of nematodes (Jiang *et al*., 2013; Steel *et al*., 2013). Among the treatments used, cow and goat manure effectively stimulated populations of free-living nematodes, especially the bacterivores. However, goat manure was the most effective in stimulating higher abundances of free-living nematodes. This could be attributed to the nutritious food resources available in this amendment.

5.5 Conclusion

In summary, this work outlines a high diversity of free-living nematodes associated with sweet potato. The organic amendments that were used revealed varying effects on specific nematode genera. Seasonal changes in temperature and moisture may have influenced the abundance of these nematodes. Notably, goat manure showed the highest potential in stimulating the population densities of free-living nematodes. Furthermore, irrespective of the low number of omnivorous and predacious nematodes, organic amendments increased their abundance compared to control primarily in the short rains season.

CHAPTER SIX

SYNTHESIS

6.0 General Overview

Sweet potato is an important food crop consumed in Kenya and throughout Africa. However, yields are greatly reduced by plant parasitic nematodes among other pests. Management of nematodes in sweet potato fields in Kenya is mainly through the use of nematicides and crop rotation which have limitations. The use of resistant sweet potato cultivars along with other low-cost organic nematode management strategies is the most economical, effective, and environmentally safe method of managing parasitic nematodes associated with sweet potato in Kenya.

Investigation of the performance of sweet potato cultivar, SPK 004 in fields with a natural infestation of root-knot nematodes revealed that this cultivar was very resistant to *Meloidogyne* species. This was demonstrated by a low mean galling index that ranged between 2.667 and 6.00 for both untreated and nematicide treated SPK 004 and control plots, respectively. Findings from this study confirmed greenhouse findings, where this cultivar was found to be very resistant to *Meloidogyne incognita*. This resistant cultivar may be used in sweet potato infested fields and rotation with non-host crops for the management of root-knot nematodes. This will be useful in reducing production costs, overreliance on nematicides, and for the improvement of quality and market value of storage roots. In addition, the cultivar recorded high dry matter content, total and marketable yields which are important attributes preferred by consumers. This crop can be utilized in bridging the food security gap in Kenya.

High diversity of plant parasitic and free-living nematodes was observed across treatments in both seasons. However, differences in the abundance of specific genera in the two seasons were observed. Seasonal variability in nematode genera abundance could be attributed to the differences in temperature and moisture levels that directly and indirectly affect nematode abundance. *Meloidogyne*, *Pratylenchus*, *Rotylenchulus*, *Scutellonema*, *Tylenchus*, and *Ditylenchus* were the major parasitic nematodes of economic importance recorded in this study. These species attack sweet potato at different growth stages resulting in significant yield losses and reduction in the quality and quantity of sweet potato.

Principal response curve analysis revealed that treatment effects on nematode genera over time varied between the two seasons. All treatments reduced the number of plant parasitic nematodes at different times. Reduction of PPN by these amendments at the distinct sweet potato growth stages is important in improving the overall yields since most damage by PPN occurs at specific developmental phases. Goat manure treatment exhibited the most pronounced effect on economically important PPN in sweet potato across the two seasons. Renyi diversity profiles revealed that all treatments had low diversity of omnivores and predators in both seasons except in marigold treatment which indicated a high diversity of predators. Despite the low diversity, the abundance of some predatory and omnivorous nematodes increased after the application of marigold and intercropping with maize.

The treatments had varying effects on soil food web indices and nematode metabolic footprints. Goat manure recorded high values of structure index and low plant parasitic index values indicating that the soil food web in goat manure treated plots was well-structured with moderate ability to suppress PPN. Low maturity index values were expressed in marigold treated plots, which might have resulted from the enrichment effect of the green manure and is an indication of an extremely disturbed ecosystem. Fluctuations in channel index values were observed between the two seasons indicating a shift from fungal to bacterial decomposition due to the influence of environmental factors on the organic amendments. Low basal index values were recorded in the two seasons indicating that the treatments did not severely affect the soil food web. High enrichment index values were recorded in marigold plots and they are characteristic of bacterial-mediated decomposition.

Nematode metabolic footprints provide an estimate of nematode’s contribution to various ecosystem functions and services based on biomass and metabolic activity of nematodes within each functional guild. Higher values of enrichment footprint recorded in marigold treated plots suggested that this treatment might have provided more labile and readily available resources for enrichment opportunists thus significantly increasing their abundance. Significantly higher values of predatory and omnivore footprints were recorded in cow manure plots and non-significant high structure footprint values were recorded in goat manure plots. The high values of these footprints are indicative of the level of PPN regulation which may have been due to an increase in the availability of prey resulting from the addition of organic resources. The functional metabolic footprint categorized plots under maize- sweet potato intercrops as structured in short rains season while all the other plots were degraded in both seasons. However, goat manure bordered a structured ecosystem in long rains season while cow manure bordered a structured ecosystem in both seasons. Degraded plots revealed a depleted food web with insufficient resources to support the nematode communities while the structured plots are indicative of a more complex ecosystem that has higher trophic groups with high connectance between fungal, omnivore and predatory channels which is beneficial in pest regulation.

Variations in the abundance and diversity of free-living nematodes were observed in this study. High populations of bacterivores were recorded in goat manure and cow manure treated plots. This may be attributed to increased food resources associated with organic amendments. In this study, relatively low numbers of omnivorous and predacious nematodes were observed. Among the organic amendments, goat manure was more efficient in increasing the populations of free-living nematodes. This probably may be attributed to the nutritious resources present in this amendment.

6.1 Conclusions

From the results of this study, it can be concluded that:

- Sweet potato cultivar, SPK 004 is very resistant to *Meloidogyne* species.
- Reduced population of plant parasitic nematodes and increased numbers of free-living nematodes were found in goat manure treated plots.
- Overall, the use of resistant cultivars along with the low-cost organic amendments is effective.

6.2 Recommendations

Based on the findings,

- Sweet potato cultivar, SPK 004 may be utilized in sweet potato fields with a high infestation of *Meloidogyne* species to minimize the overall yield losses.
- Farmers may consider adopting the locally available low-cost organic amendments such as goat manure to manage plant-parasitic nematodes and stimulate free-living nematodes populations that play key functions in the soil.
- Further studies should be conducted to help understand the mechanism behind the suppression of parasitic nematodes as well as an increase in free-living nematodes in goat manure.
- While these strategies may be applicable at small-scale farming levels, it is imperative to verify their effectiveness on a large-scale level.

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