Soil macrofauna functional groups and their effects on soil structure, as related to agricultural management practices across agroecological zones of Sub-Saharan Africa

Fredrick Ouma Ayuke

Thesis committee

Thesis supervisor

Prof. Dr. Lijbert Brussaard
Professor of Soil Biology and Biological Soil Quality, Wageningen University

Thesis co-supervisors

Dr. Mirjam M. Pulleman,
Researcher, Department of Soil Quality, Wageningen University
Dr. Bernard Vanlauwe,
Senior Researcher, TSBF-CIAT, Nairobi, Kenya
Prof. Dr. Johan Six,
Professor, UC-Davis, California, USA

Other members

Prof. Dr. Ir. A. van Huis, Wageningen University
Dr. Ir. W.B. Hoogmoed, Wageningen University
Prof. Dr. Ir. R. Merckx, Catholic University, Leuven, Belgium
Dr. D. Odee, Centre for Ecology and Hydrology, Penicuik, UK

This research was conducted under the auspices of the C. T. de Wit Graduate School of Production Ecology and Resource Conservation

Soil macrofauna functional groups and their effects on soil structure, as related to agricultural management practices across agroecological zones of Sub-Saharan Africa

Fredrick Ouma Ayuke

Thesis
submitted in fulfilment of the requirements
for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr. M.J. Kropff,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Friday 11 June 2010
at 4 p.m. in the Aula.

Fredrick Ouma Ayuke
Soil macrofauna functional groups and their effects on soil structure, as related to agricultural management practices across agroecological zones of Sub-Saharan Africa

Thesis, Wageningen University, Wageningen, NL (2010)
With references, with summaries in Dutch and English

ISBN 978-90-8585-687-0

DEDICATION

To the memory of ***Matilda Nigh****t and* ***Dr. Elly A. Ochola***

You had great influence on some of my decisions and you were never wrong. You inspired me to take this path, but never lived to see me reach the destination.

Propositions (Stellingen)

(1)

Earthworms and termites play a crucial in the processes of soil aggregation and carbon and nitrogen stabilization, but earthworms more so than termites (**this thesis**).

(2)

The degree of influence of earthworms and termites on soil processes depends on management intensity (**this thesis**).

(3)

To control pests, it is better to understand their life-strategies than to produce biocides to eliminate them.

(4)

Unless decisive action is taken to assist small-scale farmers to grow more and more valuable crops, food security in Africa will remain elusive.

(5)

From whom to whom much has been given, more is expected.

(6)

The roots of education are bitter, but the fruits are sweet.

Propositions accompanying the PhD thesis **‘Soil macrofauna functional groups and their effects on soil structure, as related to agricultural management practices across agroecological zones of sub-Saharan Africa’**

Fredrick Ouma Ayuke

Wageningen, 11th June 2010

Abstract

This study aimed at understanding the effects of crop management practices on soil macrofauna and the links with soil aggregation and soil organic matter dynamics, which is key to the improvement of infertile or degrading soils in Sub-Sahara Africa. Soil macrofauna, especially earthworms and termites, are important components of the soil ecosystem and, as ecosystem engineers, they influence the formation and maintenance of soil structure and regulate soil processes, such as organic matter decomposition and nutrient dynamics.

In comparison with natural systems, earthworm and termite diversity and abundance were low in fallow, high soil-carbon (C) and low soil-C arable treatments in 12 long-term trial fields across the sub-humid to semi-arid tropical zones in Eastern and Western Africa. Continuous crop production had significant negative effects on earthworm diversity, but little effect on termite diversity, as compared to long-term fallow. Agricultural management resulting in high soil C increased earthworm and termite diversity as compared to low-C soil. Long-term application of manure in combination with fertilizer resulted in higher earthworm diversity and biomass, associated with improved soil aggregation and enhanced C and N stabilization within this more stable soil structure. These practices therefore result in the dual benefits of improving soil physical and chemical properties.

A micromorphological study of undisturbed soil thin sections showed that fallowing, conservation tillage plus residue application (in East Africa) and hand-hoeing plus manure (in West Africa) enhanced biogenic soil structure formation, resulting in a well developed soil structure and a continuous pore system characterized by many faunal channels. In contrast, intensive tillage and absence of organic inputs resulted in soil with less biogenic soil structural features.

Farmers in Nyabeda, West-Kenya, were aware of the activities and nesting habits of termites, but 90% percent of the farmers perceived termites as pests.

This study has shown that the soil macrofauna, especially earthworms, and, to a lesser extent termites, are important drivers of stable soil aggregation in Sub-Saharan agroecosystems, with beneficial effects on soil physical and chemical properties. However, their beneficial impact on soil aggregation is reduced with increasing management intensity and associated soil disturbance due to cultivation. This knowledge is important in designing agricultural management systems aimed at increasing long-term soil fertility in Sub-Saharan Africa.

TABLE OF CONTENTS

CHAPTER ONE

General introduction

Belowground biodiversity

Biodiversity has become a key issue in agronomic and environmental policies and research since the Rio de Janeiro summit in 1992. This event highlighted the importance of biodiversity conservation for sustainable development (CBD, 2001) by emphasizing different benefits people obtain from biodiversity. Biodiversity is a potential reserve of genes for plant breeding and new compounds for medicine and other so-called ecosystem goods as well as services such as water and climate regulation that are key to human well-being (Paoletti et al., 1992; Altieri, 1999; Duelli et al., 2003; Clergue et al., 2005; Millenium Ecosystem Assessment, 2005). Although biodiversity loss has been high on the science and policy agendas in the last 2-3 decades, most of the conservation efforts have been directed to, often endangered, aboveground plant and animal species of aesthetic value, whereas the less visible fauna and flora, such as soil macro- and mesofauna, bacteria and fungi have been widely ignored. Yet, soil contains some of the most diverse assemblages of organisms, the vast majority of which are still undescribed, but whose functions contribute to maintain life on earth (Lavelle, 1996; Altieri, 1999; CBD, 2001). The beneficial effects of soil fauna on plant production have largely been neglected by agronomists, in contrast to their harmful roles as potential pest species. As a consequence, there is a general lack of knowledge on the beneficial roles of soil fauna in crop production systems and the management of soil fauna in conventional agricultural systems generally comes down to pest control, including widespread use of pesticides (ICIPE, 1997).

Soil invertebrate fauna as a key component of ecosystems

Characterization of soil invertebrate fauna

Soil fauna comprise a large variety of life forms and adaptive strategies. All animals ranging from microscopic amoebae and ciliates to arthropods (e.g. beetles and millipedes) and mammals (e.g. rats) that spend at least part of their life within the soil can be considered as part of the soil fauna (Dangerfield, 1993).

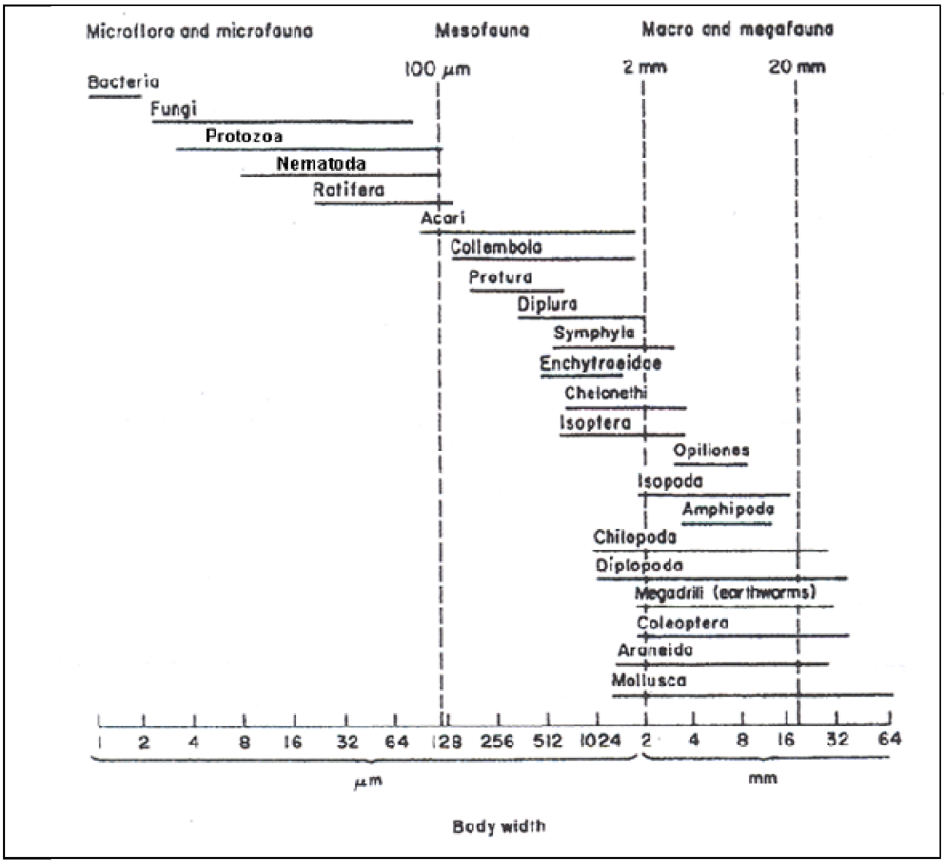

Figure 1. Classification of soil organisms based on body size. From Swift et al. (1979).

Soil invertebrates can be described in terms of size (macro-, meso- and microfauna; Swift et al., 1979, Lavelle, 1988; Figure 1), taxonomic composition (order, family, genus or species), guild structure or trophic level (Lavelle, 1988; Lavelle et al., 1994b). A guild has been defined as a group of species of organisms that exploit the same class of environmental resources in a similar way (Brussaard, 1998). This definition groups together species that significantly overlap in their niche requirements without regard to taxonomic position.

Among the three size categories, macrofauna are the most conspicuous with the greatest potential to modify the soil environment through their activities (Lavelle et al., 1994b; Jouquet et al., 2006). Especially earthworms and termites are widely recognized for their role in soil structure formation, organic matter incorporation and decomposition and nutrient mineralization. Lavelle (1996, 1999) and Jones et al. (1994) consider these organisms “ecosystem engineers’’, defined as organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials; in so doing they modify, maintain and create habitats. Earthworms and termites ingest organic matter or a mixture of mineral soil and organic matter and create channels and nests in the soil, thus creating solid organo-mineral structures that may persist longer than the organisms that produced them. They developed highly efficient digestion systems based on internal mutualism with microflora and protozoa that live in their gut. Earthworms and termites constitute >90% of the biomass of the invertebrate fauna in soils of sub-Saharan Africa (Brown et al., 1996).

Role of soil macrofauna in soil functioning

Soil invertebrates are important determinants of biological, chemical and physical characteristics. They enhance biodegradation and humification of organic residues in several ways: (1) by breaking down organic residues and increasing surface area for microbial activity, (2) by producing enzymes which break down complex bio-molecules into simple compounds to form humus and (3) by improving the soil environment for microbial growth and soil-plant interactions (Lal, 1988; Brussaard and Juma, 1996; Swift et al., 1996; Tian et al., 1997a).

The diversity and abundance of the structures produced by soil ecosystem engineers impact on the physical properties of soils, i.e. overall aggregation, porosity, water infiltration and retention and resistance to erosion (Lavelle, 1999, Figure 2). The channels created by earthworms improve soil structure, aeration, water infiltration and water availability to plants (Lavelle et al., 1994a; Tinzara and Tukahirwa, 1995; Blanchart et al., 1999; Lavelle, et al., 1999; Brown et al., 2004). Earthworms play an important role in the formation of soil organic matter (SOM) enriched macroaggregates (Lavelle et al., 1999; Six et al., 2004; Bossuyt et al., 2004; Pulleman et al., 2004; 2005), which can physically protect occluded organic matter against microbial decay, and, upon disintegration, release occluded carbon and nutrients (Blanchart et al., 1993; 2004; Bossuyt et al., 2005). Earthworm casts are enriched in SOM, N, P, K, and Ca as compared to bulk soil (Fitzpatrick, 1986, Jiménez and Thomas, 2001; Mora et al., 2003) and, hence, serve as a reservoir of (micro) nutrients. Apart from promoting soil physical and chemical properties, earthworms also promote nodulation (Doube et al., 1994), dispersal of mycorrhizal fungi (Harinikumar et al., 1994) and even disease suppression and dispersal (Szczech et al., 1993).

Termites mediate the synthesis and breakdown of soil organic matter and influence water infiltration and availability to plants by modifying soil structure (Wielemaker, 1984; Kooyman and Onck, 1987; Asawalam et al., 1999; Mando et al., 1999; Sarr et al., 2001). They influence soil physical properties through the construction of mounds, nests, galleries and surface sheeting (Mando et al., 1996; Asawalam et al., 1999; Sarr et al., 2001; Figure 2) and also by transporting materials, thereby producing passages, which improve drainage and aeration (Lavelle at al., 1994b; Mando, 1997a, b; Mando, 1998; Ouédraogo et al., 2006). Mound-building termites form stable microaggregates that physically protect occluded organic matter against rapid decomposition and reduce soil erosion and crust formation (Jungerius et al., 1999; Jouquet et al., 2002).

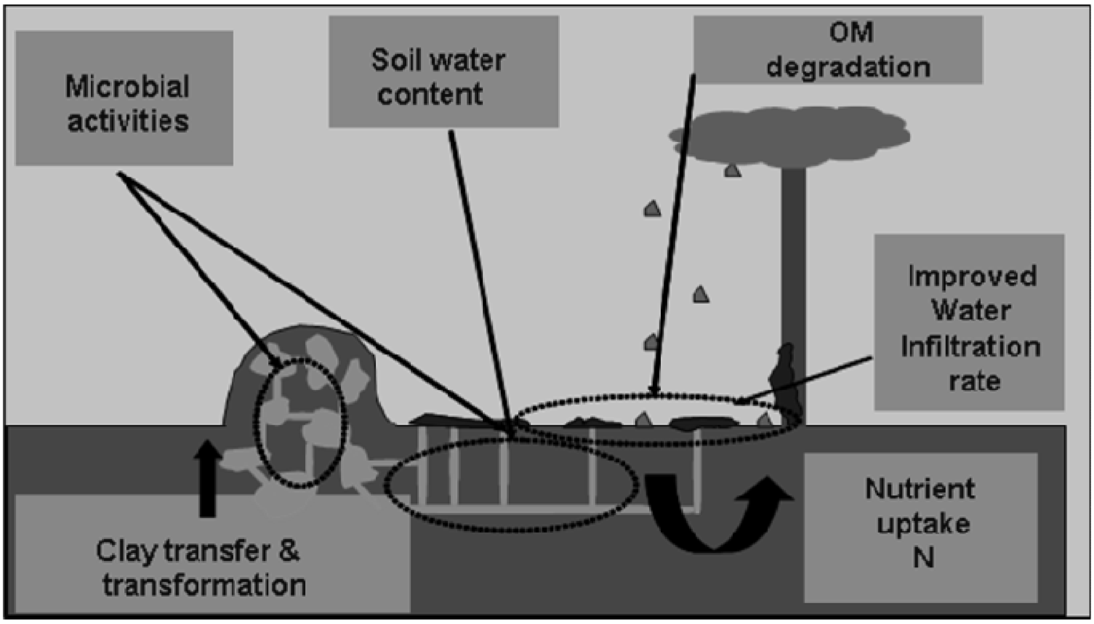

Figure 2. The concept of ecosystem engineering by termites (courtesy of Soulemayne Konate).

The importance of termites in the decomposition of plant matter in natural ecosystems is well documented (Martius, 1994; Mando and Brussaard, 1999). Collin, (1981, 1983) established that in the tropical rainforests of Nigeria and Malaysia termites play a significant role in both decomposition and litter removal. Mando and Brussaard (1999) found that termites alone could account for up to 80% of litter disappearance in one year. Termites play a significant role in soil nutrient availability and cycling through interactions with other soil organisms, e.g. bacteria and fungi, most of whom they avail food to (Jouquet et al., 2002). Soil from termite mounds is sometimes used as fertilizer in tropical cropping systems because of a high accumulation of nutrients (Anderson and Wood, 1984; Nyamapfene, 1986; Swift et al., 1989; Lopez-Hernandez, 2001). Despite the potentially beneficial role of termites, termite pest problems have been identified as a major constraint to increasing yields of crops in sub-Saharan Africa (Smale 1995, Sekamatte et al. 2003, Sileshi et al. 2005). The challenge therefore remains to better understand the interactions between agricultural management practices and soil macrofauna (e.g. termites) in order to find ways to enhance soil fertility and crop yields.

Effects of management on soil macrofauna in tropical agroecosystems

Introduction

In large parts of sub-Saharan Africa, pests, weeds, diseases and soil fertility decline are major biophysical causes of low per capita food production (Sanchez, 2002; SP-IPM, 2004). Degradation processes such as loss of soil carbon and nutrient depletion in general can occur quickly and are difficult to reverse (Sanchez et al., 1989). Moreover, loss in yield cannot be corrected by the use of fertilizers in economies where cash flow is minimal. Under such circumstances, Integrated Soil Fertility Management (ISFM) i.e. integration of fertilizers with organic resources has been regarded as a feasible alternative in low-input systems, compensating for the high costs of fertilizers (Vanlauwe et al., 2009). Manipulation of the soil environment via tillage, application of organic residues and manipulating soil fauna are among the factors affecting SOM dynamics under cropping systems (Six et al., 1999, 2002). In low-input agricultural systems, soil fauna has been found to play a crucial role in soil organic matter dynamics, in soil physical properties improvement, and in nutrient release for crop production (Ouédraogo, 2004). However, soil macrofauna composition, abundance and activity, hence their impacts on soil processes, vary depending on residue inputs and soil management practices (Mackay and Kladivko, 1985; Lavelle et al., 1994a; Tinzara and Tukahirwa, 1995; Choo and Baker, 1998; Pulleman et al., 2004). Management practices (e.g. crop rotation, tillage, organic resource use and application of agrochemicals such as pesticides, herbicides and inorganic fertilizers) can cause positive or negative changes in species composition, community structure and population sizes. Some of the negative effects of management practices may be long-lasting and result in a decline in the abundance and/or biomass of soil macrofauna populations, or eliminate or reduce key species, i.e.

species that play a disproportionate role in ecosystem processes (Dangerfield, 1993; Beare et al., 1997). Figure 3 shows a hierarchical model of inter-correlated factors that determine soil biodiversity and processes.

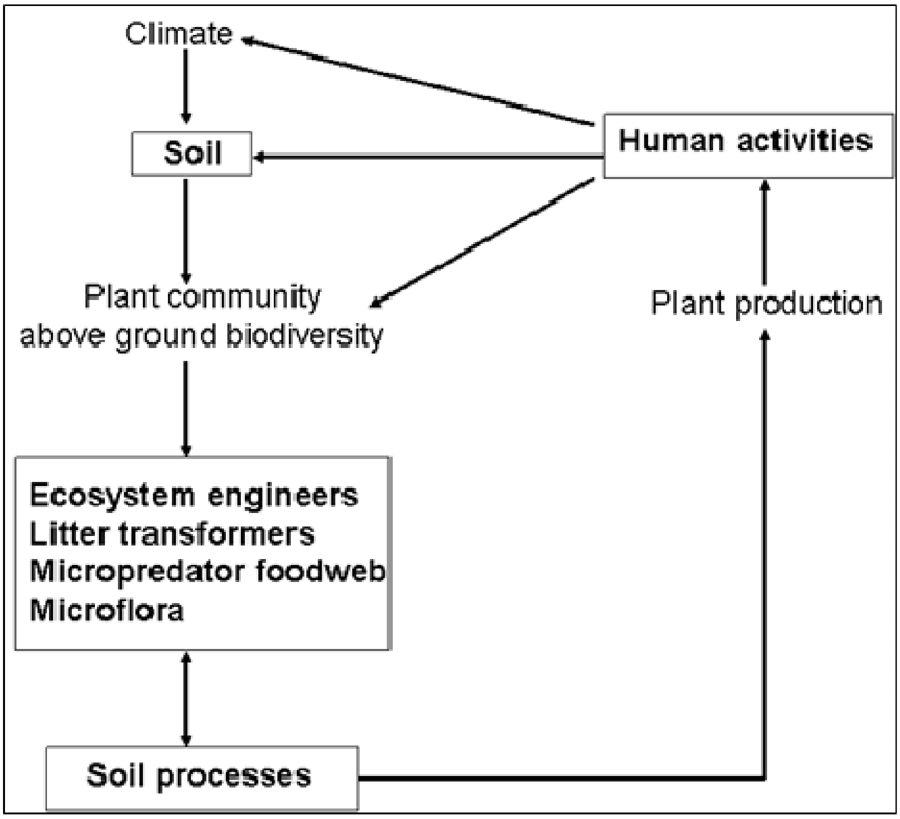

Figure 3. A hierarchical model of factors that determine soil biodiversity and soil processes (modified from Lavelle *et al.*, 1993).

Climate, soil texture and management have also been indicated to influence the activity of soil macrofauna (e.g. earthworms and termites) that produce biogenic structures (Brussaard et al., 2007). It can therefore be postulated that differential land management effects on soil macrofauna functional groups will translate into differential effects on the structures they produce, thus affecting soil organic matter, soil aggregation, porosity and water and nutrient availability to plants. As such, the diversity of biostructures produced by ecosystem engineers represents the major functional attribute whereby macro-invertebrate diversity influences soil functioning (Lavelle, 1996). Nevertheless, little is known on their diversity in agricultural soils across different climate and soil conditions and agricultural management practices in low input cropping systems.

Recent studies revealing the intimate relations between aggregate turnover and SOM dynamics indicate the need for agricultural management that balances macro- and microaggregate turnover in order to optimize their protective (soil and SOM stabilization) versus productive (nutrient release) functions (Brussaard et al., 2007). Given that the dynamics of biogenic structures affect water, C and nutrient fluxes (Anderson 1988, Mando 1997b, Bossuyt et al., 2004; 2005; Pulleman et al., 2003, 2005) with consequent effect on plant production, Brussaard et al., 2007 propose the use of water and nutrient use efficiencies of crops and cropping systems as bioassays of the success of management of the soil macrofauna in agriculture aimed at an optimal balance between the protective and productive functions of soil aggregates.

Henceforth, I will address the most important management practices affecting the soil macrofauna and their roles in ecosystem functioning in more detail.

Organic resource management

Organic resources in the form of plant litter or decomposed organic matter is utilized by a wide range of organisms and their predators within natural ecosystems. This results in complex food webs and habitat structures with many interactions between soil and litter- or organic matter-dwelling species. Application of plant residues (Newman, 1988; Ayuke et al., 2003; Fonte et al., 2009) and addition of farmyard manure (Adejuyigbe, 1994) have been found to increase the abundance of earthworms. Although organic residues over short periods increase macrofauna populations, effects on macrofauna diversity are small (Mando, 1998; Ayuke et al., 2003; Ouédraogo et al., 2004). Whether long-term additions of organic residues of varying quality can influence the diversity and abundance of soil macrofauna in arable cropping systems and, hence, soil functions like organic matter retention, stable aggregation and water infiltration, offers scope for further studies. Macrofauna manipulation studies investigating organic resource and soil biota interactions in cropping systems under field conditions are few. Mando et al. (1996) and Mando (1998) showed that mulch-induced termite recolonization led to a rapid increase in water infiltration, water use efficiency, nutrient release and crop performance on Sahelian crusted soils. Ouédraogo et al. (2006) found that soil fauna enhanced the water and nitrogen use efficiency of crops, especially with the addition of high-quality residues.

In low-input agroecosystems in which organic residues form chief sources of nutrients, the composition and activity of soil fauna, including their effects on nutrient availability, are likely to be regulated by litter quality (Tian et al., 1997b; Wardle and Lavelle, 1997). According to Mafongoya et al. (1998) and Palm et al. (2001), “resource quality" is defined by the organic constituents (lignin, polyphenols) and nutrient contents (nitrogen and phosphorus) of the materials. Resource quality parameters and indices (lignin, polyphenols, and nitrogen) that govern decomposition and nutrient release in natural ecosystems were identified by Swift et al. (1979) and Melillo et al. (1982). Since then, numerous studies have reported resource quality, decomposition and nutrient release patterns for a variety of organic residues used in tropical agroecosystems (Palm, 1995; Cadisch and Giller, 1997; Heal et al., 1997; Mafongoya et al., 1998). From these studies, a predictive understanding of decomposition and nutrient release patterns has emerged (Cadisch and Giller, 1997; Palm et al., 1997), resulting in the development of an organic resource database (ORD) by Palm et al. (2001) and subsequent validation of residue quality-driven decision support system (DSS) by Vanlauwe et al. (2002).

In spite of these developments, it is not well understood how these resource quality parameters relate to soil faunal composition, abundance and activity. Tian et al. (1995) integrated C to N ratio, lignin and polyphenol content of plant residues into a quality index (PRQI) and tried to correlate this index to soil fauna (termite, earthworm and ant) density, but they did not specify critical levels or the utility of PRQI for selection of plant materials in order to stimulate fauna activities (Mafongoya et al., 1998). Although a few studies have reported the effects of organic resource quantity and quality on the diversity and abundance of soil fauna (Lavelle et al., 1997; Tian et al., 1997b), their interactions and derived benefits, if known, largely remain untapped, especially in low-input smallholder agriculture. For example, Rouland et al. (2003) could not explain the food preferences by termites in a manipulative experiment using litter amendments of various qualities, such as acacia leaves, millet canes, ground millet, combretum wood and cattle manure.

Tillage

Improvements of root penetration, water infiltration and soil moisture storage, weed control and supply of nutrients from rapid decomposition of organic matter, are considered the most beneficial contributions of tillage to crop production (Hoogmoed, 1999; Wander and Yang, 2000; Lampurlanes and Cantero-Matinez, 2003; Antil et al., 2005). However, over the last decades, no-till systems are increasingly promoted and adopted as an alternative management system that could restore or sustain soil fertility in the long term. Particulate organic matter (POM) and microbial biomass have been shown to be the components of SOM that are most sensitive to cropping system management (Vanlauwe et al., 1998; Six et al., 1999; Wander and Young, 2000). For example, Doran et al. (1998), Mrabet et al. (2001), Six et al. (2002), Wu et al. (2003) and Al-Kaisi and Yin (2005) have shown that no-till management results in less loss of soil carbon, nitrogen and phosphorus in the topsoil over time. Changes in soil C and N due to tillage can result from several mechanisms such as redistribution, mixing and dilution with depth and enhanced biological oxidation of SOM (Warkentin, 2001; Pedro, et al., 2001; Hulugalle et al., 2002; Ouédraogo, 2004) and erosion of the top soil (Warkentin, 2001; Steiner, 2002).

Tillage is also known to adversely affect arthropods and other invertebrates that inhabit the soil (Roper and Gupta, 1995; Steiner, 2002; Clapperton, 2005). Numerous studies have demonstrated that tillage practices can have a significant influence on the abundance and distributions of soil fauna (Farrar and Crossley, 1983; Moore et al., 1984; Chikara et al., 2004). House and Parmelee (1985) and Smith (2001) showed that soil arthropods and earthworm densities were higher under no-tillage than in conventional tillage systems, while Tian *et al.* (1997b) and Chakara et al. (2004) reported lower earthworms populations in tilled land than in bush fallows or no-till land. Underlying causes are the destruction of nests and burrows occupied by soil invertebrates and alterations of the amount and location of the food supply and increased soil moisture and temperature fluctuations by tillage operations (Kladivko, 2001).

Crop rotation/intercropping

Crop rotations are fundamental to sustainable cropping systems (KRC, 1998; Wu et al., 2003; Al-Kaisi and Yin, 2005; Clapperton, 2005). Associated benefits include: improved soil structure and associated soil physical properties, increase in SOM, improved soil nutrient and moisture contents of the soil (Roper and Gupta, 1995; Wu et al., 2003; Al-Kaisi and Yin, 2005), weed and disease and pest control, reduced soil erosion and an increase in flora and fauna diversity and numbers (KRC, 1998). Under crop rotation, greater biomass or activity of soil microorganisms such as bacterial-feeding protozoans, heterotrophic rhizospere microorganisms, dinitrifying and nitrifying bacteria (Collins et al., 1992) or collembola (Anderson, 1987) and reduction of pest and disease-causing organisms (Roper and Gupta, 1995) have been reported. However, little is known of the response of earthworms and termites to crop diversification.

Damage to crops by termites has become a major constraint to increasing yields of, e.g., maize and sorghum which are the staple foods for millions of people in sub-Saharan Africa (Wood et al., 1980; Smale, 1995; Sekamatte et al., 2003; Sileshi et al., 2005). Arguably, crop rotation and intercropping promote litter availability and diversity in space and time and may therefore prevent termites from reaching pest status. For example, in cereal-legume intercrops lower damage by termites has been reported (Hominic, 1999; Sekamatte et al., 2003; Sileshi and Mafongoya, 2003). Blair et al., (1996) and Wardle and Lavelle (1997) reported that it is difficult to predict the direction in which increased litter diversity affects the diversity of soil fauna and associated litter decomposition. Yet, litter mixing has been proposed as one of the options to optimize rates of short- and long-term nutrient release and to maintain SOM (Mafongoya et al., 1998). Clearly, there is scope for further research on litter diversity under crop rotation/intercropping as related to crop damage and litter decomposition.

Scope of the study

Despite advances made in understanding the links between soil macrofauna and agricultural productivity, this component of biodiversity is still very much a “black box”. An understanding of the link between soil macrofauna and management on soil aggregation and SOM dynamics is key in the improvement and management of soils with low fertility. This thesis proposes to link soil biodiversity to soil functioning through the diversity of the soil structures produced by ‘ecosystem engineers’ like earthworms and termites, i.e. organisms, which physically modify and create habitats for other soil organisms and plant roots.

In a survey of 12 long-term field trials across the sub-humid to semi-arid agro-ecological zones of West Africa (Tamale: Ghana, Ibadan: Nigeria, Farakoba and Saria I-III: Burkina Faso, Sadore: Niger) and East Africa (Embu, Kabete, Impala and Nyabeda: Kenya and Lilongwe: Malawi), soil macrofauna were systematically quantified and then related to agroecological (including soil) characteristics and agricultural management systems. In-depth studies were also conducted in a long-term trial at Kabete, Kenya, to assess the effects of management (organic resource management and mineral fertilizer use) on earthworm and termite taxa and functional group diversity. An assessment was made of how this functional diversity is reflected in the diversity of biogenic structures and the relative abundance of biogenic (= soil fauna-formed) structures, soil aggregation and SOM dynamics. A micromorphological approach was used to describe and quantify macrofauna-induced biogenic structures in soil thin sections by comparing management systems differing in tillage intensity and with or without organic amendments (manure/crop residues) in long-term field trials at Nyabeda (Kenya) and Saria III (Burkina Faso).

This study is part of a larger WOTRO/NWO programme testing the general hypothesis that the diversity of earthworms and termites and the soil structures they produce, optimizes SOM dynamics with consequent positive impacts on N and water availability and synchronization with crop demand, thereby enhancing crop performance.

In the context of the WOTRO programme, the results were expected to show how and to what extent the productivity and sustainability of tropical agro-ecosystems can be improved by stimulating the soil macrofauna (especially earthworms and termites) biodiversity and activity through the judicious use of organic resources and soil cultivation and associated management practices.

Our study thus aimed at assessing:

1. How agricultural management affects earthworm and termite diversity across sub-humid to semi-arid tropical zones.

2. The influence of soil macrofauna on soil aggregation and SOM dynamics in agro-ecosystems of sub-Saharan Africa as influenced by management practices.

3. How management practices (e.g. tillage and use of organic inputs) influence macrofauna-induced biogenic structures in East and West African soils.
4. Disclosing farmers' knowledge and perception on the roles of termites in Western Kenya.

Description of the study sites

The study was conducted in 12 long-term field trials across the sub-humid to semi-arid agro-ecological zones of East Africa (Embu, Kabete, Impala and Nyabeda in Kenya and Chitala in Malawi) and West Africa (Tamale in Ghana, Ibadan in Nigeria, Sadore in Niger and Farakoba, Saria I, II and III in Burkina Faso; (Figure 4). A general characterization of the sites including climate and soils is presented in Table 1 of chapter 2. The long-term trials were established 7-50 years ago and are aimed at testing different management options for arable crop production (e.g. organic, mineral or organic + mineral inputs, crop rotation and tillage). Treatments selected for both survey and in-depth studies are indicated in the individual chapters of the thesis.

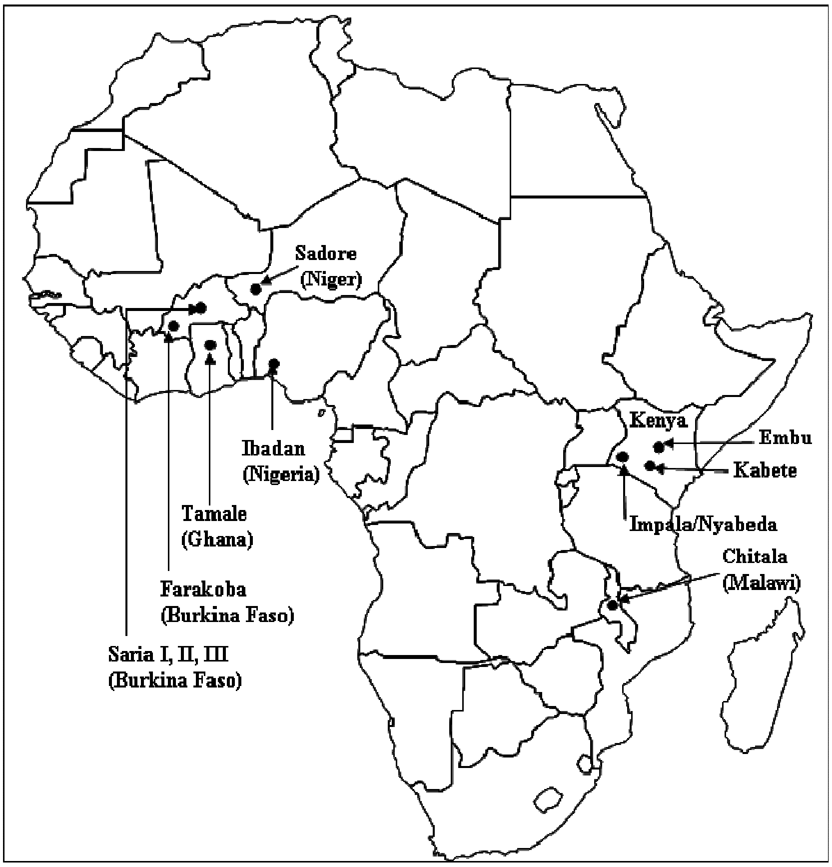

Figure 4. Location of research sites in East and West Africa (Saria consists of Saria I, II, III).

Outline of the thesis

This thesis is composed of 7 chapters. Chapter 2 examines how agricultural management affects earthworm and termite diversity across sub-humid to semi-arid tropical zones. In 12 long-term agricultural field trials in East and West Africa, treatments with high and low soil organic C were chosen to represent contrasts in long-term soil management effects, including tillage intensity, organic matter and nutrient management and crop rotations. High soil C was considered to reflect relatively favorable conditions, and low soil C less favorable conditions for soil macrofauna. For each trial, a fallow representing a relatively undisturbed reference was also sampled.

In chapters 3, 4 and 5, the relations between soil fauna and ecosystem functioning are examined in arable and fallow systems. In chapter 3, a broad regional study is reported, which examined how management intensity affects soil macrofauna, and how macrofauna in turn influence soil aggregation in agro-ecosystems of sub-Saharan Africa. In chapter 4, a long-term trial at Kabete, Kenya, was selected to examine in detail the interactive effects of soil fertility management and soil macrofauna diversity on soil aggregation and SOM dynamics in arable cropping systems. Differently managed arable systems were compared to a long-term green fallow system representing a relatively undisturbed reference. In chapter 5, a micromorphological approach is used to describe and quantify macrofauna-induced structures in thin sections of undisturbed soil samples from long-term field experiments in East and West Africa. Management systems differing in tillage intensity and with or without organic amendments (manure/crop residues) are compared. Chapter 6 describes farmers' knowledge on the occurrence and behavior of termites, farmers' perception of the importance of termites in their cropping systems and the management of termite activities in their farm fields in Nyabeda, Western Kenya. Chapter 7 provides a general, integrated discussion of the results described in the previous chapters against the background of existing theories and concepts.

CHAPTER TWO

Agricultural management affects earthworm and termite diversity across sub-humid to semi-arid tropical zones

F.O. Ayuke [a*, b], M.M. Pulleman [a], B. Vanlauwe [b], R.G.M. de Goede [a], J. Six [c]., C. Csuzdi [d], L. Brussaard [a]

[*a] *Department of Soil Quality, Wageningen University, P.O Box 47, NL-6700 AA Wageningen, The Netherlands*
[b] *Tropical Soil Biology and Fertility (TSBF) Institute of CIAT, P.O Box 30677-00100, Nairobi, Kenya*
[c] *Department of Plant Sciences, University of California, Davis, CA 95616, USA*
[d] *Systematic Zoology Research Group of HAS and Hungarian Natural History Museum, Baross str. 13, H-1088 Budapest, Hungary*

*Corresponding author: (0317) 486524; Fax: (0317) 419000

Email: fredrick.Ayuke@wur.nl or fredrick.ayuke@yahoo.com*

Submitted to Agriculture, Ecosystems and Environment

Abstract

Soil invertebrate fauna, in particular earthworms and termites, play an important role in the decomposition of organic residues and the formation of soil structure and therefore affect soil quality for crop production. Little is known, however, on their diversity in agricultural soils across different climate and soil conditions, and agricultural management in low input cropping systems. Earthworm and termite diversity were studied in 12 long-term agricultural field trials across the sub-humid to semi-arid tropical zones of Eastern and Western Africa. In each trial, treatments with high and low soil organic C were chosen to represent contrasts in long-term soil management effects, including tillage intensity, organic matter and nutrient management and crop rotations. High soil C was considered to reflect relatively favourable conditions, and low soil C less favourable conditions for soil macrofauna. For each trial, a fallow representing a relatively undisturbed reference was also sampled. Monolith and transect sampling were used for termite assessments while earthworms were collected through monolith sampling only. Data were subjected to Redundancy Analysis and Analysis Of Variance to investigate effects of environmental variables and agricultural management on earthworm and termite taxonomic richness and diversity, respectively. Twenty taxa of earthworms in 3 families (Ocnerodrilidae, Acanthodrilidae and Eudrilidae) were found. Trophic groups were predominantly epigeic and endogeic. No anecic earthworms were present. Twenty taxa of termites belonging to two families (Termitidae and Rhinotermitidae) were found. Trophic groups were dominated by group II termites (i.e. wood, litter and grass feeders; fungal growers). Taxonomic abundance and distribution of termite and earthworm species were influenced by climate and soil type, as reflected in their association with rainfall and temperature, texture, and total soil C, which in turn correlated with altitude, longitude and latitude. Arable cropping has significant negative effects on earthworm, but little effect on termite diversity as compared to long-term fallow. Under continuous crop production, higher earthworm and termite diversity is observed under agricultural management that had resulted in high-C *versus* low-C soils. We conclude that fewer species of earthworms and termites are favored under agricultural management that leads to lower soil C. Results indicate that the soil disturbance that goes with continuous crop production is more detrimental to earthworms than to termites, when compared to the fallow.

Key words: Soil biodiversity, earthworms, termites, agriculture, crop management, soil carbon

Introduction

Crop yields in large parts of Sub-Saharan Africa (SSA) are low due to declining soil fertility associated with continuous cropping and sub-optimal fertilizer use. With the liberalization of trade and introduction of structural adjustment programmes, fertilizer costs have increased and most small-scale farmers can no longer afford them, while the challenge of increasing and maintaining crop yields to sustain the growing population in most countries south of the Sahara has remained. Technologies such as improved fallow systems (Sileshi and Mafongoya, 2006; Walker et al., 2007) and use of organic inputs (Mafongoya et al., 1998; Ouédraogo et al., 2001; Vanlauwe et al., 2002) have been demonstrated to increase crop yields, but often organic resources used alone provide insufficient nutrients to build up longer-term soil fertility and sustain crop yields (Palm et al., 2001). Integrated Soil Fertility Management (ISFM), i.e. combined use of organic and inorganic fertilizers has been recommended for increasing nutrient use efficiency (NUE) among farmers in SSA (Palm et al., 1997; Vanlauwe et al., 2009). The challenge in such low input systems is to develop ways of managing organic matter to optimize the maintenance of soil organic matter (SOM), improve soil structure and enhance water and nutrient use efficiencies. Soil invertebrate fauna, especially earthworms and termites can considerably contribute to these processes, hence improved understanding and manipulation of their composition and activities would appear to be one of the ways in which balanced decomposition and humification of organic residues, maintenance of soil structure and aggregate stability and other ecological functions can be restored in degraded soils (TSBF, 2001, SP-IPM, 2004; Brussaard et al., 2007). In a wider sense, the elucidation of biodiversity of soil organisms has high priority in global biodiversity research, as it appears to be key to understanding their role in soil ecosystem processes and services (Altieri, 1999; CBD, 2001; Clergue et al., 2005).

Several studies have indicated that earthworms and termites sustain agricultural productivity through their beneficial impact on soil ecosystem services (Kooyman and Onck, 1987; Vikram, 1994; Mando et al., 1999; Brown et al., 2004;

Fonte et al., 2009). Earthworms play an important role in the incorporation of organic materials into the soil matrix and in the formation of soil pores and stable macroaggregates which tend to be enriched in SOM (Blanchart et al., 1999; Scullion and Malik, 2000; Six et al., 2004; Pulleman et al., 2005; Bossuyt et al., 2005). Termites equally mediate the redistribution and decomposition of organic matter and soil particles through the construction of mounds, nests, galleries and surface sheeting (Collins, 1981; Martius, 1994; Mando, 1997; Asawalam et al., 1999; Brauman, 2000), thereby influencing nutrient and soil water availability to plants, but their impacts on (differentially managed) agricultural soils are still poorly understood (Jungerius et al., 1999; Mando and Brussaard, 1999; Jouquet et al., 2007).

Changes in diversity and density of macrofauna (earthworms and termites) across geographic regions and landscapes have received very little attention, with some studies giving conflicting results about the influence of climate. For example, Collins (1980) and Gathorne-Hardy et al. (2001) noted higher termite taxonomic richness and abundance in low rainfall areas, whereas Buxton (1981) observed a reverse trend. Therefore, knowledge and analysis of the spatial distribution of different taxa of earthworms and termites in agricultural soils across climatic regions and soil types is necessary to determine to what extent and how their diversity and activities are affected by climate versus agricultural land use and management.

Site-specific studies by Kooyman and Onck (1987), Eggleton et al. (1996), Okwakol (2000), Birang et al. (2003) and Curry et al. (2002) have indicated that deforestation, soil disturbance and increased intensity of agriculture are among the management practices that negatively impact macrofauna species richness and abundance in general. Clearance and tillage of habitats result in destruction of nests and nesting sites, especially for earthworms and termites, thus exposing them to harsh environmental conditions and/or predators (Brust et al., 1986; House and Parmelee, 1985; Chan, 2001; Barros et al., 2002). Soil management practices such as use of organic inputs and crop diversification through rotation favor macrofauna diversity due to improvement in the abiotic conditions and increased substrate supply (Tian et al., 1997; Ayuke et al., 2003; Curry, 2004; Osler et al., 2008, Fonte et al., 2009). Although research has continued to demonstrate that tillage and other agronomic practices (e.g. mulching, organic and inorganic fertilizer applications, cover crop management, crop rotation and rotation pattern) influence changes in invertebrate communities (Brust et al., 1986; Ferguson et al., 1984; Lambert et al., 1987; Smith et al., 1988; Zehnder and Linduska, 1987), such studies mostly targeted aboveground fauna and effects on belowground invertebrate communities in cropped soils are little understood, especially in the case of termites. This study, therefore, aimed at:

1. Quantifying earthworm and termite diversity and identifying taxa or trophic groups in natural fallows and agricultural soils across a transect of sub-humid to semi-arid tropical zones.

2. Evaluating the environmental (climate and soil) factors that influence distribution patterns of earthworm and termite species.

3. Evaluating the extent to which contrasting agricultural management, resulting in different soil organic C levels, affects earthworm and termite diversity.

We hypothesized that the biodiversity of earthworms and termites will:

1. Decrease with increasing temperature and decreasing precipitation,

2. Be lower in agricultural than in fallow systems,

3. Be higher under long-term agricultural management that had led to high-C soils than where it had led to low-C soils.

Material and methods

Study sites and sampling strategy

The study was conducted in 12 long-term field trials across the sub-humid to semi-arid tropical zones of Eastern Africa (Embu, Kabete, Impala and Nyabeda in Kenya and Chitala in Malawi) and Western Africa (Tamale in Ghana, Ibadan in Nigeria, Sadore in Niger and Farakoba, Saria I, II and III in Burkina Faso). A general characterization of the sites, including climate and soils, is presented in Table 1. The long-term trials were established in the past one to four decades and aimed at testing different management options for arable crop production such as organic versus mineral inputs, crop rotation, and tillage. In our sampling scheme, the arable treatments that, according to previously available data, had resulted in the highest and lowest soil organic carbon (SOC) contents were included (Table 2). The SOC content is known to increase due to improved long-term management practices, such as reduced tillage (Six et al., 1999; Grandy and Robertson, 2006; McVay et al., 2006; Pikul et al., 2009), organic matter and nutrient inputs (Ouédraogo et al., 2001; Palm et al., 2001; Vanlauwe et al., 2002; Antil et al., 2005) and crop rotations (Wu et al., 2003). These management practices have been found to also have a beneficial effect on soil macrofauna activity (Tian et al., 1997; Mando and Brussaard, 1999; Ayuke et al., 2003; Fonte et al., 2009). High soil C was expected to represent relatively favorable conditions, while low soil C was expected to reflect the least favorable conditions for soil macrofauna (earthworms and termites). A fallow located nearby the arable fields was considered to represent a reference with relatively favorable conditions for macrofauna (no tillage, continuous plant cover and high residue inputs) compared to arable systems. Depending on site, the fallows consisted of green fallow, forest or shrubland, which may or may not have been used for crop production in the past, but had been undisturbed for at least 10 years at the time of sampling. No insecticides were applied in the fields we sampled for this study.

Table 1. Location and characteristics of the study sites.

Environmental Parameters	**Sites**									
	Embu, Kenya	**Kabete, Kenya**	**Impala, Kenya**	**Nyabeda, Kenya**	**Chitala, Malawi**	**Ibadan, Nigeria**	**Tamale, Ghana**	**Sadore, Niger**	**Farakoba, Burkina Faso**	**Saria I, II, III, Burkina Faso**
Altitude asl. (m)	1480	1700	1337	1420	606	200	185	250	405	300
Latitude and Longitude	0° 30′ S; 37° 30′ E	1° 15' S; 36° 41' E	0° 08' N; 34° 25' E	0° 06' N; 34° 36' E	13° 40' S; 34° 15' E	7° 30' N; 3° 54' E	9° 25' N; 1° 00' W	13° 15' N; 2° 17' E	11° 06' N; 4° 20' W	12° 16' N; 2° 09' E
Mean Annual temp (°C)	20	18	23	23	22	27	29	33	28	33
Mean annual rainfall (mm)	1450 Bimodal	1000 Bimodal	1800 Bimodal	1800 Bimodal	800 Unimodal	1200 Bimodal	1200 Unimodal	550 Unimodal	850 Unimodal	800 Unimodal
Climate (FAO)	Sub-humid	Sub-humid	Humid	Humid	Sub-humid	Humid	Semi-arid	Semi-arid	Sudano-Sahelian	North-Sudanian
Soil type (FAO)	HUMIC NITISOL	HUMIC NITISOL	HUMIC FERRALSOL	HUMIC FERRALSOL	TYPIC FERRALSOL	DYSTRIC REGOSOL	FERRIC LUVISOL	FERRALIC ARENOSOL	FERRIC LUVISOL	FERRIC LIXISOL
†Texture sand, silt, clay (%)	Clay 3, 22, 75	Clay 11, 22, 67	Clay 13, 17, 70	Clay 9, 21, 70	Sandy clay 60, 5, 35	Sandy 87, 6, 7	Sandy 90, 4, 6	Sandy 92, 3, 5	Loamy sand 74, 19, 7	Sandy loam 53, 36, 11

†Source: Zida et al., Unpublished.

Table 2. Description of selected sites and their soil C content (g kg^{-1} soil) at 0-15^a, 15-30^b cm depths. # refers to management treatments: 1 = crop rotation, 2 = tillage management, 3 = organic inputs, 4 = inorganic fertilizer.

Trial site	**Year established**	**Treatments**		
		Fallow	**High-C**	**Low-C**
Embu	1993	Fallow-woodland/shrubland since 1993; Soil C=40.0^a, 28.4^b	#1=Cont. maize, 2=Hand hoeing, 3=*Leucaena leucocephala* (5 Mg ha^{-1}), 4=no fertilizer; Soil C=27.5^a, 24.9^b	#1=Cont. maize, 2=Hand hoeing, 3=no organic inputs, 4=no fertilizer; Soil C=24.6^a, 23.9^b
Kabete	1976	Fallow-Bushland since trial establishment in 1976; Soil C=23.7^a, 20.8^b	#1=Maize-bean rotation, 2=Hand hoeing, 3=10 t ha^{-1} manure, 4=CAN (120 kg N ha^{-1}) and TSP (52.8 kg P ha^{-1}) fertilizers; Soil C=21.9^a, 17.2^b	#1. Maize-bean rotation, 2=Hand hoeing, 3= no organic inputs, 4=no fertilizer; Soil C=17.7^a, 16.2^b
Impala	2000	Fallow-shrubland nearby since trial establishment in 2000; Soil C=24.5^a, 16.9^b	#1=Maize-*Tephrosia candida* relay/rotation, 2=Hand hoeing, 3=*T. candida* residues (5 Mg ha^{-1}), 4= Blanket P , no N fertilizer; Soil C=27.9^a, 21.8^b	#1= Cont. maize, 2=no till, 3=no organic inputs, 4=no fertilizer; Soil C=22.0^a, 21.2^b
Nyabeda	2003	Fallow-shrubland nearby since trial establishment in 2003; Soil C=28.2^a, 16.6^b	#1. Maize-soybean rotatn, 2=Hand hoeing, 3=Maize stover residues (2 Mg ha^{-1}), 4=NPK fertilizer (60:60:60); Soil C=23.2^a, 17.8^b	#1=Maize-soybean rotation, 2=no till, 3=no organic inputs, 4=NPK fertilizer (60:60:60); Soil C=20.8^a, 17.9^b
Chitala	1995	Grass fallow since trial establishment in 1995; Soil C=13.6^a, 9.4^b	#1=Maize-pigeon pea rotation, 2=Tractor till, 3=Crop residues: stem + leaves, 4=$(NH_4)_2SO_4$ fertilizer (96 kg N ha^{-1} yr^{-1}); Soil C=8.8^a, 9.9^b	#1=Cont. maize, 2=Tractor till, 3=no organic inputs, 4=no fertilizer; Soil C=8.2^a, 7.1^b
†Ibadan	1996	Bushland fallow since 1986 adjacent to the experimental plots; Soil C=12.4^a, 7.5^b	#1=Maize-cowpea rotation, 2= Minimum tillage-light surface hoeing, 3=*S. siamea* (5 Mg ha^{-1}), 4=fertilizer-NPK (60:30:30 kg ha^{-1} yr^{-1}); Soil C=10.6^a, 6.7^b	#1=Maize-cowpea rotation, 2=Minimum tillage-light surface hoeing, 3=no organic inputs, 4=no fertilizer; Soil C=5.7^a, 3.9^b

Table 2 (Continued). Description of selected sites and their soil C content (g kg−1 soil) at 0-15a, 15-30b cm depths. # refers to management treatments: 1 = crop rotation, 2 = tillage management, 3 = organic inputs, 4 = inorganic fertilizer.

Tamale	1996	Grass fallow strip since 1996; Soil C=9.0^{a}, 4.8^{b}	#1=Cont. maize, 2=Zero till-hand pulling/slashing of weeds, 3=no organic inputs, 4=no fertilizer; Soil C=5.7^{a}, 3.7^{b}	#1=Cont. maize, 2=Bullock plough-hand hoeing of weeds, 3=no organic inputs, 4=no fertilizer; Soil C=3.1^{a}, 2.6^{b}
Sadore	1986	Fallow-shrubland within the experimental site since 1986; Soil C=1.5^{a}, 1.2^{b}	#1=Cont. millet, 2= Hand hoeing, no ridging, 3=residues applied, 4=fertilizer (13 kg P ha^{-1}), no N; Soil C=1.4^{a}, 1.2^{b}	#1=Millet-cowpea rotation, 2= Animal traction + ridging , 3=residues applied, 4=fertilizer (30kg N, 13 kg P ha^{-1}); Soil C=1.0^{a}, 0.9^{b}
Farakoba	1993	Grass fallow within the experimental site since trial; establishment in 1993; Soil C=3.6^{a}, 2.9^{b}	#1. Cont. sorghum, 2=Tractor till, 3=compost (5 Mg ha^{-1}), 4=PK fertilizer (25:14); Soil C=3.6^{a}, 2.4^{b}	#1. Cont. sorghum, 2=tractor till, 3=no organic inputs; Soil C=2.7^{a}, 2.3^{b}
Saria I	1960	Grass- fallow since trial establishment in 1959 (Common for all the Sarias); Soil C=3.3^{a}, 3.1^{b}	#1=Sorghum-cowpea rotation, 2=Tractor till, 3=manure (5 Mg ha^{-1} every 2 yrs), 4=NPK fertilizer (100 kg ha^{-1}) and Urea (50 kg ha^{-1}) every 2 years; Soil C=2.6^{a}, 3.7^{b}	#1=Cont. sorghum, 2=Tractor till, 3=manure (5 Mg ha^{-1} every 2 yrs), 4=NPK fertilizer (100 kg ha^{-1}) and Urea (50 kg ha^{-1}) every 2 years; Soil C=3.3^{a}, 3.2^{b}
Saria II	1980	See Saria I	#1=Cont. sorghum, 2=Tractor till, 3=10 Mg ha^{-1} manure, 4=fertilizer- 23kg N ha^{-1}; Soil C=3.5^{a}, 3.3^{b}	#1=Cont. sorghum, 2=Tractor till, 3=no organic inputs, 4=no fertilizer; Soil C=1.8^{a}, 2.5^{b}
Saria III	1990	See Saria I	#1. Cont. sorghum, 2=Oxen plough, 3=Manure (10 Mg ha^{-1}), 4=NPK fertilizer (100 kg ha^{-1} yr^{-1}) and Urea (50 kg ha^{-1} yr^{-1}); Soil C=2.4^{a}, 3.3^{b}	#1=Cont. sorghum, 2=Hand hoeing (5cm depth), 3=Manure (10 Mg ha^{-1}), 4=NPK fertilizer (100 kg ha^{-1} yr^{-1}) and Urea (50 kg ha^{-1} yr^{-1}); Soil C=2.2^{a}, 3.0^{b}

Note: Soil C data source: Western Africa (Zida et al., unpublished), †Ibadan (Vanlauwe et al., 2002); Eastern Africa (from monolith soils).

Macrofauna sampling protocols

Monolith sampling and transect sampling were used for termite assessments while earthworms were collected through monolith sampling only. Sampling was done six to eight weeks after planting (July-September, 2006 in the Western Africa sites and February-June 2007 in Eastern Africa sites). A total of 108 monoliths and 108 transects (3 treatments × 3 replications × 12 sites = 108) was taken across all the trial sites.

Monolith sampling of soil macrofauna (earthworms and termites) was done according to the standard TSBF method (Swift and Bignell, 2001; Bignell et al., 2008). One soil monolith of 25 cm × 25 cm × 30 cm depth was randomly taken in each plot replicate (n = 3). The extracted soil was separated into two depth layers (0-15 and 15-30 cm), and earthworms and termites were collected by hand-sorting on plastic trays. Transect sampling for termites was done alongside the monolith sampling. In each sampling plot, a 20 × 2 m transect (or 5 × 2 m sections depending on the dimension of the plots) was randomly laid out. Each transect or section was sampled sequentially (by two trained persons for 30 minutes) and the following microhabitats which are common sites for termites were searched manually: surface soil to 5 cm depth; the soil between large buttress roots if any; the inside of branches and twigs; the soil within and beneath rotten logs and smaller pieces of dead wood; subterranean nests, mounds, carton sheeting and runways on vegetation (Jones and Eggleton, 2000; Swift and Bignell, 2001).

Macrofauna preservation, identification and classification into trophic groups

Earthworms were killed in 75% alcohol, then fixed in 4% formaldehyde and stored in sealed vials before being transported to the laboratory for identification and enumeration. Earthworms were indentified at the Department of Invertebrate Zoology of the NMK, Nairobi, Kenya, using appropriate keys and reference specimens in the NMK collections. Adult earthworms were identified to species or where this proved difficult, to numbered morphospecies. Unidentified specimens were sent to the Natural History Museum in Budapest, Hungary, for further analysis. Voucher specimens are being held at the NMK, Nairobi.

Earthworms were allocated to functional groups, based on their habitat, food choice, feeding behaviour and ecophysiology (Lavelle et al., 1998; Swift and Bignell, 2001):

- Epigeics (those that live and feed near the soil surface; they affect litter comminution and nutrient release);
- Anecics (those that transport organic residues from the surface into vertical burrows and actively mix them with soil; considerable amounts of soil, mineral elements and organic matter may be redistributed through these activities, accompanied by physical effects on soil structure and hydraulic properties) and
- Endogeics (those foraging on organic matter and dead roots in the soil profile, forming largely horizontally-orientated burrows).

Termites were preserved in 75% alcohol and stored in sealed vials before being transported to the laboratory for taxonomic analysis and enumeration. Termites were identified at the Department of Invertebrate Zoology of the National Museums of Kenya (NMK), Nairobi, Kenya, using appropriate keys and reference specimens in the NMK collections. Mature or adult termites, particularly the soldiers and workers were considered for identification. They were identified to species or, where this proved difficult, to numbered morphospecies.

Most alates/juvenile termites could not be identified beyond order. Voucher specimens of our collections are currently being held at NMK.

Termites are classified on the basis of their food choice, feeding habits and nesting behaviour (Jones and Eggleton, 2000; Swift and Bignell, 2001). These include:

- Soil feeders (those that occur in the soil profile, the organic layer and/or feed on organic matter associated with mineral soil, apparently with some degree of selection of silt and clay fractions);
- Wood feeders (those that feed on wood and excavate galleries in larger items of wood litter which may become colony centres; this group includes termites having arboreal, subterranean or epigeal nests but feeding elsewhere, such as Macrotermitinae, cultivating fungus gardens);

- Soil/wood interface feeders (those that feed in highly decayed wood which has become friable and soil-like, or predominantly within soil under logs or soil plastered on the surface of rotting logs or mixed with rotting leaves);
- Litter feeders (those that forage for leaf litter, live or dry standing grass stems and small woody items, usually cutting the material before consumption or transport to the nest; these include most subterranean and mound-building Macrotermitinae, as well as certain Nasutitermitinae that forage on the surface of the ground, and at least one lower termite, *Hodotermes mossambicus*, with a similar habit);
- Specialized and incidental feeders (this category follows listing of termite foods given by Wood (1978), including species of various specialized habits.

In our study, we placed termites into one of four feeding groups based on visual observation notes taken while in the field and/or in line with classifications by Donovan et al. (2001) and Eggleton et al. (2002):

- Feeding group I-lower termites (wood, litter and grass feeders);
- Feeding group II-higher termites (wood litter and grass feeders);
- Feeding group III-higher termites (very decayed wood or high organic content soil;
- Feeding group IV-higher termites (low organic content soil: true soil feeders).

Assessments of earthworm and termite diversity

Biological assessments included identity at the genus and species level and abundance (numbers of individuals per unit area). As for diversity, taxonomic richness (*S*) and the Shannon-Wiener diversity index (H') were calculated. Taxonomic richness (*S*) was calculated as the number of taxa per monolith and transect sample (pooled together from each experimental plot). The Shannon-Wiener diversity index (H') was calculated as $H' = -\sum (\mathrm{p}i \ln \mathrm{p}i)$, where p*i* is the proportion of the *i*th taxonomic group, estimated as n*i*/N; where n*i* is the number of individuals of the *i*th species and N the total number of individuals within the sample (Magurran, 1988). Shannon-Wiener diversity index assumes that: 1) individuals are randomly sampled from a large population, and 2) all species are represented in the sample. The index combines both species richness (total number of taxa present) and abundance. As such, if calculated for a number of samples, the Shannon-Wiener index will be normally distributed making it possible to use parametric statistics such as ANOVA (Magurran, 1988).

Data from transects were pooled and combined with data from the monoliths to capture total termite species and estimate taxonomic richness in each treatment, but quantitative and statistical analyses on data that are expressed on an areal basis (per m^2) were based on monolith data only.

Statistical analyses

The data obtained were subjected to analysis of variance (ANOVA) using GENSTAT 11.1 (2009). Levene's test was used to assess homogeneity in the data (Field, 2005; Kirkpatrick and Feeney, 2005). Due to non-homogeneity of variances in the termite and earthworm data (diversity indices and abundance), data were square root transformed $(x + 0.5)^{1/2}$. Levels of significance were evaluated using Fisher's least significant difference (LSD).

The strength and statistical significance of species-environment relationships were analyzed with the programme CANOCO 3.1 (Ter Braak, 1988; 1990; Ter Braak and Verdonschot, 1995). With CANOCO, a preliminary detrended correspondence analysis (DCA) was conducted to determine the length of the gradient, test the homogeneity of the data in taxonomic abundance and decide on which ordination analysis to apply. In this study, length of gradient determined by DCA was <4 for the first axis, so we opted for the linear ordination technique Redundancy Analysis (RDA). RDA was used to investigate the correlative relationships of environmental variables (latitude, longitude, altitude, average temperature, precipitation, clay, sand and soil carbon) with both earthworm and termite abundance at species level. Forward selection was applied to assess the significance and strength of each environmental variable within the RDA. The first variable selected was that with the highest marginal eigenvalue (i.e. its explanatory fit to the species and site data if added as the only environmental variable in the analysis). Subsequently, the environmental variables were entered one at a time in order of the magnitude of their conditional eigenvalues (i.e. additional fit after adding previous variables), until none of the remaining variables significantly explained additional variation in species abundance. In the subsequent analysis only those environmental variables with conditional statistical significance in the above RDA were included. Overall contribution of each of the variables to description of the variation in macrofauna data was tested by a Monte-Carlo test based on 999 random permutations. Since our samples were never assumed to be independent of each other, we restricted permutations to a split-plot design, such that sites were treated as whole plot factors, while treatments within sites were treated as split plot factors (Ter Braak and Smilauer, 1998).

Results

Taxonomic richness and functional groups

A total of 20 earthworm taxa belonging to three families (Ocnerodrilidae, Acanthodrilidae and Eudrilidae) were found across the 12 sites (Table 3). Acanthodrilidae and Eudrilidae families were each represented by 8 taxa, and Ocnerodrilidae, by 4 taxa. The richness of the earthworm taxa varied across the sites, with Ibadan showing the highest taxonomic richness (11 taxa), followed by Kabete and Impala (6 taxa). Earthworm taxa were dominated by epigeic worms (14 taxa), while relatively few endogeic worms (6 taxa) were found. No anecic worms were present (Table 3).

A total of 20 termite taxa belonging to two families (Termitidae and Rhinotermitidae) were found across the 12 sites (Table 4). The majority of these (15 taxa) belonged to the family Termitidae. This family was dominated by the subfamily Macrotermitinae with 9 taxa recorded and the subfamily Termitinae in which 4 taxa were observed (Table 4). Only the *Microtermes* spp. were found at all 12 sites. Although all the sites had few termite taxa, the Chitala site appeared to be taxonomically the richest (7 taxa), followed by Farakoba and Saria I-III (6 taxa).

The termites collected across the different sites are known to feed on a wide range of food sources. In terms of feeding groups, all four categories were represented. The assemblages were dominated by group II foragers (wood, litter, grass feeders, fungus growers), most of which (15 taxa) were in the family Termitidae, followed by group I (wood, litter and grass) feeders in the family Rhinotermitidae, represented by 3 taxa. Specialized soil feeders (groups III and IV) were least diverse, each being represented by one taxon of the subfamily Termitinae (Table 4).

Table 3. Earthworm taxonomic richness and functional diversity based on monolith method.

		Site											
		Eastern Africa					Western Africa						
Taxonomic group	**Functional group**[a]	**Embu**	**Kabete**	**Impala**	**Nyabeda**	**Chitala**	**Ibadan**	**Tamale**	**Sadore**	**Farakoba**	**Saria I**	**Saria II**	**Saria III**
Ocnerodrilidae													
Nematogenia lacuum	Endogeic	+	+	-	+	-	-	-	-	-	-	-	-
Gordiodrilus robustus	Endogeic	-	-	-	-	-	+	-	-	-	-	-	-
Gordiodrilus wemanus	Endogeic	-	+	+	+	-	-	-	-	-	-	-	-
Gordiodrilus marcusi	Endogeic	-	-	-	-	-	+	-	-	-	-	-	-
Acanthodrilidae													
Millsonia inermis	Endogeic	-	-	-	-	-	+	-	-	-	+	+	-
Millsonia guttata	Endogeic	-	-	-	-	-	-	+	-	-	-	-	-
Dichogaster (Dt.) saliens	Epigeic	+	-	+	-	-	-	-	-	-	-	-	-
Dichogaster (Dt.) affinis	Epigeic	-	+	+	+	-	+	-	-	-	+	-	+
Dichogaster (Dt.) bolaui	Epigeic	-	+	+	-	-	-	-	-	-	-	-	-
Dichogaster (Dt.) modiglianii	Epigeic	-	-	+	-	-	-	-	-	-	-	-	
Dichogaster (Dt.) spec nov 1	Epigeic	-	-	-	-	-	+	-	-	-	-	-	+
Dichogaster (Dt.) spec nov 2	Epigeic	-	-	-	-	+	-	-	-	-	-	-	-
Eudrilidae													
Polytoreutus annulatus	Epigeic	+	+	-	-	-	-	-	-	-	-	-	-
Hyperiodrilus africanus	Epigeic	-	-	-	-	-	+	+	-	+	-	-	-
Hyperiodrilus spec nov	Epigeic	-	-	-	-	-	+	+	-	+	-	-	-
Eudrilus buettneri	Epigeic	-	-	-	-	-	+	-	-	+	-	-	-
Ephyriodrilus afroccidentalis	Epigeic	-	-	-	-	-	+	-	-	-	-	-	-
Eminoscolex violaceus	Epigeic	-	-	+	+	-	-	-	-	-	-	-	-
Stuhlamannia spec nov	Epigeic	-	+	-	-	-	+	-	-	-	-	-	-
Lavellea spec nov	Epigeic	-	-	-	-	-	+	-	-	+	-	-	-
Taxonomic richness (*S*)		**3**	**6**	**6**	**4**	**1**	**11**	**3**	**0**	**4**	**2**	**1**	**2**

[a]Based on classification by Lavelle et al. (1998); Swift and Bignell (2001). +/- denotes presence or absence, respectively.

Table 4. Termite taxonomic richness and functional groups based on monolith and transect methods.

Taxonomic group	Functional group[a]	Food type[b]	Possible pest[c]	Site											
				Eastern Africa					Western Africa						
				Embu	Kabete	Impala	Nyabeda	Chitala	Ibadan	Tamale	Sadore	Farakoba	Saria I	Saria II	Saria III
Rhinotermitidae-Rhinotermitinae															
Captotermes intermedias	I	WLG	Yes	-	-	-	-	-	-	+	-	-	-	-	-
Schedorhinotermes lamanianus	I	WLG	Yes	-	-	-	-	+	-	-	-	-	-	-	-
Rhinotermitidae-Psammotermitinae															
Psammotermes hybostoma	I	WLG	Yes	-	-	-	-	-	-	-	+	-	-	-	-
Termitidae-Nasutitermitinae															
Nasutitermes spec	II	WLG	Yes	-	-	-	-	+	-	-	-	-	-	-	-
Trinevitermes spec	II	LG	Yes	-	-	-	-	-	-	+	-	+	+	+	+
Termitidae-Macrotermitinae															
Ancistrotermes cavithorax	II	WLG	Yes	-	-	-	-	-	+	+	-	+	-	-	-
Macrotermes nr. Vitrialatus	II	FWLG	Yes	-	-	-	-	+	-	-	-	-	-	-	-
Macrotermes subhyalinus	II	FWLG	Yes	-	-	-	-	-	-	-	-	-	+	+	+
Macrotermes herus	II	FWLG	Yes	-	-	-	+	-	-	-	-	-	-	-	-
Microtermes pusillas	II	FWLG	Yes	-	-	-	+	-	-	-	-	-	-	-	-
Macrotermes spp.	II	FWLG	Yes	-	-	-	-	+	-	-	-	-	-	-	-
Microtermes spp.	II	FWLG	Yes	+	+	+	+	+	+	+	+	+	+	+	+
Odontotermes magdalenae	II	FWLG	Yes	-	-	-	-	-	-	-	-	-	+	+	+
Odontotermes spp.	II	FWLG	Yes	+	+	-	-	+	-	+	+	+	-	-	-
Pseudacanthotermes spiniger	II	FLG	No	-	-	+	+	-	-	-	-	-	-	-	-
Pseudacanthotermes spp	II	FLSD	Yes	+	+	-	-	-	+	-	-	+	-	-	-
Termitidae-Termitinae															
Amitermes-Amitermes stephensoni	II	WLSD	Yes	-	-	-	-	-	-	-	-	-	+	+	+
Microcerotermes parvulus	II	WLG	Yes	-	-	-	-	+	-	-	+	+	+	+	+
Termes-Termes baculi	III	WS	No	-	-	-	-	-	+	-	-	-	-	-	-
Cubitermes- Tubeculitermes spec	IV	S	No	-	-	+	+	-	-	-	-	-	-	-	-
Taxonomic richness (*S*)				**3**	**3**	**3**	**5**	**7**	**4**	**5**	**4**	**6**	**6**	**6**	**6**

(W=wood; L=leaf litter; S=soil; D=Dung/manure; F=fungus grower; G=dead/dry grass. [a]based on classification by Bignell and Eggleton (2000); Donovan et al. (2001) and Eggleton et al. (2002). [b] based on field notes/observation. [c]based on observations by Kooyman and Onck (1987); Jannette (2002). +/- denotes presence or absence, respectively.

Correlations between earthworm species abundances and environmental parameters

Of the eight variables (latitude, longitude, altitude, average temperature, precipitation, soil clay content, soil sand content, and soil carbon) initially entered into the RDA, six (precipitation, average temperature, soil carbon, altitude, longitude and latitude) were significantly correlated with earthworm taxonomic abundance ($p < 0.001$). The eigenvalues of the first and second RDA axes constrained to the environmental variables were 0.261 and 0.069, respectively, and the two axes explained 33% of the variation in earthworm taxa distribution (Figure 1A). The sum of all canonical eigenvalues showed that the environmental variables that significantly contributed to the description of the variation in the earthworm fauna (latitude, longitude, altitude, temperature, precipitation and soil carbon content) explained 42% of the total variation observed (data not shown). The first axis is mainly a temperature/altitudinal gradient ($r = -0.83$ and 0.86 respectively), while the second axis is a precipitation/latitudinal gradient ($r = 0.12$ and -0.16 respectively) (Figure 1A). Axis 1 separates cooler, higher-altitude sites from hotter, lower-altitude sites. Earthworm taxa were less abundant on the higher, cooler altitudes that are characteristic of the sites sampled in Eastern Africa (Figure 1A and 1B).

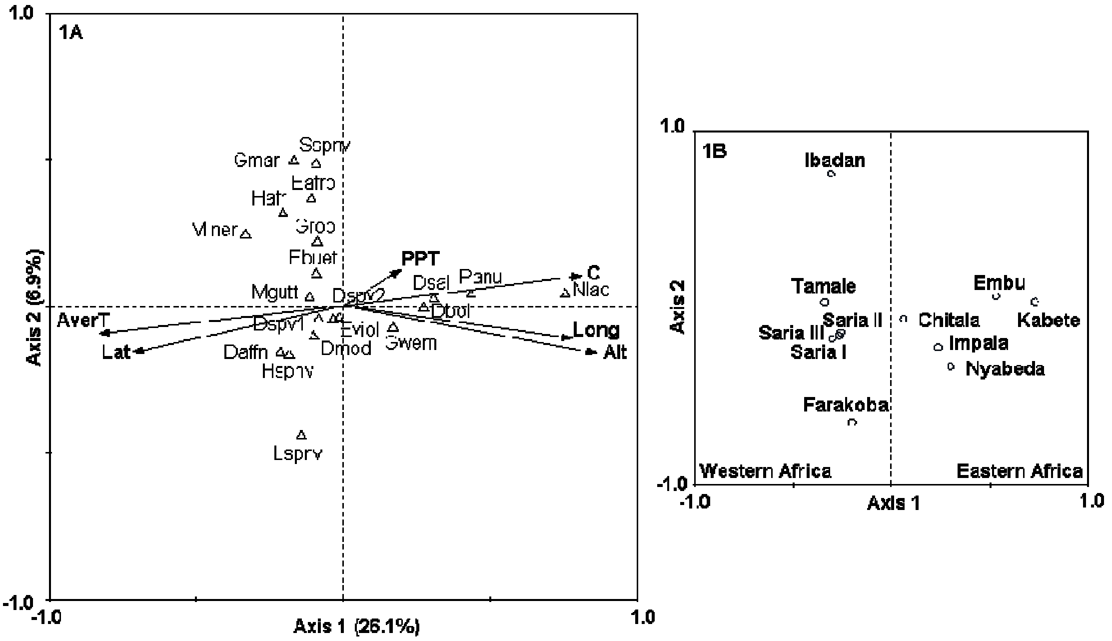

Figure 1. RDA biplot showing correlation between earthworm species abundance and selected environmental variables. Earthworm taxa are represented by triangles, while environmental parameters are represented by pointed arrows. Sites are represented by open symbols.

Earthworm species abbreviations: *Nematogenia lacuum* **(Nlac),** *Gordiodrilus robusta* **(Grob),** *Gordiodrilus wemanus* **(Gwem),** *Gordiodrilus marcusi* **(Gmar),** *Polytoreutus annulatus* **(Panul),** *Hyperiodrilus africanus* **(Hafr),** ***Hyperiodrilus sp*** **nov (Hspnv),** *Eudrilus buettneri* **(Ebuet),** *Ephyriodrilus afroccidentalis* **(Eafro),** *Eminoscolex violaceus* **(Eviol),** *Stuhlmannia sp* nov **(Sspnv),** *Lavellea sp* nov **(Lspnv),** *Millsonia inermis* **(Miner),** *Millsonia guttata* **(Mgutt),** *Dichogaster (Dt.) saliens* **(Dsal),** *Dichogaster (Dt.) affinis* **(Daffn),** *Dichogaster (Dt.) bolaui* **(Dbol),** *Dichogaster (Dt.) modiglianii* **(Dmod),** *Dichogaster (Dt.) sp* nov 1 (**Dspv1),** *Dichogaster (Dt.) sp* nov 2 **(Dspv2). Environmental abbreviations:** Altitude **(Alt),** average temperature **(AverT)**, carbon **(C),** latitude **(Lat)**, Longitude **(Long)**, Precipitation **(PPT)**.

Correlations between termite species abundances and environmental parameters

For termites, eigenvalues of the first and second RDA axes constrained to the environmental variables were 0.135 and 0.067, respectively, and the two axes explained 20.2% of variation in termite taxa distribution (Figure 2A). The sum of all canonical eigenvalues showed that the environmental variables that significantly contributed to the description of the variation in the termite fauna (precipitation, longitude, average temperature, soil sand content and latitude), explained 25% of the total variation observed (data not shown). The first axis is a precipitation/latitudinal gradient (r = 0.81 and −0.63 respectively), while the second axis is a temperature/texture/longitudinal gradient (r = −0.84, −0.77 and 0.85 respectively). A higher than average taxa occurred on the warmer/drier side (Figure 2A). Axis 2 mainly separates Eastern and Western Africa with mean rainfall being higher, and temperature lower in Eastern Africa and termite taxa were less abundant in most of the sites here (Figure 2B).

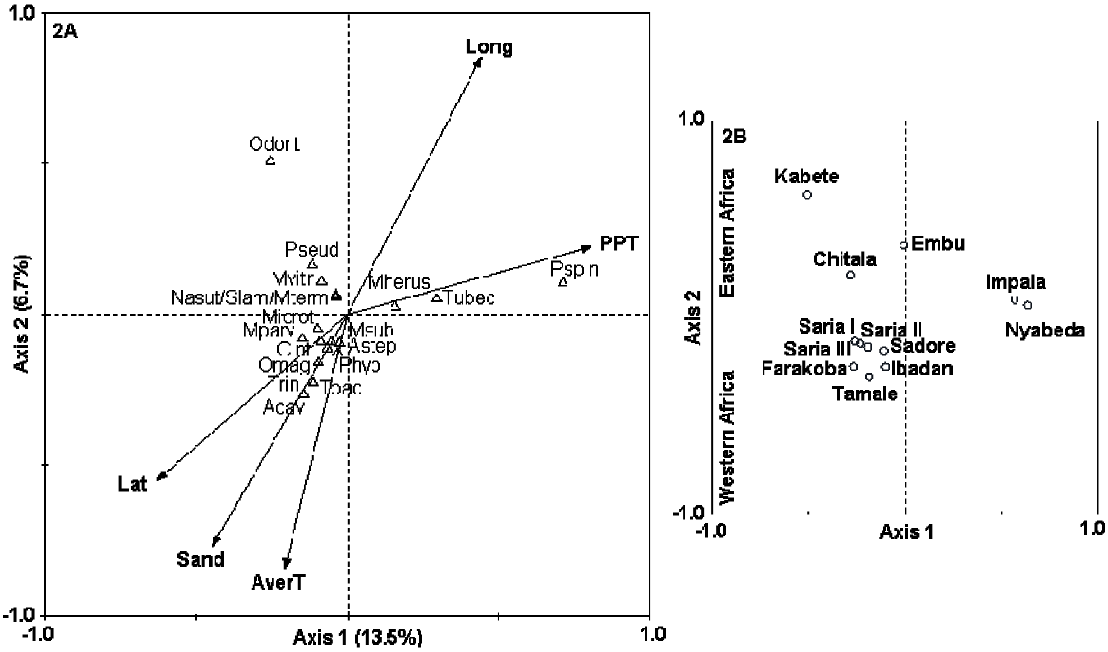

Figure 2. RDA biplot showing correlation between termite species abundance and selected environmental variables. Termite taxa are represented by triangles, while environmental parameters are represented by pointed arrows. Sites are represented by open symbols.

Species abbreviations: *Amitermes stephensoni* **(Astep)**, *Ancistrotermes cavithorax* **(Acav)**, *Captotermes intermedias* **(Cint)**, *Macrotermes nr. Vitrialatus* **(Mvitr)**, *Macrotermes subhyalinus* **(Msub)**, *Macrotermes herus* **(Mherus)**, *Macrotermes* sp **(Mterm)**, *Microcerotermes parvulus* **(Mparv)**, *Microtermes* sp **(Microt)**, *Nasutitermes* sp **(Nasut)**, *Trinevitermes sp* **(Trinv)**, *Odontotermes magdalenae* **(Odom)**, *Odontotermes* sp **(Odont)**, *Psammotermes hybostoma* **(Phyb)**, *Pseudacanthotermes spiniger* **(Pspn)**, *Pseudocanthotermes* sp **(Pseud)**, *Schedorhinotermes lamanianus* **(Slam)**, *Termes baculi* **(Tbac)**, *Tubeculitermes* sp **(Tubec)**. **Environmental abbreviations:** Average temperature **(AverT)**, latitude **(Lat)**, Longitude **(Long)**, Precipitation **(PPT)**.

Diversity indices

Mean earthworm Shannon-Wiener diversity index across sites was significantly higher in the fallow (0.40) than in the high-C treatments (0.17), where, in turn, the index was significantly higher than in the low-C (0.12) treatments. However, not at all sites the diversity indices followed the order fallow > high-C > low-C treatment (Table 5). Hence, site-treatment interactions were also significant. Also, there were significant differences in diversity between sites (Table 5).

Mean termite diversity indices showed a pattern similar to that of earthworms, also following the order fallow > high-C > low-C treatments. Whereas the difference between high-C and low-C treatments was significant, this was not the case for the difference between fallow and high-C treatments (Table 5). Also, not at all sites the diversity indices followed the order high-C > low-C treatment (Table 5). Hence, site-treatment interactions were also significant.

Macrofauna abundance

Differences in mean earthworm abundance showed the same pattern as differences in mean diversity, but the difference between high-C and low-C treatments was not significant (Table 5). In contrast, termite abundance was highly variable across treatments and mean abundance did not differ among treatments (fallow, high-C and low- C (Table 5). Termite abundance, in contrast to termite diversity, differed significantly between sites.

Table 5. Macrofauna (termite and earthworm) diversity indices and abundances across fallow and arable systems of Eastern and Western Africa.

	Earthworm						**Termite**					
	Treatment											
	Fallow	**High-C**	**Low-C**	**Fallow**	**High-C**	**Low-C**	**Fallow**	**High-C**	**Low-C**	**Fallow**	**High-C**	**Low-C**
Site	**Shannon diversity (H′)**			**Abundance (no m^{-2})**			**Shannon diversity (H′)**			**Abundance (no m^{-2})**		
Embu	0.60^{a}	0.00^{b}	0.17^{b}	1264^{a}	32^{b}	27^{b}	0.01^{a}	0.12^{a}	0.03^{a}	139^{a}	528^{a}	32^{a}
Kabete	0.74^{a}	0.33^{b}	0.00^{b}	363^{a}	395^{a}	272^{a}	0.13^{a}	0.03^{a}	0.16^{a}	203^{b}	1029^{a}	384^{ab}
Impala	0.90^{a}	0.15^{b}	0.21^{b}	165^{a}	32^{b}	16^{b}	0.37^{a}	0.05^{ab}	0.00^{b}	987^{a}	43^{b}	1104^{a}
Nyabeda	0.08^{a}	0.00^{a}	0.00^{a}	117^{a}	11^{ab}	0^{b}	0.20^{a}	0.15^{a}	0.00^{a}	475^{a}	208^{ab}	0^{b}
Chitala	0.30^{a}	0.00^{a}	0.00^{a}	53^{a}	5^{a}	5^{a}	0.41^{a}	0.15^{ab}	0.08^{b}	752^{ab}	117^{b}	1744^{a}
Ibadan	0.41^{b}	0.99^{a}	0.51^{b}	96^{b}	933^{a}	117^{b}	0.61^{a}	0.34^{a}	0.00^{b}	320^{b}	1483^{a}	0^{b}
Tamale	0.67^{a}	0.21^{b}	0.00^{b}	37^{a}	32^{a}	16^{a}	0.03^{a}	0.00^{a}	0.20^{a}	149^{b}	1179^{a}	32^{b}
Sadore	0.00^{a}	0.00^{a}	0.00^{a}	0^{a}	0^{a}	0^{a}	0.12^{a}	0.13^{a}	0.23^{a}	256^{a}	181^{a}	0^{a}
Farakoba	0.49^{a}	0.11^{b}	0.00^{b}	453^{a}	59^{b}	11^{b}	0.13^{b}	0.75^{a}	0.00^{b}	59^{b}	693^{a}	160^{ab}
Saria I	0.21^{a}	0.12^{a}	0.00^{a}	69^{a}	27^{a}	21^{a}	0.27^{a}	0.00^{a}	0.00^{a}	112^{a}	0^{a}	0^{a}
Saria II	0.21^{a}	0.12^{a}	0.00^{a}	69^{a}	11^{a}	0^{a}	0.27^{a}	0.27^{a}	0.00^{a}	112^{a}	256^{a}	0^{a}
Saria III	0.21^{ab}	0.00^{b}	0.53^{a}	69^{a}	80^{a}	59^{a}	0.27^{a}	0.00^{a}	0.02^{a}	112^{a}	11^{a}	112^{a}
Mean	**0.40^{a}**	**0.17^{b}**	**0.12^{c}**	**230^{a}**	**135^{b}**	**45^{b}**	**0.22^{a}**	**0.17^{a}**	**0.06^{b}**	**306^{ab}**	**477^{a}**	**297^{b}**
SV	df	F-ratio	P-value	df	F-ratio	P-value	df	F-ratio	P-value	df	F-ratio	P-value
Site	11	4.09	<0.001	11	10.07	<0.001	11	1.57	0.126	11	2.74	0.005
Treatment	2	12.33	<0.001	2	20.37	<0.001	2	6.39	0.003	2	2.54	0.086
Site*treat	22	1.97	0.017	22	4.73	<0.001	22	2.31	0.004	22	2.35	0.004
Residual	70			70			70			70		

Means of H′ or abundance followed by same lower case letters within rows are not statistically significant at $p<0.05$.

Discussion

Soil C in the fallow treatments was higher than in the arable treatments, except for Impala and Saria I. Differences between high-C and low-C in some cases, especially Saria I were relatively small (Table 2). Variability in soil C across sites was large and sites in Eastern Africa generally had higher soil C than sites in Western Africa (Table 2). Wherever differences in macrofauna diversity between treatments were significant, results can, therefore, be considered robust.

Influence of environmental factors on diversity patterns of earthworm and termites

The number of taxa of both earthworms and termites was low in most of the sites. Taxonomic richness ranged between 0-11 for earthworms and 3-7 for termites, while diversity indices for both earthworms and termites ranged between 0-0.99 across sites. The number of termite taxa collected in our sites was lower than the range of 10-24 recorded by Kooyman and Onck (1987) and Eggleton et al. (1996, 2002) across fallow and arable fields of Western Kenya and around the Mbalmayo forest reserve in Cameroun, respectively. However, it conforms with the range of 3-10 taxa recorded by Okwakol (2000) across arable sites in Uganda. The diversity indices for both macrofauna groups were in most cases lower than those across fallow and arable fields (0.94-1.95) as recorded by Birang et al. (2003).

Highly significant correlations were observed between macrofauna taxonomic richness, and environmental variables, reflecting the influence of climate and soil type. The two RDA biplots for earthworms (Figure 1) and termites (Figure 2) separated the relatively cooler, wetter, more clayey Eastern Africa sites from the warmer, drier, more sandy Western Africa sites. Contrary to our hypothesis, more than average earthworm and termite taxa were found under relatively warmer, drier conditions. This is not in line with the observation that earthworm and termite species richness increases with increase in rainfall or soil moisture, as generally found at least in temperate climates (Bohlen et al., 1995; Gathorne-Hardy et al., 2001; Curry, 2004). However seasonality of rainfall in the tropical regions means rainfall amount per season is more important than annual total (Mainoo et al., 2008). We attribute lower taxonomic richness among the sites in Eastern Africa to less favourable conditions arising from high rainfall and low temperatures at higher altitudes. These observations are consistent with those of Collins (1980) and Gathorne-Hardy et al. (2001), who noted that low rainfall areas harbour more termite taxa, especially of the subfamily Macrotermitinae. It, however, contradicts findings by Buxton, (1981), who observed an increase in the number of termite species with increasing rainfall and Oniagu (1979), who noted higher termite abundances during the wet season. Widespread presence of *Microtermes* spp. across all sites illustrates how widely adapted these are to varying climatic conditions and management practices. This may partly be attributed to their nesting habits and also their ability to utilize a wide variety of food resources which include wood, litter, soil and dung. These termites were observed to build both aboveground mounds as well as underground tunnels that can extend many metres, probably a strategy to avoid harsh conditions while foraging. This is in contrast to group I feeders which nest and feed on the same or nearby pieces of wood, and group III feeders that commonly make nests on the ground to feed on surrounding humus or humified soil (Bignell and Eggleton, 2000; Gathorne-Hardy et al., 2001). Some termite and earthworm taxa, however, were better represented under cool and wet conditions, in agreement with our hypothesis (Figure 1A and 2A).

Effect of contrasting agricultural management on earthworm and termite diversity

In agreement with our hypothesis, higher earthworm diversity was recorded in the fallow than in the agricultural systems. Similarly, under continuous crop production, higher earthworm diversity was observed under agricultural management that had resulted in high-C than low-C soils. This indicates that earthworms are sensitive to disturbances associated with agriculture and agricultural land use intensity, and that their role can be significantly enhanced by applying management practices that increase soil C in arable systems. Relative impact of individual management practices remains to be investigated. Earthworms sampled in our study were largely comprised of the epigeic, to a smaller extent the endogeic and none of the anecic taxa. Epigeic earthworms, which need organic inputs as mulch, and endogeic species which are capable of utilizing low-quality organic residues as food, will have been favoured by the addition of organic resources as used in many of our sites. Anecic earthworms were lacking across all sites. Anecic earthworms tend to be few in tropical soils in general, due to low litter availability as a result of higher decomposition rates at higher temperatures (Lavelle et al. (1999), and in arable fields in particular because they tend to be more sensitive to disturbance and tillage (Curry, 2004). Natural or relatively undisturbed agro-ecosystems offer suitable conditions for food and shelter for macrofauna (Barros et al., 2002; Eggleton et al., 2002; Birang et al., 2003). Soil disturbance alters the habitat and the distribution of food resources. Consequently, macrofauna populations often decline (Kooyman and Onck, 1987; Crossley et al., 1992; Lavelle et al., 1992; Black and Okwakol, 1997).

Contrary to our hypothesis, little difference in termite diversity was observed between fallow and high-C arable systems. We attribute this to the wide feeding and foraging habit of most of the species sampled. Very few typical soil feeders (group IV) were found. Rather, a large proportion of the termites sampled in this study belong to feeding group II and to a smaller extent to feeding group I and III. These groups are largely foragers of wood, litter, soil, dung/manure and grass. They were probably scavenging for food all over the plots and, hence, were sampled uniformly across treatments. In agreement with our hypothesis, higher termite diversity was recorded in agricultural management that had resulted in high-C than in low-C soils. We suggest that the foraging groups utilizing organic residues as food were favoured by the addition of organic resources characteristic of many of our high C treatments.

Conclusions

This study, conducted in 12 long-term agricultural field trials across the sub-humid to semi-arid tropical zones of Eastern and Western Africa, provides new insights on diversity of earthworms and termites in SSA, since it is the first time that a study like this is done on this scale.

We have shown that:

1. Earthworm and termite diversity and abundance were low in fallow, high-C and low-C agricultural treatments in 12 long-term trial fields across the sub-humid to semi-arid tropical zones in Eastern and Western Africa. This is in contrast to most typical native or undisturbed forest ecosystems of the tropical zones;

2. Environmental variables contributed 42% and 25% of variation observed in earthworm and termite taxonomic abundance, respectively. Earthworm and termite taxa were less abundant in the relatively cooler, wetter, more clayey sites

characteristic of Eastern Africa, compared to the warmer, drier, more sandy Western Africa sites;

3. Continuous crop production has significant negative effects on earthworms, but little effect on termite diversity, as compared to long-term fallow, and agricultural management resulting in high-C increases earthworm and termite diversity as compared to low-C.

4. We conclude that fewer species of earthworms and termites are favored under agricultural management that leads to lower soil C. Results indicate that soil disturbance that goes with continuous crop production is more detrimental to earthworms than to termites as compared to fallow.

Acknowledgements

This study was supported by WOTRO Science for Global Development of The Netherlands Organization for Scientific Research (NWO). We thank our partners, especially the scientists and field technicians of the Tropical Soil Biology and Fertility Institute of the International Centre for Tropical Agriculture (TSBF-CIAT, Kenya), Kenya Agricultural Research Institute (KARI), Kenya Forestry Research Institute (KEFRI), Kenyatta University, Kenya, International Institute of Tropical Agriculture (IITA, Nigeria), International Center for Soil and Agricultural Development (IFDC, Burkina Faso), Institute of Natural Environmental and Agricultural Research (INERA, Burkina Faso), Savanna Agricultural Research Institute (SARI, Ghana), Chitedze Agricultural Research Station (Malawi), International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, Niger), National Museums of Kenya and Natural History Museums (Hungary), who agreed to work with us and have allowed us to use their experimental sites and facilities for this study.

CHAPTER THREE

The influence of soil macrofauna on soil aggregation in agro-ecosystems of sub-Saharan Africa depends on management intensity

F.O. AYUKE [a*, b], B. VANLAUWE [b], M.M. PULLEMAN [a], D.W. ODEE [c, d], L. BRUSSAARD [a], J. SIX [e]

[*a] *Department of Soil Quality, Wageningen University, P.O Box 47, NL-6700 AA Wageningen, The Netherlands*

[b] *Tropical Soil Biology and Fertility (TSBF) Institute of CIAT, P.O Box 30677-00100, Nairobi, Kenya*

[c] *NERC Centre for Ecology and Hydrology, CEH Edinburgh, Bush Estate, Penicuik, Midlothian EH26 0QB, UK*

[d] *Kenya Forestry Research Institute (KEFRI), P.O Box 20412-00200*

[e] *Department of Plant Sciences, University of California, Davis, CA 95616, USA*

*Corresponding author: (0317) 486524; Fax: (0317) 419000

Email: fredrick.Ayuke@wur.nl or fredrick.ayuke@yahoo.com*

Submitted to European Journal of Soil Science

Abstract

The effects of soil macrofauna on soil organic matter (SOM) and soil structure are rarely considered when developing sustainable management practices. We investigated the relative importance of earthworms and termites, in addition to soil- and climatic factors in influencing soil aggregation in 12 long-term field experiments in East and West Africa. Aggregate size distribution, SOM and soil texture, as well as the diversity, abundance and biomass of earthworms and termites were measured in arable systems under contrasting management and a nearby fallow. Aggregate stability indices, SOM, and diversity, abundance and biomass of earthworms and termites were generally higher in the fallows compared to the arable systems. Factor analysis indicated that under fallow, 45.9% of the sample variation was explained by factor I, which was related to SOM, precipitation, clay content and earthworm indices, and 17.8% by factor II, which was related to termite indices. Under arable systems, 42.4% of the sample variation was explained by factor I, which related to SOM, precipitation and clay and 20% by factor II, which related to earthworms and termites. Regression analysis indicated that under fallow, the two factors explained 92.6% for total macroaggregates (TM) and 87.5% for microaggregates within macroaggregates (mM). Under arable cropping, the two factors explained 98% for TM and 100% for mM. We conclude that earthworms, and to a smaller extent termites, are important drivers of soil aggregation, together with climate, SOM and soil texture. However, the benefits of soil macrofauna for aggregation are reduced with increasing management intensity and soil disturbance due to cultivation, whereas the relative contribution of SOM and clay is increased.

Introduction

Soil degradation of arable land through loss of soil organic matter (SOM) and soil structural stability results from soil tillage and the removal of plant biomass. In many tropical cropping systems, little or no agricultural residues are returned to the soil as these are either burnt to clear the ground for crop planting, utilized as fuel, or grazed by livestock (Karanja et al., 2006; Chivenge et al., 2007). The loss of SOM and the associated deterioration of soil physical, chemical and biological soil fertility associated with continuous cropping, and sub-optimal fertilizer use frequently result in a decline in biomass productivity and crop yields and present great challenges to many farmers in sub-Saharan Africa (SSA) (Sanchez et al., 1997). One of the major challenges in such low input systems is to develop ways of managing organic matter to optimize the maintenance of SOM, improve soil structure and enhance water and nutrient use efficiencies. Integrated soil fertility management (ISFM), i.e. the combined use of organic and inorganic fertilizers, has been recommended for increasing nutrient use efficiency (NUE) and with long-term stabilization of SOM (Vanlauwe et al., 2002). One aspect of ISFM, that is often ignored, is that it offers perspective for the manipulation of community composition and activities of soil invertebrate fauna through the judicious management of organic inputs. Especially the stimulation of earthworm and termite activity may contribute to decomposition and humification of organic residues, maintenance of soil structure and aggregate stability, and overall restoration of degraded soils (Brussaard et al., 2007).

The roles played by soil fauna in soil processes are widely recognized, but rarely taken into account when developing sustainable crop and soil management options. Earthworms and termites are the most abundant groups of macrofauna in tropical soils and are considered important soil ecosystem engineers (Lavelle et al., 1997; Black and Okwakol, 1997). Earthworms have been reported to play an important role in the incorporation of organic materials into the soil matrix and in the formation of soil pores and stable macroaggregates (Blanchart et al., 1999; Scullion and Malik, 2000; Pulleman, *et al.,* 2005b) and thereby have profound effects on soil ecosystem functions. Their feeding, burrowing and excretion activities regulate the mineralization of carbon and nutrients, both directly and indirectly via an effect on aggregate dynamics in which occluded organic matter can be physically protected (Tisdall and Oades, 1982; Bossuyt et al, 2005). Earthworms and termites are also important for soil water dynamics and soil erosion control (Mando, 1997; Blanchart et al., 2004; Jouquet et al., 2008). With respect to the benefits of stable soil aggregates for SOM stabilization, microaggregates are key because of their role in long-term protection of SOM (Six et al., 2004). The potential beneficial role of earthworms on SOM incorporation and soil aggregation in agricultural soils has been relatively well established (Bossyut et al., 2005; Pulleman et al, 2005a, b; Coq et al., 2007; Fonte et al., 2009), whereas the impact of termite activity on (differentially managed) agricultural soils is very poorly understood (Black and Okwakol; Jouquet et al., 2002). Termites, especially mound builders, use soil materials rich in clay to construct their nests (Jouquet et al., 2002). During nest construction they excrete organo-mineral complexes as fecal pellets that are enriched in organic matter (Jungerius et al., 1999). So termites exert effects on soil physical properties through the construction of mounds, nests, galleries and surface sheeting (Mando, 1997; Asawalam et al., 1999).

Despite the potential significant benefits of soil macrofauna for soil aggregation and related soil processes, there is a general lack of knowledge on the significance of soil macrofauna abundance and diversity (specifically in termites and earthworms) for stable soil aggregation under different climatic and soil conditions in Sub Saharan-Africa, nor how this relationship is affected by management intensity and associated soil disturbance due to agricultural activities. Studies by Eggleton et al. (2002), Okwakol (2000) and Birang et al. (2003) have indicated that soil disturbance and increased intensity of agriculture negatively impact macrofauna groups (i.e. earthworms and termites) compared with undisturbed or less managed ecosystems such as natural forests or natural fallows. Least intensively managed sites (e.g. fallow) favor soil macrofauna probably because of less soil disturbance and possibly due to high accumulations of SOM compared to arable systems characterized by high soil disturbance (tillage), addition of inorganic mineral inputs or low organic inputs. Although numerous studies have shown that SOM and physical soil properties decline following the conversion of untilled native ecosystems to agricultural land (De Gryze et al., 2004; Grandy and Robertson, 2006), very few have quantitatively considered the interactive effects between SOM and soil macrofauna diversity in affecting soil ecosystem functions (Six et al., 2004). As such, quantitative understanding of these relationships is needed in order to predict changes in soil ecosystems due to management and global change.

This study specifically aimed at: 1) investigating the multicollinearity between soil and climatic factors, soil fauna and aggregate stability, 2) assess the extent to which soil macrofauna explains differences in aggregation across a wide range of climatic and soil conditions in SSA, and 3) compare these relationships between arable and fallow systems representing different levels of management intensity.

Materials and Methods

Study sites and sampling strategy

The study was conducted in 12 long-term field trials across the sub-humid to semi-arid tropical zones of Eastern Africa (Embu, Kabete, Impala and Nyabeda in Kenya and Chitala in Malawi) and Western Africa (Tamale in Ghana, Ibadan in Nigeria, Sadore in Niger and Farakoba, Saria I, II and III in Burkina Faso). A general characterization of the sites, including climate and soils, is presented in Table 1. The long-term trials were established between 1960 and 2003 and aimed at testing different management options for arable crop production such as organic versus mineral inputs, crop rotation, and tillage. In our sampling scheme, the fallow, high-C and low-C treatments represent a gradient in management intensity that corresponds with a gradient in soil C. Arable treatments that, according to previously available data, had resulted in the highest and lowest soil organic carbon (SOC) contents were included (Table 2). Depending on site, the fallows consisted of grass fallow, forest or shrubland, which may or may not have been used for crop production in the past, but had been undisturbed for at least 10 years before the time of sampling. No insecticides were applied in the fields we sampled for this study.

Table 1. Location and characteristics of the study sites.

	Sites									
Environmental Parameters	**Embu, Kenya**	**Kabete, Kenya**	**Impala, Kenya**	**Nyabeda, Kenya**	**Chitala, Malawi**	**Ibadan, Nigeria**	**Tamale, Ghana**	**Sadore, Niger**	**Farakoba, Burkina Faso**	**Saria I, II, III, Burkina Faso**
Altitude asl. (m)	1480	1700	1337	1420	606	200	185	250	405	300
Latitude and Longitude	0° 30′ S; 37° 30′ E	1° 15' S; 36° 41' E	0° 08' N; 34° 25' E	0° 06' N; 34° 36' E	13° 40' S; 34° 15' E	7° 30' N; 3° 54' E	9° 25' N; 1° 00' W	13° 15' N; 2° 17' E	11° 06' N; 4° 20' W	12° 16' N; 2° 09' E
Mean Annual temp (°C)	20	18	23	23	22	27	29	33	28	33
Mean annual rainfall (mm)	1450 Bimodal	1000 Bimodal	1800 Bimodal	1800 Bimodal	800 Unimodal	1200 Bimodal	1200 Unimodal	550 Unimodal	850 Unimodal	800 Unimodal
Climate (FAO)	Sub-humid	Sub-humid	Humid	Humid	Sub-humid	Humid	Semi-arid	Semi-arid	Sudano-Sahelian	North-Sudanian
Soil type (FAO)	HUMIC NITISOL	HUMIC NITISOL	HUMIC FERRALSOL	HUMIC FERRALSOL	TYPIC FERRALSOL	DYSTRIC REGOSOL	FERRIC LUVISOL	FERRALIC ARENOSOL	FERRIC LUVISOL	FERRIC LIXISOL
†Texture sand, silt, clay (%)	Clay 3, 22, 75	Clay 11, 22, 67	Clay 13, 17, 70	Clay 9, 21, 70	Sandy clay 60, 5, 35	Sandy 87, 6, 7	Sandy 90, 4, 6	Sandy 92, 3, 5	Loamy sand 74, 19, 7	Sandy loam 53, 36, 11

†Source: Zida et al., Unpublished.

Table 2. Description of selected sites. # refers to management treatments: 1 = crop rotation, 2 = tillage, 3 = organic inputs, 4 = inorganic fertilizer

		Treatments		
		Fallow	**High-C**	**Low-C**
Trial site	**Year established**			
Embu	1993	Fallow-woodland/shrubland since 1993	#1=Cont. maize, 2=Hand hoeing, 3=*Leucaena leucocephala* (5 Mg ha^{-1}), 4=no fertilizer	#1=Cont. maize, 2=Hand hoeing, 3=no organic inputs, 4=no fertilizer
Kabete	1976	Fallow-Bushland since trial establishment in 1976	#1=Maize-bean rotation, 2=Hand hoeing, 3=10 Mg ha^{-1} manure, 4=CAN (120 kg N ha^{-1}) and TSP (52.8 kg P ha^{-1}) fertilizers	#1. Maize-bean rotation, 2=Hand hoeing, 3= no organic inputs, 4=no fertilizer
Impala	2000	Fallow-shrubland nearby since trial establishment in 2000	#1=Maize-*Tephrosia candida* relay/rotation, 2=Hand hoeing, 3=*T. candida* residues (5 Mg ha^{-1}), 4= Blanket P , no N fertilizer	#1= Cont. maize, 2=no till, 3=no organic inputs, 4=no fertilizer
Nyabeda	2003	Fallow-shrubland nearby since trial establishment in 2003	#1. Maize-soybean rotatn, 2=no till, 3=Maize stover residues (2 Mg ha^{-1}), 4=NPK fertilizer (60:60:60)	#1=Maize-soybean rotation, 2=hand hoeing, 3=no organic inputs, 4=NPK fertilizer (60:60:60)
Chitala	1995	Grass fallow since trial establishment in 1995	#1=Maize-pigeon pea rotation, 2=Tractor till, 3=Crop residues: stem + leaves, 4=$(NH_4)_2SO_4$ fertilizer (96 kg N ha^{-1} yr^{-1})	#1=Cont. maize, 2=Tractor till, 3=no organic inputs, 4=no fertilizer
Ibadan	1996	Bushland fallow since 1986 adjacent to the experimental plots	#1=Maize-cowpea rotation, 2=Minimum tillage-light surface hoeing, 3=*S. siamea* (5 Mg ha^{-1}), 4=fertilizer-NPK (60:30:30 kg ha^{-1} yr^{-1})	#1=Maize-cowpea rotation, 2=Minimum tillage-light surface hoeing, 3=no organic inputs, 4=no fertilizer

Table 2. (Continued) Description of selected sites. # refers to management treatments: 1 = crop rotation, 2 = tillage, 3 = organic inputs, 4 = inorganic fertilizer.

Tamale	1996	Grass fallow strip since 1996	#1=Cont. maize, 2=Zero till-hand pulling/slashing of weeds, 3=no organic inputs, 4=no fertilizer	#1=Cont. maize, 2=Bullock plough-hand hoeing of weeds, 3=no organic inputs, 4=no fertilizer
Sadore	1986	Fallow-shrubland within the experimental site since 1986	#1=Cont. millet, 2= Hand hoeing, no ridging, 3=residues applied, 4=fertilizer (13 kg P ha^{-1})	#1=Millet-cowpea rotation, 2= Animal traction + ridging , 3=residues applied, 4=fertilizer (30kg N, 13 kg P ha^{-1})
Farakoba	1993	Grass fallow within the experimental site since trial; establishment in 1993	#1. Cont. sorghum, 2=Tractor till, 3=compost (5 Mg ha^{-1}), 4=PK fertilizer (25:14)	#1. Cont. sorghum, 2=tractor till, 3=no organic inputs
Saria I	1960	Grass- fallow since trial establishment in 1959 (Common for all the Sarias)	#1=Sorghum-cowpea rotation, 2=Tractor till, 3=manure (5 Mg ha^{-1} every 2 yrs), 4=NPK fertilizer (100 kg ha^{-1}) and Urea (50 kg ha^{-1}) every 2 years	#1=Cont. sorghum, 2=Tractor till, 3=manure (5 Mg ha^{-1} every 2 yrs), 4=NPK fertilizer (100 kg ha^{-1}) and Urea (50 kg ha^{-1}) every 2 years
Saria II	1980	See Saria I	#1=Cont. sorghum, 2=Tractor till, 3=10 Mg ha^{-1} manure, 4=fertilizer- 23kg N ha^{-1}	#1=Cont. sorghum, 2=Tractor till, 3=no organic inputs, 4=no fertilizer
Saria III	1990	See Saria I	#1. Cont. sorghum, 2=Oxen plough, 3=Manure (10 Mg ha^{-1}), 4=NPK fertilizer (100 kg ha^{-1} yr^{-1}) and Urea (50 kg ha^{-1} yr^{-1})	#1=Cont. sorghum, 2=Hand hoeing (5cm depth), 3=Manure (10 Mg ha^{-1}), 4=NPK fertilizer (100 kg ha^{-1} yr^{-1}) and Urea (50 kg ha^{-1} yr^{-1})

Soil sampling, pretreatment and analysis

One soil monolith (25 × 25 × 30 cm) sample per plot (n = 3) was taken 8 weeks after planting (July-September 2006 in West Africa and May-July 2007 in East Africa). The extracted soil was hand-sorted for macrofauna. Termite specimens were preserved in 75% alcohol and earthworms in 75% alcohol + 4% formaldehyde before being transported in sealed vials to the laboratory for identification, enumeration and biomass determination. Biological assessments included abundance (numbers of individuals per unit area), and biomass (fresh weight per unit area) per sample. As for diversity, the Shannon-Wiener diversity index (H′) was calculated as $H' = -\sum (p_i \ln p_i)$, where pi is the proportion of the ith taxonomic group, estimated as ni/N; where ni is the number of individuals of the ith species and N the total number of individuals within the sample (Magurran, 1988).

A representative subsample (about 500 g) of the 0-15 and 15-30 cm soil depth layers of the monolith was gently passed through a 10mm sieve by breaking up the soil along natural planes of weakness, air-dried and stored at room temperature. The soil was then separated into four water stable aggregate size fractions: (i) large macroaggregates (>2000 µm), (ii) small macroaggregates (250 µm-2000 µm), (iii) microaggregates (53–250 µm), and (iv) silt + clay sized particles (<53 µm), using the method described by Elliott (1986). Briefly, 80 g of air-dried soil was transferred to a 2 mm sieve, placed in a recipient filled with deionized water, and left to slake for 5 minutes (Figure 1). After which the 2 mm sieve was manually moved up and down 50 times in 2 minutes. The procedure was repeated using the material that passed through the 2 mm sieve, using a 250 µm sieve and subsequently a 53 µm sieve. A representative 250 ml subsample was taken from the suspension containing the <53 µm silt and clay sized particles to determine the weight of the smallest fraction. Soil aggregates retained on each sieve were backwashed into pre-weighed containers, oven-dried at 105°C over-night and weighed. The weights of the large macroaggregates and small macroaggregates were added to calculate the total amount (TM) of macroaggregates (>250 µm).

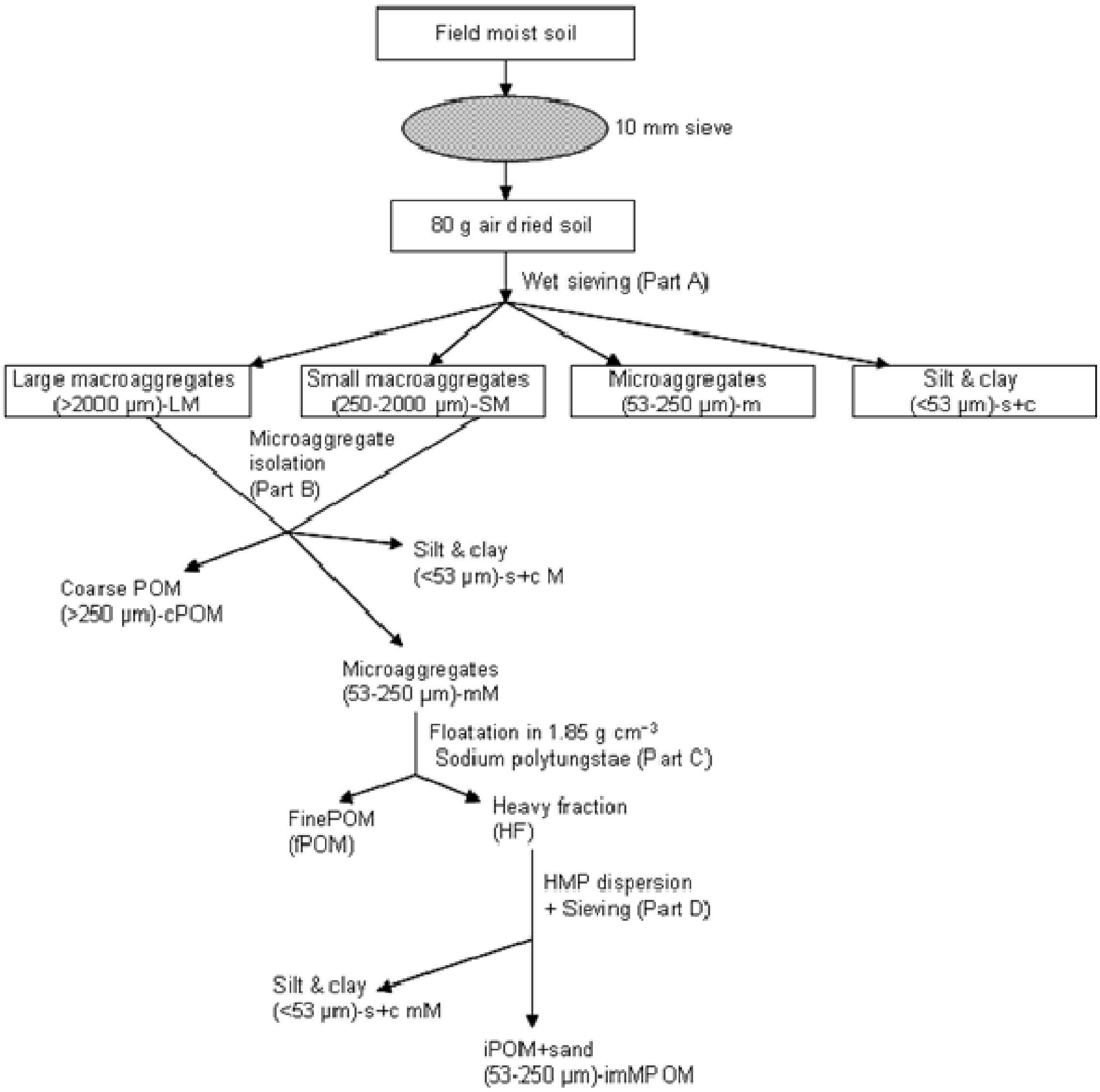

Figure 1 Fractionation scheme to isolate aggregate and sand fractions. Adapted from Six et al., (2000).

After wet sieving, oven drying and weighing, the large and small macroaggregates retained were combined according to their relative weight/proportion and used for the separation of microaggregates within macroaggregates (mM) as follows: Microaggregates (53-250 µm) occluded within macroaggregates were isolated using a device described by Six et al. (2000) which completely breaks up macroaggregates with minimal disruption of microaggregates. About 5 g of the macroaggregates were transferred to the device holding a 250 µm mesh screen and shaken with 50 glass beads (diameter 4 mm) until all macroaggregates were broken. The microaggregates released were immediately flushed through the 250 µm sieve and deposited onto a 53-µm sieve by a continuous flow of water through the device. The material on the 53 µm sieve was then wet sieved as described above, 50 times in 2 minutes, to isolate the stable microaggregates (mM) from the silt and clay (Figure 1). The microaggregate fractions (53-250 µm) were oven-dried (60°C) for 48 hours and weighed. Sand and coarse particulate organic matter (cPOM) retained on the 250 µm mesh screen were washed off, oven-dried, and weighed; the weight of this fraction was used for sand correction of total macroaggregates. A subsample of the stable microaggregate (mM) fraction was dispersed by overnight shaking in sodium hexametaphosphate (5 g L-1) and sieving over a 53 µm sieve, oven dried and weighed to determine the fine sand content of this fraction.

It should be noted that sand correction is needed because it normalizes soil samples with different amounts of total sand in order to correct for the effect of sand on the measurements of aggregate distribution and structural stability of the soil. Sand correction of the total macroaggregate (TM) fraction and the mM fraction was done as follows:

Sand corrected TM:
[g TM/100 g soil] − ([g cPOM + sand/100 g TM]/100 × [g TM/100 g soil]).
Sand corrected mM:
[g mM/100g TM] − ([g fine sand/100 g mM]/100 × [g mM/100 g TM]).

For measurement of total soil organic C and N content, 1-2 g of the whole soil samples (before fractionation) was taken and ground. About 30 mg of the samples were weighed out in aluminium capsules and sent to the University of California at Davis for C and N analysis with a PDZ Europa Integra C-N isotope ratio mass spectrometer (Cheshire, United Kingdom).

Textural data (clay and sand), and some C and N data were derived from secondary sources and also previous studies conducted at the sites (see Table 3).

Statistical analysis

The data obtained were subjected to analysis of variance (ANOVA) using GENSTAT (2009). Levels of significance among the interactions were evaluated using Fischer’s least significant difference (LSD). Multivariate statistics was conducted using XLSTAT (XLSTAT PRO, 2009), following procedures by De Gryze *et al.* (2007) in which they used factor analysis to assess controls on aggregation. Briefly, at first, simple Pearson correlations among all the selected variables were calculated and their significance tested ($p < 0.05$) to obtain a general overview of the relationships between the different variables. Because of multicollinearity among the variables, we employed factor analysis to obtain orthogonal and standardized variables using the factor procedures of SAS (SAS Library, 1995). Initial estimates of the factors were made on principal components using Kaiser-Guttman rule, such that those factors with eigenvalues (variance) >1 were retained and rotated using varimax procedure. Using a rule of thumb as recommended by SAS Library (1995), factors that had loadings >0.5 in absolute value were considered significant. They were subsequently used in multiple regression to test their impact on the quantity of macroaggregates.

Results

Variation in the soil properties

(a) Water stable aggregate indices, total soil C and N

Mean percent total macroaggregates were generally higher in the fallow than in the arable (high-C and low-C), and the differences between high-C and low-C treatments were significant for most of the eastern Africa sites (e.g. Kabete, Impala and Nyabeda) (Table 3). The amount of microaggregates within macroaggregates (mM) was variable, with site having the most influence on the percent mM. For instance, the arable systems of Embu and Nyabeda had a higher percentage of mM than fallow, whereas Kabete showed a reverse trend (Table 3).

As a general trend, mean total soil C was higher in the fallow than in arable cropping systems, but not all sites followed the order fallow > high-C > low-C (Table 3). Site-treatment interactions were also significant, as were differences among sites (Table 3). Mean total N showed similar trends as soil C (Table 3).

Table 3. Soil aggregate fractions and chemical properties across fallow and arable systems of East and West Africa (averaged for 0-30cm)

	Soil aggregate fractions						**Soil chemical properties**					
	Treatment											
	Fallow	**High-C**	**Low-C**	**Fallow**	**High-C**	**Low-C**	**Fallow**	**High-C**	**Low-C**	**Fallow**	**High-C**	**Low-C**
Site	**Total macroaggregates (% of total soil)**			**Micro within macroaggregates (% of total macroaggregate)**			**Total C / g kg−1**			**Total N / g kg−1**		
†Embu	75.9^{a}	48.7^{b}	47.5^{b}	55.0^{b}	71.3^{a}	72.9^{a}	34.2^{a}	26.2^{b}	24.2^{b}	3.0^{a}	2.3^{b}	2.1^{c}
†Kabete	56.0^{a}	49.1^{b}	41.5^{c}	75.8^{a}	69.8^{b}	72.1^{b}	22.3^{a}	19.6^{ab}	16.9^{b}	2.0^{a}	1.7^{b}	1.4^{c}
†Impala	72.9^{a}	74.5^{a}	64.6^{b}	57.1^{a}	56.5^{a}	58.0^{a}	20.7^{b}	24.8^{a}	21.6^{b}	1.9^{b}	2.2^{a}	1.8^{b}
†Nyabeda	80.9^{a}	61.8^{b}	52.8^{c}	53.2^{a}	57.7^{a}	55.2^{a}	22.4^{a}	20.3^{b}	18.2^{b}	2.1^{a}	1.8^{b}	1.7^{b}
†Chitala	15.6^{a}	14.6^{a}	15.1^{a}	ND*	ND*	ND*	11.5^{a}	9.3^{b}	7.6^{b}	0.8^{a}	0.6^{a}	0.6^{a}
††Ibadan	5.0^{a}	8.6^{a}	5.8^{a}	ND*	ND*	ND*	10.0^{a}	8.7^{a}	4.8^{b}	1.1^{a}	0.7^{b}	0.3^{c}
‡Tamale	23.7^{a}	7.7^{b}	6.6^{b}	ND*	ND*	ND*	6.9^{a}	4.7^{b}	2.9^{b}	0.5^{a}	0.4^{a}	0.2^{b}
‡Sadore	ND*	ND*	ND*	ND*	ND*	ND*	1.4^{a}	1.3^{a}	1.0^{a}	0.1^{a}	0.1^{a}	0.1^{a}
‡Farakoba	20.0^{a}	12.7^{b}	12.3^{b}	ND*	ND*	ND*	3.3^{a}	3.0^{a}	2.5^{a}	0.2^{a}	0.2^{a}	0.2^{a}
‡Saria I	ND*	ND*	ND*	ND*	ND*	ND*	3.2^{a}	3.2^{a}	3.2^{a}	0.2^{a}	0.2^{a}	0.2^{a}
‡Saria II	ND*	ND*	ND*	ND*	ND*	ND*	3.2^{a}	3.4^{a}	2.2^{a}	0.2^{a}	0.2^{a}	0.1^{a}
‡Saria III	ND*	ND*	ND*	ND*	ND*	ND*	3.2^{a}	2.9^{a}	2.6^{a}	0.2^{a}	0.2^{a}	0.2^{a}
SV	df	F-ratio	P-value	df	F-ratio	P-value	df	F-ratio	P-value	df	F-ratio	P-value
Site	11	579.1	<0.001	7	1939.3	<0.001	11	483.7	<0.001	11	527.3	<0.001
Treatment	2	59.1	<0.001	2	4.6	0.013	2	42.3	<0.001	2	53.0	<0.001
Site*treat	22	9.6	<0.001	14	6.4	<0.001	22	5.6	<0.001	22	7.1	<0.001
Residual	70			46			70			70		

Means followed by same lower case letters within rows across treatments are not statistically significant at $p<0.05$. *ND= Not determined due to high sand proportion, hence all of the total macroaggregate was actually coarse sand; Soil C data source: †Eastern Africa (from monolith soils). ‡Western Africa (Zida et al., unpublished), ††Ibadan (Vanlauwe et al., 2002).

(b) Taxonomic richness and functional groups

Twenty taxa of earthworms in 3 families (Ocnerodrilidae, Acanthodrilidae and Eudrilidae) were found across the 12 sites (Table 4). Trophic groups were predominantly epigeic and endogeic. No anecic earthworms were present. Twenty taxa of termites belonging to two families (Termitidae and Rhinotermitidae) were found. Trophic groups were dominated by group II termites (i.e. wood, litter and grass feeders; fungal growers) (Table 4).

(c) Macrofauna diversity indices, abundance and biomass

Arable cropping had significant negative effects on earthworms, but little effect on termite diversity, compared to long-term fallow. Agricultural management resulting in high-C soils increased earthworm and termite diversity compared to low-C soils. Mean earthworm Shannon-Wiener diversity index was significantly higher in the fallow (0.40) than in the high-C treatments (0.17), where, in turn, the index was significantly higher than in the low-C (0.12) treatments. Across sites, interaction (site by treatment) effects were observed because not at all the sites followed the diversity indices the order fallow > high-C > low-C. Also, there were significant differences in diversity between sites (Table 5). Arable systems of sites such as Embu, Kabete, Impala, Tamale and Farakoba had significantly lower earthworm diversity indices than the fallow systems, and this trend was similar for termites in sites such as Impala, Chitala and Ibadan (Table 5).

Differences in mean earthworm abundance showed the same pattern as differences in mean diversity, but the difference between high-C and low-C treatments was not significant (Table 5). In contrast, termite abundance was highly variable across treatments. Termite abundance, in contrast to termite diversity, differed significantly between sites (Table 5).

Table 4. Earthworm and termite taxonomic richness and functional groups based on monolith and transect methods

Earthworm taxa		**Termite taxa**		
Taxonomic group	**Functional group** [a]	**Taxonomic group**	**Functional group** [b]	**Food type** [c]
Ocnerodrilidae		**Rhinotermitidae-Rhinotermitinae**		
Nematogenia lacuum	Endogeic	*Captotermes intermedias*	I	WLG
Gordiodrilus robustus	Endogeic	*Schedorhinotermes lamanianus*	I	WLG
Gordiodrilus wemanus	Endogeic	**Rhinotermitidae-Psammotermitinae**		
Gordiodrilus marcusi	Endogeic	*Psammotermes hybostoma*	I	WLG
Acanthodrilidae		**Termitidae-Nasutitermitinae**		
Millsonia inermis	Endogeic	*Nasutitermes* spec	II	WLG
Millsonia guttata	Endogeic	*Trinevitermes* spec	II	LG
Dichogaster (Dt.) saliens	Epigeic	**Termitidae-Macrotermitinae**		
Dichogaster (Dt.) affinis	Epigeic	*Ancistrotermes cavithorax*	II	WLG
Dichogaster (Dt.) bolaui	Epigeic	*Macrotermes nr. Vitrialatus*	II	FWLG
Dichogaster (Dt.) modiglianii	Epigeic	*Macrotermes subhyalinus*	II	FWLG
Dichogaster (Dt.) spec nov 1	Epigeic	*Macrotermes herus*	II	FWLG
Dichogaster (Dt.) spec nov 2	Epigeic	*Microtermes pusillas*	II	FWLG
Eudrilidae		*Macrotermes* spp.	II	FWLG
Polytoreutus annulatus	Epigeic	*Microtermes* spp.	II	FWLG
Hyperiodrilus africanus	Epigeic	*Odontotermes magdalenae*	II	FWLG
Hyperiodrilus spec nov	Epigeic	*Odontotermes* spp.	II	FWLG
Eudrilus buettneri	Epigeic	*Pseudacanthotermes spiniger*	II	FLG
Ephyriodrilus afroccidentalis	Epigeic	*Pseudacanthotermes* spp	II	FLSD
Eminoscolex violaceus	Epigeic	**Termitidae-Termitinae**		
Stuhlamannia spec nov	Epigeic	*Amitermes-Amitermes stephensoni*	II	WLSD
Lavellea spec nov	Epigeic	*Microcerotermes parvulus*	II	WLG
		Termes-Termes baculi	III	WS
		Cubitermes- Tubeculitermes spec	IV	S

[a] Based on classification by Swift & Bignell (2001). (W=wood; L=leaf litter; S=soil; D=Dung/manure; F=fungus grower; G=dead/dry grass. [b] Based on classification by Eggleton *et al.* (2002). [c] based on field notes/observation. [c] based on observations by Kooyman & Onck (1987).

Earthworm and termite biomass were also variable across treatments. Mean earthworm biomass was significantly higher in the fallow than in the high-C soils, but the difference between high-C and low-C soils was not significant (Table 5). No significant differences were observed in mean termite biomass. Effects of site and site-treatment interactions were significant ($p < 0.05$), while treatment effect was not significant.

Table 5. Macrofauna (earthworm and termite) diversity indices, abundance and biomass across fallow and arable systems of Eastern and Western Africa

Earthworms

	Shannon indices (H')			**Abundance / number m−2**			**Biomass / g m−2**		
	---------------------------**Treatments**	-----------------------------	-----------------------------	-----------------------------	-----------------------------	-----------------------------	-----------------------------	-----------------------------	-----------------------------
Site	Fallow	High-C	Low-C	Fallow	High-C	Low-C	Fallow	High-C	Low-C
Embu	0.60^{a}	0.00^{b}	0.17^{b}	1264^{a}	32^{b}	27^{b}	8.40^{a}	0.50^{a}	0.30^{a}
Kabete	0.74^{a}	0.33^{b}	0.00^{b}	363^{a}	395^{a}	272^{a}	8.00^{a}	19.00^{a}	4.70^{a}
Impala	0.90^{a}	0.15^{b}	0.21^{b}	165^{a}	32^{b}	16^{b}	20.30^{a}	0.40^{a}	0.80^{a}
Nyabeda	0.08^{a}	0.00^{a}	0.00^{a}	117^{a}	0^{b}	16^{b}	0.60^{a}	0.00^{a}	5.60^{a}
Chitala	0.30^{a}	0.00^{a}	0.00^{a}	53^{a}	5^{b}	5^{b}	1.60^{a}	0.01^{a}	0.01^{a}
Ibadan	0.41^{b}	0.99^{a}	0.51^{b}	96^{b}	933^{a}	117^{b}	30.70^{a}	52.8^{a}	18.80^{a}
Tamale	0.67^{a}	0.21^{b}	0.00^{b}	37^{a}	32^{a}	16^{a}	128.00^{a}	2.30^{b}	0.40^{b}
Sadore	0.00^{a}	0.00^{a}	0.00^{a}	0^{a}	0^{a}	0^{a}	0.00^{a}	0.00^{a}	0.00^{a}
Farakoba	0.49^{a}	0.11^{b}	0.00^{b}	453^{a}	59^{b}	11^{b}	33.50^{a}	4.20^{b}	5.00^{b}
Saria I	0.21^{a}	0.12^{a}	0.00^{a}	69^{a}	27^{a}	21^{a}	19.40^{b}	78.80^{a}	24.70^{b}
Saria II	0.21^{a}	0.12^{a}	0.00^{a}	69^{a}	11^{a}	0^{a}	19.40^{a}	16.40^{a}	0.00^{a}
Saria III	0.21^{ab}	0.00^{b}	0.53^{a}	69^{a}	80^{a}	59^{a}	19.40^{a}	4.30^{a}	32.30^{a}
Mean	**0.40**^{a}	**0.17**^{b}	**0.12**^{c}	**230**^{a}	**134**^{b}	**47**^{b}	**24.1**^{a}	**14.9**^{b}	**7.7**^{b}
SV	df	F-ratio	P-value	df	F-ratio	P-value	df	F-ratio	P-value
Site	11	4.09	<0.001	11	10.07	<0.001	11	4.66	<0.001
Treatment	2	12.33	<0.001	2	20.37	<0.001	2	7.00	0.002
Site*treat	22	1.97	0.017	22	4.73	<0.001	22	2.30	0.005
Residual	70			70			70		

Termites

Site	Fallow	High-C	Low-C	Fallow	High-C	Low-C	Fallow	High-C	Low-C
Embu	0.01^{a}	0.12^{a}	0.03^{a}	139^{a}	528^{a}	32^{a}	0.39^{a}	3.45^{a}	0.08^{a}
Kabete	0.13^{a}	0.03^{a}	0.16^{a}	203^{b}	1029^{a}	384^{ab}	0.75^{b}	6.21^{a}	1.39^{b}
Impala	0.37^{a}	0.05^{b}	0.00^{b}	987^{ab}	43^{b}	1104^{a}	3.02^{a}	0.10^{b}	6.20^{a}
Nyabeda	0.20^{a}	0.15^{a}	0.00^{a}	475^{a}	208^{ab}	0^{b}	2.40^{a}	0.01^{a}	0.00^{a}
Chitala	0.41^{a}	0.15^{b}	0.08^{b}	752^{ab}	117^{b}	1744^{a}	6.94^{a}	0.19^{b}	1.23^{b}
Ibadan	0.61^{a}	0.34^{b}	0.00^{c}	320^{b}	1483^{a}	0^{b}	0.42^{a}	2.84^{a}	0.00^{a}
Tamale	0.03^{a}	0.00^{a}	0.20^{a}	149^{b}	1179^{a}	32^{b}	0.28^{a}	1.40^{a}	0.04^{a}
Sadore	0.12^{a}	0.13^{a}	0.23^{a}	256^{a}	181^{a}	0^{a}	0.23^{a}	0.21^{a}	0.00^{a}
Farakoba	0.13^{b}	0.75^{a}	0.00^{b}	59^{a}	693^{a}	160^{a}	0.05^{a}	0.90^{a}	0.10^{a}
Saria I	0.27^{a}	0.00^{a}	0.00^{a}	112^{a}	0^{a}	0^{a}	0.41^{a}	0.00^{a}	0.00^{a}
Saria II	0.27^{a}	0.27^{a}	0.00^{a}	112^{a}	256^{a}	0^{a}	0.41^{a}	0.26^{a}	0.00^{a}
Saria III	0.27^{a}	0.00^{a}	0.02^{b}	112^{a}	11^{a}	112^{a}	0.41^{a}	0.06^{a}	0.36^{a}
Mean	**0.22**^{a}	**0.17**^{a}	**0.06**^{b}	**306**^{a}	**462**^{a}	**297**^{a}	**1.31**^{a}	**1.30**^{a}	**0.78**^{a}
SV	df	F-ratio	P-value	df	F-ratio	P-value	df	F-ratio	P-value
Site	11	1.57	0.126	11	2.74	0.005	11	2.32	0.017
Treatment	2	6.39	0.003	2	2.54	0.086	2	1.41	0.250
Site*treat	22	2.31	0.004	22	2.35	0.004	22	1.95	0.019
Residual	70			70			70		

Means followed by the same lower case letters within rows across treatments are not statistically significant at $p < 0.05$.

Correlation analysis

Higher multicollinearity was observed in the fallow compared to the arable systems (Table 6). The quantity of total macroaggregates was significantly positively correlated with precipitation (r = 0.86 under fallow versus 0.84 under arable), total N and total C (r = 0.90 under fallow vs 0.94 under arable), amount of clay (r = 0.86 under fallow vs 0.81 under arable), earthworm diversity (r = 0.36 under fallow), earthworm abundance (r = 0.53 under fallow), and termite biomass (r = 0.26 under arable). The quantity of total macroaggregates was significantly negatively correlated with average temperature (r = −0.80 under fallow vs −0.79 under arable), sand (r = −0.86 under fallow vs −0.79 under arable) and earthworm biomass (r = −0.25 under arable). No significant correlations were observed between termite diversity and abundance and total macroaggregates under both systems (Table 6). Similar results to those for total macroaggregates were observed with mM (Table 6). Macrofauna parameters, such as earthworm diversity and abundance, were more highly correlated with mM under fallow than under arable cropping. Whereas precipitation, total C and N correlated more highly with mM under arable cropping than under fallow, a reverse trend was observed with amount of clay. The quantity of mM positively correlated with precipitation (r = 0.68 under fallow vs 0.71 under arable), total C (r = 0.86 under fallow vs 0.94 under arable), total N (r = 0.86 under fallow vs 0.95 under arable), and amount of clay (r = 0.87 under fallow vs 0.79 under arable) and termite biomass (r = 0.26 under arable). The quantity of mM was significantly negatively correlated with average temperature (r = −0.80 under fallow and arable) and sand (r = −0.87 under fallow vs 0.80 under arable) (Table 6).

Table 6. Correlation matrix (Pearson) between selected variables measured on soil samples (0-15, 15-30cm) in fallow and arable systems of East and West Africa. Values in bold* are significantly different from 0 with a significance level alpha = 0.05; TH = termite Shannon index; EH = earthworm Shannon index; TN = termite abundance, EN = earthworm abundance, TB = termite biomass, EB = earthworm biomass, AT = average temperature, PPT = precipitation, TOC = total soil C, TON = total soil N, TM = total macroaggregate (sand corrected); mM = microaggregate within macroaggregate (sand corrected)

Variables	TH	EH	TN	EN	TB	EB	AT	PPT	TOC	TON	clay	Sand
							Fallow system (n = 36)					
EH	−0.23											
TN	**0.41**	−0.05										
EN	−0.28	**0.40**	−0.10									
TB	**0.41**	−0.05	**0.56**	0.13								
EB	−0.16	**0.49**	**−0.37**	0.03	**−0.37**							
AT	0.02	**−0.41**	−0.28	**−0.55**	**−0.41**	0.19						
PPT	0.04	0.33	0.31	**0.33**	0.23	0.04	**−0.59**					
TOC	−0.08	**0.35**	0.21	**0.62**	0.26	−0.23	**−0.87**	**0.75**				
TON	−0.06	**0.34**	0.21	**0.61**	0.20	−0.22	**−0.84**	**0.78**	**0.99**			
clay	−0.01	0.32	**0.33**	**0.49**	**0.46**	**−0.33**	**−0.85**	**0.64**	**0.89**	**0.85**		
Sand	0.14	**−0.33**	−0.24	**−0.50**	**−0.34**	0.23	**0.74**	**−0.67**	**−0.83**	**−0.79**	**−0.96**	
TM	0.15	**0.36**	0.25	**0.53**	0.25	−0.14	**−0.80**	**0.86**	**0.90**	**0.90**	**0.86**	**−0.86**
mM	−0.12	**0.33**	0.26	**0.50**	0.18	0.26	**−0.80**	**0.68**	**0.86**	**0.86**	**0.87**	**−0.87**
							Arable system (n = 72)					
EH	0.05											
TN	**0.27**	**0.30**										
EN	0.18	**0.56**	**0.35**									
TB	0.09	**0.29**	**0.77**	**0.35**								
EB	0.07	**0.60**	0.13	**0.60**	0.16							
AT	0.01	−0.01	**−0.33**	−0.20	**−0.33**	0.20						
PPT	−0.13	0.09	0.06	0.01	0.20	−0.17	**−0.59**					
TOC	−0.11	−0.00	0.16	0.10	**0.31**	−0.18	**−0.84**	**0.81**				
TON	−0.11	−0.00	0.15	0.10	**0.30**	−0.18	**−0.82**	**0.81**	**1.00**			
clay	−0.19	−0.16	0.16	−0.07	0.23	**−0.25**	**−0.84**	**0.62**	**0.87**	**0.85**		
Sand	0.21	0.17	-0.11	0.06	-0.21	0.20	**0.77**	**−0.65**	**−0.86**	**−0.84**	**−0.95**	
TM	−0.12	−0.05	0.14	0.01	**0.26**	**−0.25**	**−0.79**	**0.84**	**0.94**	**0.94**	**0.81**	**−0.79**
mM	0.13	−0.06	0.09	0.08	**0.26**	−0.20	**−0.80**	**0.71**	**0.94**	**1.00**	**0.79**	**−0.80**

Factor analyses

Lack of split loading between the identified factors indicated low redundancy among the selected variables (SAS Library, 1995). The factor analysis (using Kaiser-Guttman rule) produced two factors (with factor eigenvalues >1) that explained 63.7% of the total variation in aggregation under fallow, and two factors, that explained 62.4% of total variation under arable systems (Table 7). The first factor under fallow systems was significantly positively related to earthworm diversity (loading coefficient = 0.5) and abundance (0.6), precipitation (0.7), total C and N (1.0 in both cases) and amount of clay (0.9), but negatively related to average temperature and sand (loading coefficients = −0.9 in both cases). The second factor under fallow systems was positively related to termite diversity (0.5), abundance (0.6) and biomass (0.7), but negatively to earthworm biomass (−0.8). The first factor under arable systems was negatively related to average temperature and sand (loading coefficients of −0.9 in both cases), but positively related to precipitation (0.7), total C and N (1.0 in both cases) and clay content (0.9). The second factor under arable systems was related to earthworm diversity and abundance (loading coefficients = 0.7 in both cases), earthworm biomass (0.6), termite abundance (0.8) and biomass (0.6). Under fallow fields, 45.9% of the total sample variation in aggregation was explained by the amount of SOM (total C and N), climate (precipitation), texture (amount of clay) and the earthworm indices, and 17.8% was explained by the termite indices (Table 7). Under arable systems, 42.6% of the total sample variation was explained by the amount of SOM (total C and N), climate (precipitation) and texture (amount of clay) and 20% by both earthworm and termite indices (Table 7).

Multiple regression analysis

Multiple regression analysis indicated that under fallow and arable systems, a greater percentage of the variation in the quantity of aggregation was accounted for by the first factor (Table 7). Under fallow systems, the first factor explained 88.5% for total macroaggregates and 82.6% for mM, while the second factor explained 4.1% for total macroaggregates and 4.9% for mM. Under arable cropping systems, the first factor explained 90.4% for total macroaggregates and 91.3% for mM. The second factor explained 7.6% for total macroaggregates and 8.7% for mM (Table 7). Under the fallow systems, the two factors explained 92.6% for total macroaggregates and 87.5% for mM. Under the arable cropping systems, the two factors explained 98% for total macroaggregates and 100% for mM.

Table 7. Factor pattern analysis for aggregation (total macroaggregation (TM) and percent microaggregate within macroaggregate (mM)) after Varimax rotation. Loading coefficients > 0.5 are in bold face. TH = termite Shannon index, EH = earthworm Shannon index, TN = termite abundance, EN = earthworm abundance, TB=termite biomass, EB = earthworm biomass, AT = average temperature, PPT = precipitation, TOC = total soil C, TON = total soil N

Variable	**Treatment**			
	Fallow system (n=36)		**Arable system (n=72)**	
	Factor I	**Factor II**	**Factor I**	**Factor II**
TH	−0.1	**0.5**	−0.1	0.2
EH	**0.5**	−0.4	−0.1	**0.7**
TN	0.2	**0.6**	0.2	**0.7**
EN	**0.6**	−0.3	0.0	**0.7**
TB	0.3	**0.7**	0.3	**0.6**
EB	−0.1	**−0. 8**	−0.2	**0.6**
AT	**−0.9**	−0.2	**−0.9**	−0.1
PPT	**0.7**	0.1	**0.7**	0.0
TOC	**1.0**	0.1	**1.0**	0.0
TON	**1.0**	0.1	**1.0**	0.0
Clay	**0.9**	0.3	**0.9**	−0.1
Sand	**−0.9**	−0.1	**−0.9**	0.1
Factor eigenvalues	5.6	2.0	5.1	2.4
Explained variance (%)	45.9	17.8	42.6	20.0
Possible attributes	SOM, Texture, Climate, Earthworm (Shannon diversity & abundance)	Termite (Shannon diversity, abundance & biomass)	SOM, Texture, Climate	Termite (abundance & biomass), Earthworm (Shannon diversity, abundance and biomass)
Multiple regression analysis with aggregate fractions and factors with loading coefficients >0.05 (%variance accounted for by factors)				
TM (sand corrected)	88.5	4.1	90.4	7.6
mM	82.6	4.9	91.3	8.7

Discussion

In this study, we aimed to investigate the interrelationship between soil properties, soil fauna and the degree of soil aggregation (i.e. total macroaggregates and percent mM). We specifically measured soil aggregation and the variables presumed to influence aggregation under fallow and arable systems. Significant amounts of multicollinearity were noted among the selected variables. As rightly pointed out by De Gryze et al. (2007), these factors are often strongly inter-correlated, making it difficult to separate different driving mechanisms for macroaggregation. Therefore, we used factor analysis to understand the underlying mechanisms in aggregation in each of the two systems. This method ensures that the factors relating to aggregation are uncorrelated and independent (SAS Library, 1995; De Gryze et al., 2007).

Factor analysis detected two factors under fallow systems and also two under arable systems. Under fallow systems, factor I selected clayey soils in relatively wet and cool climates with high SOM, where earthworms thrive and aggregation is high, whereas factor II selected soils with high termite influence. Therefore, both factors indicate the importance of soil macrofauna for aggregation, but termites clearly come in as a secondary factor. Under arable systems, factor I also selects the soils in relatively wet and cool climates with high SOM and clay content, but the primary role of earthworms in aggregation is nullified, probably due to cultivation. Consequently, this study demonstrates that macrofauna explain a large amount of variability associated with aggregation. Hence, their activities are important drivers of stable macroaggregation, in conjunction with climatic conditions, SOM and texture, and these factors are all interrelated. However, their degree of influence depends on soil management (Fonte et al., 2007). Management practices such as tillage, organic matter amendments and crop rotation influence soil structural stability (Haynes et al., 1991; Ramani et al., 1997; Picollo et al., 1997). The role of macrofauna, especially earthworms and to a small extent termite was more pronounced in the fallow fields compared to the arable systems. Fallow systems represent relatively undisturbed conditions with permanent soil cover, in which mechanical soil disturbance is minimal and organic matter accumulation is relatively high. These conditions, in addition to the cool and moist climate are suitable for macrofauna activities. Hence, they contribute to the significant positive correlations with indices of aggregation. Although earthworms and termites affect aggregation positively in arable systems, they do so only as secondary factors. Activities in arable systems are influenced by variations in soil disturbance and the quantity of organic inputs or by the heterogeneous nature of soil management typical of most of the sites we studied. As such, lower macrofauna influence in arable systems could be linked to soil disturbance and corresponding lower food supply. Soil tillage indirectly affects soil aggregate stability, mainly through its influence on soil fauna, soil moisture, and on the redistribution of SOM (Tisdall and Oades, 1982). Tillage breaks down aggregates and also exposes organic matter to microbial attack, thus stimulating oxidation and loss of labile organic matter which binds microaggregates into macroaggregates (Kushwaha et al., 2001). Our results compare well with earlier studies, in which it was reported that the quantity of water stable macroaggregates positively correlated with macrofauna activities (Scullion and Malik, 2000; Pulleman et al., 2005b) and/or organic matter content (Tisdall and Oades, 1982; Chaney and Swift, 1984; Mbagwu and Picollo, 1989; Boix-Fayos et al., 2001), and amount of clay, but negatively correlated with sand content (De Gryze et al., 2006). Macrofauna (e.g. earthworms and termites), may stabilize soil structure by ingesting soil and mixing it with humified organic materials in their guts, and egesting it as casts or pellets (Blanchart et al., 2004; Bossuyt et al., 2005; Jouquet et al. 2007).

In general, increased earthworm populations and activities have been positively linked to greater aggregate stability and organic matter within aggregates (Ketterings et al., 1997; Marinissen and Hillenaar, 1997; Coq et al., 2007; Fonte et al., 2009). Gilot-Villenave et al. (1996) observed that activity of endogeic worms (e.g. *Millsonia anomala*) significantly modified the structure of the soil by increasing the proportion of large aggregates (over 2 mm in diameter). Blanchart et al. (1997), also found that *M. anomala* was responsible for the formation of macroaggregates >5.0 mm, whereas eudrilid (epigeic) earthworms egested smaller aggregates (0.5–5 mm). In our study, the sampled earthworm taxa were epigeic and endogeic and could, hence, have positively contributed to the formation of water stable aggregates. Other studies have, however, shown that some compacting species like *Pontoscolex corethrurus* modify the hydrology and functioning of soils by excreting wet casts that form compacted layers impermeable to air and water (Chauvel et al., 1999; Hallaire et al., 2000).

Termites influence soil aggregation by mixing organic polymers with inorganic soil particles, thereby modifying the physical properties of soil. Although a higher percent of water stable aggregates have been recorded in termite-inhabited compared to termite free soils (Lobry de Bruyn and Conacher, 1990), overall aggregate stabilities produced differ between termite species (Garnier-Sillam and Harry, 1995) and could also depend on the biology of the particular trophic groups

(Garnier-Sillam, 1989). Generally, termite species (e.g. *Noditermes lamanianus*) that build nests enriched with organic matter and increased exchangeable cations, result in high structural stability, and humivorous termites are reported to be more effective than fungus-growing termites (Garnier-Sillam, 1989; Garnier-Sillam and Harry, 1995). Most of the termite taxa sampled in our study sites were fungal growers and typically foragers of wood, litter, dry grass, and dung/manure. Very few soil feeders were found at our sites, resulting in less of a role of these termites in aggregation. Termites were consequently less important in explaining the variation in aggregation in both the fallow and arable systems.

Our study also showed that SOM (total C and N) and texture (clay) positively correlated with aggregation. However, in aggregate formation, SOM does not act in isolation, but in association with soil texture (Chaney and Swift, 1984). Most of the West African sites we sampled were dominated by coarse-textured sandy soils that were low in SOM. Aggregation was consequently low in these sites, especially compared to East African sites that were dominated by clay soils with relatively high SOM, thus high aggregation in the latter sites could be due to influence of oxides (e.g. iron and aluminium oxides) (Goldberg et al., 1990).

Conclusions

Our study has shown that macrofauna, especially earthworms, and to a smaller extent termites, are important drivers of stable soil aggregation, in conjunction with climate, soil organic C content and soil texture in sub-Saharan agroecosystems. However, the beneficial impact of earthworms and termites on soil aggregation is reduced with increasing management intensity and associated soil disturbance due to cultivation. We suggest that this knowledge is important in designing agricultural management systems aimed at increasing long-term soil fertility in sub-Saharan Africa.

Acknowledgements

This study was supported by Science for Global Development/WOTRO through Wageningen University and Norman Borlaug LEAP Fellowship Program through UC-Davis. We thank our partners, especially the scientists and field technicians of the Tropical Soil Biology and Fertility Institute of the International Centre for Tropical Agriculture (TSBF-CIAT, Kenya), Kenya Agricultural Research Institute (KARI), Kenya Forestry Research Institute (KEFRI), Kenyatta University, Kenya, International Institute of Tropical Agriculture (IITA, Nigeria), International Fertilizer Development Centre (IFDC, Burkina Faso), Institute of Natural Environmental and Agricultural Research (INERA, Burkina Faso), Savanna Agricultural Research Institute (SARI, Ghana), Chitedze Agricultural Research Station (Malawi), International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, Niger) and Natural History Museums (Hungary), who agreed to work with us and have allowed us to use their experimental sites for this study. We sincerely thank David Lelei and Zida Zacharie who helped with laboratory extraction of aggregate fractions.

CHAPTER FOUR

Soil fertility management and soil macrofauna: impacts on soil aggregation and soil organic matter allocation

F.O. Ayuke [a*, b], L. Brussaard [a], B. Vanlauwe [b], J. Six [c], D.K, Lelei [d], M.M. Pulleman [a],

[a] *Department of Soil Quality, Wageningen University, P.O Box 47, NL-6700 AA Wageningen, The Netherlands*

[b] *Tropical Soil Biology and Fertility (TSBF) Institute of CIAT, P.O Box 30677-00100, Nairobi, Kenya*

[c] *Department of Plant Sciences, University of California, Davis, CA 95616, USA*

[d] *Department of Land Resource Management and Agricultural Technology, University of Nairobi, P.O Box 30197, Nairobi, Kenya*

*Corresponding author: (0317) 486524; Fax: (0317) 419000

Email: fredrick.Ayuke@wur.nl or fredrick.ayuke@yahoo.com*

Submitted to Applied Soil Ecology

Abstract

Maintenance of soil organic matter (SOM) through integrated soil fertility management is important for soil quality and agricultural productivity, and for the persistence of soil faunal diversity, abundance and biomass. In turn, soil macrofauna affects SOM dynamics through organic matter incorporation, decomposition and the formation of stable aggregates that protect organic matter against rapid decomposition. Little is known about the interactive effects of soil fertility management and soil macrofauna diversity on soil aggregation and SOM dynamics in arable cropping systems. A study was conducted in a long-term trial on a Nitisol at Kabete, Central Kenya, to investigate to what extent the single and combined effects of organic inputs (maize stover or manure) and inorganic fertilizers influence soil macrofauna abundance, biomass and diversity, water stable aggregation, whole soil and aggregate-associated organic C and N, as well as the relations between these variables. Differently managed arable systems were compared to a long-term green fallow system representing a relatively undisturbed reference. Fallowing, and application of manure in combination with fertilizer, significantly enhanced earthworm diversity and biomass as well as aggregate stability and C and N pools in the top 15 cm of the soil. Earthworm abundance significantly negatively correlated with the percentage of total macroaggregates, but all earthworm parameters positively correlated with whole soil and aggregate associated C and N, unlike termite parameters. Factor analysis showed that 31.7% of the total sample variation in aggregation and C and N in total soil and aggregate fractions was explained by earthworm parameters, and 25.6% by termite parameters. Multiple regression analysis confirmed this outcome. Overall, our results indicate that fallowing and long-term application of manure in combination with fertilizer result in higher earthworm Shannon diversity and biomass, which leads to improved soil aggregation and enhanced C and N stabilization within this more stable soil structure. These practices therefore result in the dual benefits of improving soil physical and chemical properties. The negative correlation between earthworm abundance and total macroaggregates could be linked to the dominant presence of high numbers of Nematogenia lacuum in the arable treatments without organic fertilizer amendments, an endogeic species that feeds on excrements of other larger epigeic worms and produces small excrements, thus reducing the mean aggregate size. Under the conditions studied, differences in earthworm abundance, biomass and diversity were more important drivers of management-induced changes in aggregate stability and soil C and N pools than differences in termite populations.

Key words: Earthworms, termites, Shannon diversity, soil organic matter, carbon, nitrogen, soil aggregate fractions.

Introduction

In large parts of sub-Saharan Africa, the challenge of increasing crop yields to sustain the growing population is persistent. Decomposing plant residues are a major source of plant nutrients in soils with little inherent mineral fertility. In many cropping systems of Africa, organic matter is periodically returned to the soil either as litter, crop residues or as animal waste products, but the amounts and qualities differ (Karanja et al., 2006; Chivenge et al., 2009). Although such practices can enhance soil fertility or promote soil rehabilitation, organic resources alone often provide insufficient nutrients to build or maintain the long-term soil nutrient resource base (Palm et al., 2001). Integrated soil fertility management (ISFM), widely advocated in sub-Saharan Africa, recognizes the benefits of combining organic and inorganic fertilizers for sustainable nutrient management (Chivenge et al., 2009; Gentile et al., 2009; Vanlauwe et al., 2009). The beneficial effect of soil organic matter (SOM) on soil productivity through supplying plant nutrients, enhancing cation exchange capacity, improving soil aggregation and soil and water retention is well established (Six et al., 2000; Mikha and Rice, 2004; Coq et al., 2007). In addition, SOM supports various soil biological processes by being a substrate for decomposer organisms and ecosystem engineers, such as earthworms and termites, that play an important role in soil structure formation, organic matter decomposition and nutrient mineralization (Swift and Woomer, 1992; Dudal and Deckers, 1993).

Aggregate stability is a key factor for physical soil fertility and also affects SOM dynamics (Abiven et al., 2009; Six et al., 2000). Resistance of aggregates to physical stresses inversely relates to the soil’s sensitivity to crusting and erosion (Le Bissonais, 1996; Blanchart et al., 1999), positively affects seed germination and rooting of crops (Angers and Caron, 1998) and water infiltration (Le Bissonais, 1996), and determines the ability of a soil to store SOM through physical protection against rapid decomposition (Bossuyt et al., 2005). Among the soil properties influencing aggregate stability are texture, clay mineralogy, cation content, aluminium and iron oxides, SOM and soil fauna (Amézketa, 1999; Six et al., 2004). Some of these factors (e.g. SOM and soil fauna) are affected by agricultural practices such as tillage, crop rotation, residue management and fertilization regimes (Shiran et al., 2002; Su et al., 2006). In several conceptual models, the increase of aggregate stability after organic additions to the soil has been related to the decomposition dynamics of the inputs (Abiven et al., 2009).

Earthworms are considered ecosystem engineers for their role in modifying the soil environment and availing resources for other organisms (Jouquet, et al., 2006), through their impact on soil structure and soil organic matter (SOM) dynamics (Lavelle et al., 2001). Apart from speeding up initial breakdown of organic residues, they also incorporate organic matter in their casts and can thereby protect it against further rapid decomposition (Scullion and Malik, 2000; Bossuyt et al., 2005; Pulleman et al., 2005a, b). Crop performance can also be affected through the impact of worm-made aggregates and biopores on soil water dynamics and root growth. Termites also make channels in soil and influence soil aggregation by mixing organic matter with soil particles and thereby modify the physical properties of soil (Jouquet et al., 2002). Termites can form stable microaggregates by mixing soil with saliva for nest constructions or, in the case of soil-feeding termites, by excreting faecal pellets that are enriched in organic matter (Jungerius et al., 1999).

Soil aggregates, especially microaggregates (53-250µm) formed within macroaggregates (≥250 um), protect SOM against microbial decay (Tisdall and Oades, 1982; Six et al., 2000). Soil fertility and C stabilization are therefore mediated by the interactions between soil organic matter, soil structure and soil macrofaunal abundance and diversity, which depend on soil management (Six et al., 2004). For example, Pulleman et al (2005a) showed that formation of stable and strongly organic C-enriched microaggregates was reduced under arable systems compared to permanent pasture, probably due to differences in earthworm abundance an/or species composition, the nature (i.e., quality) of organic matter input and mechanical disturbance.

Although stimulation of soil macrofauna activity and diversity through the provision of organic inputs can contribute to improved soil aggregation and C and N retention in soil (Lavelle et al., 2001), so far this role of the soil macrofauna has not been quantified in the context of ISFM. A considerable number of long-term experiments have been conducted in Sub-Saharan Africa since the 1920s, giving insights in soil processes and management practices that control soil fertility (Vanlauwe et al., 2005). However, due to lack of resources, data collection is normally limited to crop yields (Kapkiyai et al., 1999; Kamoni et al., 2007), while little information is available on long-term effects of crop management on soil aggregation, C and N dynamics, and on soil macrofaunal abundance and diversity. It is also not known how different soils, such as tropical Nitisols that are high in iron and aluminum oxides, will respond to either organic or inorganic soil amendments, and how this will in turn affect soil aggregation and C and N dynamics compared to the much studied temperate soils (Elliott, 1986; Jastrow, 1996; Six et al., 1998; Six et al., 2000). It has been shown that such soils are prone to high N losses due to leaching (Gentile et al., 2009). With recent considerable interest in (belowground) biodiversity conservation and ecosystem functioning (CBD, 2001; Clergue et al., 2005), an understanding of these specific interactions and the quantitative effects of each of those management factors in the long term is needed.

This study, therefore, investigates the linkage between management factors (fallowing, organic inputs, and inorganic inputs), soil biodiversity, soil structure and SOM (C and N) dynamics in a long-term (>60 growing seasons) field trial in Central Kenya. Specifically, the study seeked to:

1) Assess the effects of crop management on i) soil aggregation and C and N dynamics, and ii) soil macrofauna parameters (earthworm and termite abundance, biomass and diversity).

2) Explore the relationships between soil aggregation, C and N dynamics, and soil macrofauna parameters.

Materials and Methods

Study site

The study was conducted in a long-term trial based at the National Agricultural Research Laboratories (NARL) in Kabete, located about 7 kilometers Northwest of Nairobi (latitude: 1° 15′ S; longitude: 36° 41′ E) at an altitude of 1740 m above sea level (Siderius and Muchena, 1977). The area receives a mean annual rainfall of 940 mm in two rainy seasons, the ‘long rains’ (March-May) and the ‘short rains’ (mid-October to December). The mean annual temperature ranges between 13 °C and 18 °C. The area falls under ecological zone III (dry sub-humid) with a precipitation to evaporation ratio (P/Eo) of about 56% (Siderius and Muchena, 1977; Jaetzold and Helmut, 1982). The area is underlain by the Limuru Quartz trachytes, an intermediate igneous rock dating back to the early Pleistocene period (Jaetzold and Helmut, 1982). The soil is classified as a Humic Nitisol (FAO) and locally referred to as Kikuyu red clay loam. The soils are well drained, deeply weathered, dark reddish brown to dark red, and with friable structure (Jaetzold and Helmut, 1982).

Experimental design

The long-term field trial was established in 1976. Different combinations of organic and mineral inputs are applied and their effects on arable crop production are compared. In our study, we compared soil properties of the arable treatments with those of a natural fallow. The cropping system consists of a maize-bean rotation, with maize (Zea mays Hybrid 512) being grown during the long rains and beans (Phaseolus vulgaris, variety Rosecoco) during the short rains.

The treatments selected for this study were:

i) Control minus or plus mineral fertilizer (C-F/C+F). No organic inputs are applied.

ii) Maize stover residues, minus or plus mineral fertilizer (R-F/R+F)

iii) Farm yard manure, minus or plus mineral fertilizer (FYM-F/FYM+F)

iv) Natural green fallow (NF).

Mineral fertilizer is applied at 120 kg N ha^{-1} yr^{-1} as Calcium Ammonium Nitrate (CAN) and 52.6 kg P ha^{-1} yr^{-1} as triple superphosphate (TSP). Initially (from 1976-1980), a compound fertilizer 20:20:0 was used as a source of N and P, but this was replaced in 1981 by CAN and TSP (Kamoni et al., 2007). Farm yard (cattle) manure is added at 10 Mg DM ha^{-1} yr^{-1} and incorporated into the soil. The fertilizers and manure are applied once per year to the maize crop only. For the treatments receiving maize residues, maize stover from the preceding crop is incorporated into the soil. Bean residues are removed from the plots, irrespective of treatment.

The treatments are replicated three times in a randomized complete block design with plots of 7 m long by 4.5 m wide. Maize and beans are sown at a spacing of 75 × 25 cm, giving a plant population of 50,000 ha−1. All the plots are tilled by hand hoeing since the inception of the experiment in 1976. The fallow constitutes a nearby shrubland that has not been tilled since the start of the trial.

Soil sampling, pretreatment and analysis

(a) Macrofauna sampling

One soil monolith sample (25 × 25 × 30 cm) per plot (n = 3) was taken in May 2007, 8 weeks after planting, and separated into two depth layers (0-15 and 15-30 cm). The extracted soil was hand-sorted for macrofauna . Termite specimens were preserved in 75% alcohol and earthworms in 75% alcohol + 4% formaldehyde before being transported in sealed vials to the laboratory for identification, enumeration and biomass determination (Bignell et al., 2008). Earthworm and termite parameters, including abundance (numbers of individuals per unit area), biomass (fresh weight per unit area) and Shannon diversity were calculated for 0-30 cm depth because fauna are mobile. The Shannon-Wiener (SW) diversity index (H′) was calculated as H′ = – ∑ (pi ln pi), where pi is the proportion of the ith taxonomic group, estimated as ni/N; where ni is the number of individuals of the ith species and N the total number of individuals within the sample (Magurran, 1988).

(b) Wet sieving

Immediately after sampling, a representative subsample (about 500 g) of the 0-15 and 15-30 cm depth layers of the monolith was gently passed through a 10 mm sieve by breaking up the soil along natural planes of weakness, air-dried and stored at room temperature. The soil was then separated into four fractions using the method described by Elliott (1986): (i) large macroaggregates (LM; ≥2000 µm), (ii) small macroaggregates (SM; 250 -2000 µm), (iii) microaggregates (m; 53–250 µm), and (iv) silt + clay sized particles (sc; ≤53 µm). Briefly, 80 g of air-dried soil was transferred to a 2 mm sieve, placed in a recipient filled with deionized water, and left to slake (Figure 1). After 5 minutes, the 2 mm sieve was manually moved up and down 50 times in 2 minutes. The procedure was repeated using the material that passed through the 2 mm sieve, using a 250 µm sieve and subsequently a 53 µm sieve. A representative 250 ml subsample was taken from the suspension containing the ≤53 µm silt and clay sized particles to determine the weight of the smallest fraction. Soil aggregates retained on each sieve were backwashed into pre-weighed containers and, together with the 250 ml subsample of the finest fraction, oven-dried at 60 °C over-night and weighed.

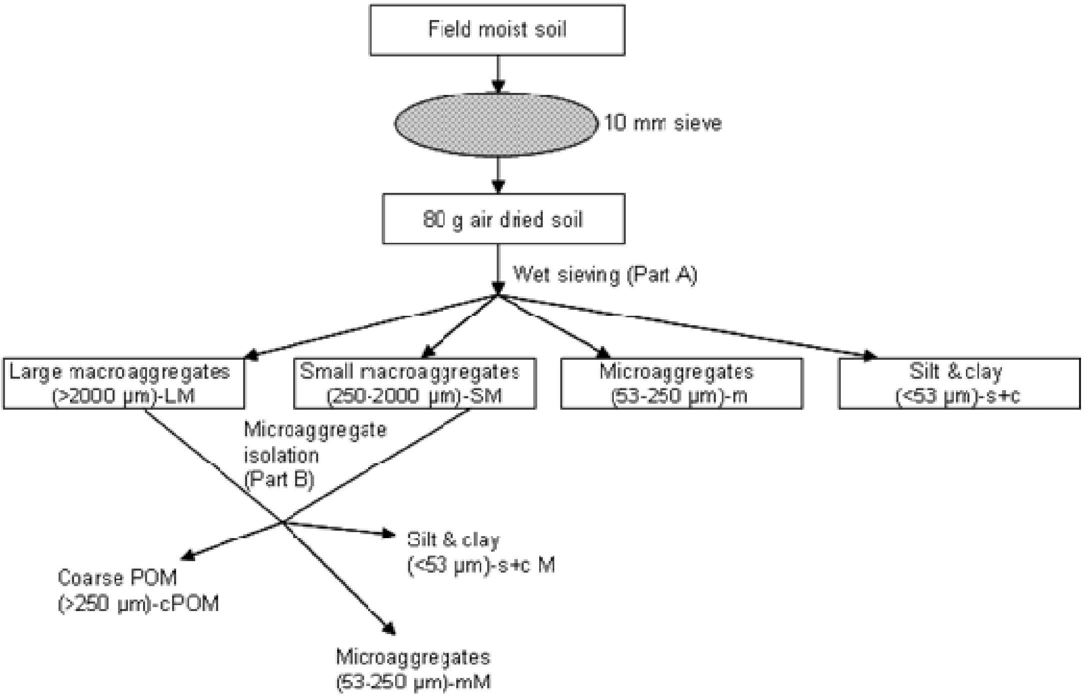

Figure 1. Fractionation scheme to separate differently sized aggregate and particulate organic matter (POM) fractions (Adapted from Six et al (2000)

(c) Macro-aggregate fractionation

After oven drying and weighing, the large and small macroaggregate fractions were combined according to their relative weight/proportion and used for the isolation of i) coarse POM + sand (cPOM; ≥250 µm), ii) microaggregates within macroaggregates (mM; 53-250 µm), and iii) silt and clay (scM; ≤53 µm). These three fractions were isolated using a device described by Six et al. (2000) which completely breaks up macroaggregates with minimal disruption of microaggregates. About 5 g of the oven-dried macroaggregates were pre-slaked overnight in 50 ml of deionized water at 4° C in order to slake the rather stable macroaggregates of the Kabete soil (Gentile et al., in press). The macroaggregates were then transferred to the device holding a 250 µm mesh screen and shaken with 50 glass beads (diameter 4 mm) until all macroaggregates were broken up. The microaggregates released were immediately flushed through the 250 µm sieve and deposited onto a 53-µm sieve by a continuous flow of deionized water through the device. The material on the 53 µm sieve was then wet-sieved as described above, 50 times in 2 minutes, to separate the stable microaggregates (mM) from the silt and clay (Figure 1). Once all the macroaggregates were broken up, all fractions retained on the 250 µm mesh screen, and silt and clay were backwashed into a pre-weighed container. All fractions were oven-dried at 60 °C for 48 hours, weighed and stored for C and N analysis.

(d) Soil C and N analysis

For measurement of soil organic C and N content, about 30 mg of the whole soil samples (before fractionation) and the aggregate fractions, and about 10 mg of the coarse sand + POM fraction were microbalanced in aluminium tin capsules, placed into capsule trays and sent to University of California at Davis for C and N analyses with a PDZ Europa Integra C-N isotope ratio mass spectrometer (Cheshire, United Kingdom).

Data analysis

We combined the LM with the SM to obtain total macroaagregates (TM), because the amount of LM was < 1% of the whole soil weight. Data on aggregate fractions and C and N (0-15 and 15-30 cm depth) and soil macrofauna parameters (Shannon-Wiener index, abundance and fresh weight; 0-30 cm depth) were subjected to analysis of variance (ANOVA) using SPSS (Kirkpatrick and Feeney, 2005). In case of the aggregate and C and N data, the two depth layers were analyzed independently. Levene's test was used to test for homogeneity of variances. In case of non-homogeneity of variances, data were log transformed (x + 1) before further analysis. The effect of the management factors organic fertilizer (none, maize residue, FYM) and mineral fertilizer (+/-) and their interactions were analyzed through two-way ANOVA. To analyse the effects at the management system level (including the fallow) one-way ANOVA was performed, where treatment constituted the independent factor. The statistical significance was determined at $P = 0.05$, and levels of significance among the different treatments (including the fallow) were evaluated using Tukey's Post Hoc Multiple comparisons test.

Multivariate statistics was conducted using XLSTAT (XLSTAT, 2009). We used correlation analysis (Pearson correlations) to establish the relationships between soil macrofauna, soil aggregation, and C and N contents. Because of multicollinearity among the variables, we employed factor analysis to obtain orthogonal and standardized variables using the factor procedures of SAS (SAS, 1995). Initial estimates of the factors were made on principal components using the Kaiser-Guttman rule, such that those factors with eigenvalues (variance) >1 were retained and rotated using varimax procedure. Using a rule of thumb as recommended by SAS (1995), factors that had loadings >0.5 in absolute value were considered significant. They were subsequently used in multiple regression to test their influence in explaining processes of aggregation, C and N stabilization in whole soil and in aggregate fractions.

Results

Water-stable aggregation

Between 85 and 90% of the soil was found in the TM and m aggregate fractions. In the layer 0-15 cm, the percentage of TM was significantly affected by organic fertilizer amendment and the interaction between organic fertilizer amendment and mineral fertilizer. This was expressed in the higher percentage of TM (45 g $100g^{-1}$) in FYM+F compared to all other arable treatments which did not differ significantly from each other (with average weight ranging between 31 and 38 g

$100g^{-1}$). A significantly higher value of TM was found in NF (55 g $100g^{-1}$) than in all arable treatments. Since the TM and the m and sc fractions are inversely related the reverse trends were found for the weight (%) of these two fractions. The amount of mM was also inversely related to the amount of TM and this fraction was negatively affected by organic fertilizer amendment. FYM+F had lower amounts of mM (1.6 g $100g^{-1}$) compared to C-F, C+F, R-F and R+F for which the amount of mM ranged between 2.1 and 2.4 g $100g^{-1}$. A significantly lower value of mM (1.4 g $100g^{-1}$) and cPOM + sand (0.1 g $100g^{-1}$) were found in NF. Percentages of scM did not differ significantly among the treatments (Table 1).

In the layer 15-30 cm, a significantly higher amount of m was observed in R+F (45.8 g $100g^{-1}$) than in R−F (28.1 g $100g^{-1}$) (Table 1). The weight (%) of the other fractions did not significantly differ among the treatments (Table 1).

The C content in whole soil and in fractions

In the layer 0-15 cm, the C content of the TM-fraction was affected by organic fertilizer amendment and was significantly higher (22 g kg^{-1} fraction) in FYM+F than in C−F, C+F and R-F (Table 2). In the layer 15-30 cm, the C content of most fractions (m, sc, mM, cPOM + sand and scM) did not differ significantly among the treatments. Although generally not significantly so, natural fallow had higher C contents in WS, and all fractions except for one, than arable treatments at both 0-15 and 15-30 cm depths (Table 2).

Table 1. Aggregate fractions as affected by management in the Kabete field trial, Kenya.

			--**Aggregate fraction (g 100 g^{-1} total soil)**--					
Depth (0-15 cm)								
Treatment	**Organic fertilizer (OF)**	**Mineral fertilizer (MF)**	**TM** (≥250 µm)	**m** (53-250 µm)	**sc** (≤ 53 µm)	**mM** (53-250 µm)	**cPOM + sand** (≥250 µm)	**scM** (≤ 53 µm)
C−F	None	−	34.19 (2.14)^{c}	51.19 (1.85)^{a}	14.61 (1.12)^{a}	2.19 (0.17)^{a}	0.37 (0.09)^{a}	0.38 (0.05)
C+F	None	+	30.67 (1.27)^{c}	55.86 (1.29)^{a}	13.47 (0.09)^{ab}	2.42 (0.15)^{a}	0.40 (0.01)^{a}	0.47 (0.05)
R−F	Residue	−	37.06 (1.80)^{c}	51.11 (1.01)^{a}	11.84 (1.28)^{ab}	2.16 (0.12)^{a}	0.31 (0.02)^{a}	0.25 (0.01)
R+F	Residue	+	35.29 (1.31)^{c}	53.41 (0.64)^{a}	11.32 (0.74)^{ab}	2.13 (0.08)^{a}	0.34 (0.02)^{a}	0.38 (0.04)
FYM−F	Manure	−	38.25 (2.70)^{c}	51.46 (2.08)^{a}	10.30 (0.76)^{b}	1.93 (0.12)^{ab}	0.33 (0.02)^{a}	0.38 (0.05)
FYM+F	Manure	+	45.04 (0.86)^{b}	45.13 (0.31)^{b}	9.83 (0.56)^{b}	1.61 (0.02)^{bc}	0.27 (0.04)^{ab}	0.33 (0.01)
NF	na	na	55.19 (0.38)^{a}	39.00 (0.26)^{c}	5.81 (0.42)^{c}	1.42 (0.01)^{c}	0.13 (0.01)^{b}	0.26 (0.00)
P-value								
One-way ANOVA (including NF)			**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	0.214
Two-way ANOVA (excluding NF)								
Organic fertilizer (OF)			**0.001**	**0.006**	**0.002**	**0.002**	0.148	0.273
Mineral fertilizer (MF)			0.737	0.849	0.328	0.715	0.992	0.301
OF × MF			**0.030**	**0.004**	0.908	0.114	0.405	0.374
Depth (15-30 cm)								
C−F	None	−	56.92 (9.27)	35.45 (7.11)^{ab}	7.63 (2.16)	1.41 (0.24)	0.13 (0.04)	0.33 (0.05)
C+F	None	+	52.21 (0.44)	41.12 (0.40)^{ab}	6.66 (0.50)	1.48 (0.03)	0.15 (0.03)	0.29 (0.03)
R−F	Residue	−	66.83 (0.64)	28.11 (0.75)^{b}	5.06 (0.12)	1.13 (0.02)	0.16 (0.01)	0.20 (0.02)
R+F	Residue	+	45.47 (7.13)	45.84 (5.35)^{a}	8.68 (1.81)	1.84 (0.30)	0.16 (0.03)	0.33 (0.06)
FYM−F	Manure	−	64.10 (0.44)	30.86 (0.27)^{ab}	5.04 (0.43)	1.38 (0.10)	0.13 (0.05)	0.20 (0.00)
FYM+F	Manure	+	64.09 (0.70)	30.56 (0.92)^{ab}	5.35 (0.68)	1.19 (0.08)	0.13 (0.04)	0.23 (0.03)
NF	na	na	64.60 (0.84)	30.68 (0.91)^{ab}	4.72 (0.26)	1.24 (0.03)	0.10 (0.01)	0.22 (0.01)
P-value								
One-way ANOVA (including NF)			0.065	**0.021**	0.164	0.087	0.763	0.434
Two-way ANOVA (excluding NF)								
Organic fertilizer (OF)			0.146	0.130	0.258	0.466	0.674	0.356
Mineral fertilizer (MF)			0.084	**0.025**	0.338	0.170	0.896	0.416
OF × MF			0.130	0.081	0.191	0.054	0.964	0.400

Within columns, means followed by the same lower case letters in superscript are not statistically significantly different at $p < 0.05$. Values in parentheses are standard errors. TM = total macroaggregates, m = microaggregates, sc = silt and clay, mM = microaggregates within macroaggregates, cPOM = coarse particulate organic matter, scM = silt and clay within macroaggregates. C-F = control minus fertilizer, C+F = control plus fertilizer, R-F = residue minus fertilizer, R+F = residue plus fertilizer, FYM-F = farm yard manure minus fertilizer, FYM+F = farm yard manure plus fertilizer, NF = natural fallow, n.a = not applicable.

Table 2. The C contents in whole soil and in fractions as affected by management in the Kabete field trial, Kenya.

Depth (0-15 cm)			-------------------------------Whole soil (g kg^{-1} soil) and aggregate fraction C (g kg^{-1} fraction) -----------------------------------						
Treatment	**Organic fertilizer (OF)**	**Mineral fertilizer (MF)**	**WS**	**TM**	**m**	**sc**	**mM**	**cPOM + sand**	**scM**
C−F	None	−	17.68 (0.87)^{b}	17.88 (1.17)^{c}	17.47 (1.17)^{b}	20.56 (1.20)	17.48 (0.79)^{bc}	10.99 (1.06)^{b}	27.62 (0.70)
C+F	None	+	17.62 (1.49)^{b}	16.98 (0.72)^{c}	16.93 (0.71)^{b}	19.18 (0.90)	16.95 (1.53)^{bc}	12.65 (3.49)^{ab}	25.40 (1.52)
R−F	Residue	−	17.31 (1.02)^{b}	16.98 (0.77)^{c}	16.94 (0.61)^{b}	19.63 (0.86)	14.96 (1.68)^{c}	15.73 (4.32)^{ab}	34.71 (9.24)
R+F	Residue	+	19.09 (0.90)^{ab}	19.57 (0.37)^{bc}	19.37 (0.90)^{ab}	23.40 (2.64)	18.90 (0.69)^{abc}	12.34 (5.32)^{ab}	31.58 (0.85)
FYM−F	Manure	−	19.38 (1.01)^{ab}	19.92 (0.67)^{bc}	19.01 (1.77)^{ab}	21.37 (1.68)	19.70 (1.10)^{abc}	14.80 (1.52)^{ab}	31.42 (5.34)
FYM+F	Manure	+	21.90 (1.09)^{ab}	22.05 (0.95)^{ab}	21.50 (0.53)^{ab}	23.17 (0.24)	21.46 (1.27)^{ab}	13.44 (1.33)^{ab}	33.61 (1.84)
NF	na	na	23.71 (0.97)^{a}	24.25 (1.28)^{a}	22.41 (0.86)^{a}	24.81 (1.15)	23.09 (1.04)^{a}	28.78 (5.02)^{a}	32.14 (2.68)
P-value									
One-way ANOVA (including NF)			**0.005**	**<0.001**	**0.008**	0.105	**0.005**	**0.050**	0.731
Two-way ANOVA (excluding NF):									
Organic fertilizer (OF)			**0.038**	**0.002**	**0.035**	0.283	**0.021**	0.735	0.278
Mineral fertilizer (MF)			0.135	0.080	0.111	0.264	0.112	0.707	0.779
OF × MF			0.492	0.106	0.288	0.247	0.231	0.746	0.778
Depth (15-30 cm)									
C−F	None	−	16.18 (0.19)	15.81 (0.42)^{b}	15.00 (0.38)	19.84 (1.04)	15.81 (0.33)	16.26 (2.64)	24.67 (0.21)
C+F	None	+	14.39 (2.27)	14.84 (1.93)^{b}	14.66 (1.59)	16.54 (1.79)	14.42 (2.16)	7.73 (1.65)	28.52 (9.96)
R−F	Residue	−	14.62 (1.68)	14.89 (1.41)^{b}	14.90 (1.38)	17.59 (0.81)	15.91 (0.42)	13.48 (5.06)	24.75 (3.80)
R+F	Residue	+	16.18 (2.48)	15.46 (0.79)^{b}	15.04 (0.77)	13.95 (2.93)	14.48 (1.35)	10.40 (1.01)	25.74 (3.27)
FYM−F	Manure	−	15.44 (1.67)	15.40 (1.65)^{b}	15.02 (1.46)	19.42 (3.12)	14.91 (1.59)	12.95 (3.49)	28.08 (7.43)
FYM+F	Manure	+	17.21 (1.51)	17.45 (1.48)^{ab}	16.84 (1.55)	20.15 (1.59)	16.56 (1.43)	10.48 (4.67)	25.59 (0.21)
NF	na	na	20.82 (1.01)	21.87 (1.27)^{a}	19.92 (1.08)	21.95 (0.90)	20.82 (1.05)	18.25 (2.21)	30.27 (4.22)
P-value									
One-way ANOVA (including NF)			0.209	**0.028**	0.088	0.157	0.055	0.351	0.982
Two-way ANOVA (excluding NF):									
Organic fertilizer (OF)			0.818	0.624	0.652	0.191	0.888	0.996	0.952
Mineral fertilizer (MF)			0.731	0.635	0.611	0.245	0.734	0.119	0.865
OF × MF			0.553	0.564	0.681	0.522	0.463	0.633	0.848

Within columns, means followed by the same lower case letters in superscript are not statistically significantly different at $p < 0.05$. Values in parentheses are standard errors. WS = whole soil, TM = total macroaggregates **(≥250 µm)**, m = microaggregates **(53-250 µm)**, sc = silt and clay **(≤53 µm)**, mM = microaggregates within macroaggregates **(53-250 µm),** cPOM = coarse particulate organic matter **(≥250 µm)**, scM = silt and clay within macroaggregates **(≤ 53 µm)**. C-F = control minus fertilizer, C+F = control plus fertilizer, R-F = residue minus fertilizer, R+F = residue plus fertilizer, FYM-F = farm yard manure minus fertilizer, FYM+F = farm yard manure plus fertilizer, NF = natural fallow, n.a = not applicable.

The N content in whole soil and in fractions

In the layer 0-15 cm, WS and TM-fraction N were significantly affected by organic fertilizer amendment. This was expressed in higher N content in FYM+F than in C-F, C+F and R-F (Table 3). The scM-fraction N was significantly affected by organic fertilizer amendment and the interaction between organic fertilizer amendment and mineral fertilizer. This was expressed in the higher N content (3 g kg−1 fraction) in R+F than in R-F (2 g kg−1 fraction). Although not statistically significant, natural fallow had higher N contents in WS and all but two of the fractions than arable treatments at both 0-15 and 15-30 cm depths (Table 3). In the layer 15-30 cm, N content in cPOM + sand and scM did not significantly differ among the treatments (Table 3).

Taxonomic richness and functional groups

In total, 6 earthworm species belonging to three families (Ocnerodrilidae, Acanthodrilidae and Eudrilidae) were found at Kabete (Table 4). Each family was represented by 2 species. The earthworm species richness varied among the treatments, with NF having the highest richness (6 taxa), followed by FYM+F (3 taxa). Earthworm species were dominated by epigeic worms (4 taxa), while relatively few endogeic worms (2 taxa) were found. No anecic worms were observed. Epigeic worms were found only in the NF and FYM+F treatment, whereas the endogeic worm (*Nematogenia lacuum*) was present in all treatments. Termites belonging to three genera and one family (Termitidae; subfamily Macrotermitinae) were found (Table 4). Although the site had few termite genera, the control treatment appeared to be taxonomically the richest (3 genera), whereas residue and manure treatments were the poorest (1 taxa). All the termite genera belonged to group II foragers (wood, litter, grass feeders, fungus growers) (Table 4).

Table 3. The N contents in whole soil and in fractions as affected by management in the Kabete field trial, Kenya.

Depth (0-15 cm)			------------------------------ Whole soil (g kg^{-1} soil) and aggregate fraction N (g kg^{-1} fraction) ------------------------------						
Treatment	**Organic fertilizer (OF)**	**Mineral fertilizer (MF)**	**WS**	**TM**	**m**	**sc**	**mM**	**cPOM + sand**	**scM**
C−F	None	−	1.52 (0.09)^{c}	1.36 (0.07)^{c}	1.45 (0.06)^{b}	1.80 (0.07)	1.42 (0.07)^{bc}	0.76 (0.10)	2.49 (0.10)^{ab}
C+F	None	+	1.50 (0.06)^{c}	1.33 (0.11)^{c}	1.42 (0.09)^{b}	1.73 (0.12)	1.39 (0.08)^{bc}	0.77 (0.24)	2.40 (0.05)^{ab}
R−F	Residue	−	1.47 (0.06)^{c}	1.39 (0.07)^{c}	1.45 (0.06)^{b}	1.71 (0.07)	1.25 (0.09)^{c}	0.83 (0.04)	2.17 (0.09)^{b}
R+F	Residue	+	1.69 (0.08)^{bc}	1.48 (0.07)^{bc}	1.56 (0.08)^{ab}	1.77 (0.11)	1.57 (0.05)^{bcd}	0.71 (0.23)	3.09 (0.03)^{a}
FYM−F	Manure	−	1.76 (0.08)^{abc}	1.64 (0.07)^{bc}	1.58 (0.15)^{ab}	1.84 (0.14)	1.72 (0.08)^{abc}	1.19 (0.12)	2.62 (0.29)^{ab}
FYM+F	Manure	+	1.97 (0.11)^{ab}	1.78 (0.05)^{ab}	1.81 (0.04)^{ab}	2.08 (0.07)	1.85 (0.10)^{ab}	1.01 (0.20)	2.66 (0.23)^{ab}
NF	na	na	2.08 (0.06)^{a}	2.03 (0.08)^{a}	1.88 (0.04)^{a}	2.15 (0.08)	1.98 (0.08)^{a}	1.61 (0.28)	2.47 (0.08)^{ab}
P-value									
One-way ANOVA (including NF)			**<0.001**	**<0.001**	**0.007**	**0.031**	**<0.001**	**0.047**	**0.027**
Two-way ANOVA (excluding NF):									
Organic fertilizer (OF)			**0.003**	**0.001**	**0.029**	0.090	**0.001**	0.122	0.434
Mineral fertilizer (MF)			0.066	0.066	0.170	0.352	0.054	0.504	**0.047**
OF × MF			0.326	0.548	0.363	0.325	0.141	0.859	**0.018**
Depth (15-30 cm)									
C−F	None	−	1.36 (0.03)^{c}	1.23 (0.01)^{b}	1.22 (0.07)^{b}	1.64 (0.02)^{ab}	1.27 (0.01)^{b}	0.76 (0.11)	2.12 (0.08)
C+F	None	+	1.22 (0.13)^{c}	1.21 (0.11)^{b}	1.21 (0.12)^{b}	1.57 (0.17)^{ab}	1.20 (0.12)^{b}	0.74 (0.11)	1.92 (0.24)
R−F	Residue	−	1.28 (0.11)^{c}	1.28 (0.12)^{b}	1.29 (0.12)^{ab}	1.64 (0.09)^{ab}	1.32 (0.03)^{b}	0.85 (0.13)	2.38 (0.45)
R+F	Residue	+	1.31 (0.06)^{c}	1.21 (0.10)^{b}	1.29 (0.10)^{ab}	1.26 (0.21)^{b}	1.22 (0.06)^{b}	0.82 (0.08)	2.50 (0.30)
FYM−F	Manure	−	1.39 (0.10)^{c}	1.28 (0.07)^{b}	1.29 (0.07)^{ab}	1.61 (0.10)^{ab}	1.29 (0.07)^{b}	0.84 (0.13)	2.00 (0.06)
FYM+F	Manure	+	1.47 (0.10)^{ab}	1.39 (0.05)^{b}	1.43 (0.06)^{ab}	1.87 (0.06)^{a}	1.35 (0.09)^{b}	0.68 (0.25)	2.16 (0.05)
NF	na	na	1.82 (0.10)^{a}	1.72 (0.06)^{a}	1.65 (0.05)^{a}	2.04 (0.04)^{a}	1.74 (0.07)^{a}	1.22 (0.04)	2.33 (0.16)
P-value									
One-way ANOVA (including NF)			**0.011**	**0.006**	**0.038**	**0.012**	**0.002**	0.193	0.592
Two-way ANOVA (excluding NF):									
Organic fertilizer (OF)			0.281	0.387	0.306	0.113	0.522	0.827	0.228
Mineral fertilizer (MF)			0.856	0.920	0.575	0.550	0.538	0.576	0.890
OF × MF			0.476	0.623	0.676	0.078	0.523	0.855	0.737

Within columns, means followed by the same lower case letters in superscript are not statistically significantly different at $p < 0.05$. Values in parentheses are standard errors. WS = whole soil, TM = total macroaggregates **(≥250 µm)**, m = microaggregates **(53-250 µm)**, sc = silt and clay **(≤53 µm)**, mM = microaggregates within macroaggregates **(53-250 µm),** cPOM = coarse particulate organic matter **(≥250 µm)**, scM = silt and clay within macroaggregates **(≤53 µm).** C-F = control minus fertilizer, C+F = control plus fertilizer, R-F = residue minus fertilizer, R+F = residue plus fertilizer, FYM-F = farm yard manure minus fertilizer, FYM+F = farm yard manure plus fertilizer, NF = natural fallow, n.a = not applicable.

Table 4. Earthworm and termite taxonomic richness across crop management systems in the Kabete field trial, Kenya

Treatment		**C-F**	**C+F**	**R-F**	**R+F**	**FYM-F**	**FYM+F**	**NF**
Organic fertilizer (OF)		None	None	Residue	Residue	Manure	Manure	na
Mineral fertilizer (MF)		−	+	−	+	−	+	na
Taxonomic group	**Functional group**[a]							
Earthworm								
Ocnerodrilidae								
Nematogenia lacuum	Endogeic	+	+	+	+	+	+	+
Gordiodrilus wemanus	Endogeic	−	−	−	−	−	−	+
Acanthodrilidae								
Dichogaster (Dt.) affinis	Epigeic	−	−	−	−	−	+	+
Dichogaster (Dt.) bolaui	Epigeic	−	−	−	−	−	+	+
Eudrilidae								
Polytoreutus annulatus	Epigeic	−	−	−	−	−	−	+
Stuhlmannia spec nov	Epigeic	−	−	−	−	−	−	+
Species richness (S)		1	1	1	1	1	3	6
Termites								
Termitidae-								
Macrotermitinae								
Microtermes spp.	G II (FWLG)	+	+	+	+	−	+	+
Odontotermes spp.	G II (FWLG)	+	+	−	−	+	+	+
Pseudacanthotermes spp.	G II (FLSD)	+	−	−	+	−	−	−
Genus richness (S)		3	2	1	2	1	2	2

C-F = control minus fertilizer, C+F = control plus fertilizer, R-F = residue minus fertilizer, R+F = residue plus fertilizer, FYM-F = farm yard manure minus fertilizer, FYM+F = farm yard manure plus fertilizer, NF = natural fallow, n.a = not applicable. Earthworm classification based on Swift and Bignell (2001): Endogeics (those foraging on organic matter and dead roots in the soil profile, forming largely horizontally-orientated burrows); Epigeics (those that live and feed near the soil surface; they affect litter comminution. and nutrient release). Termite classification based on Donovan et al. (2001) and Eggleton et al. (2002): G II = Group two; W=wood; L=leaf litter; S=soil; D=Dung/manure; F=fungus grower; G=dead/dry grass. +/- denotes presence or absence, respectively.

Macrofauna diversity, abundance and biomass

The earthworm Shannon-Wiener diversity index (SW-index) was significantly affected by organic fertilizer amendment and the interaction between organic fertilizer amendment and mineral fertilizer. FYM+F had a higher SW-index (0.33) than the other arable treatments (0.00). The fallow had a higher index (0.74) than all arable treatments (Table 5). Earthworm biomass was affected by organic fertilizer amendment in that FYM+F had a higher biomass (19 g m−2) than the other arable treatments whose biomass ranged between 1 and 5 g m−2 (Table 5). Earthworm biomass in NF did not significantly differ from those in arable treatments. Mean earthworm abundance and termite parameters (SW indices, abundance and biomass) did not show significant differences among the treatments (Table 5).

Correlation analysis and factor, and regression analyses

Positive correlations, in most cases significant, between earthworm parameters (diversity, abundance and biomass), whole soil C and N and the amounts and C and N contents of fractions, were observed with one exception: earthworm abundance negatively correlated with TM (r = -0.35) (Table 6). No significant correlations were found between any of the termite parameters (Table 6).

The factor analysis (using Kaiser-Guttman rule) produced two factors that together explained 57.3% of the total variation in aggregate and associated SOM fractions, and the C and N contents of whole soil and fractions (Table 6). Earthworm parameters (loading coefficient of biomass = 0.98, that of abundance = 0.84, and that of Shannon diversity = 0.47), positively loaded the first factor and explained 31.7% of the total sample variation in aggregation, C and N stabilization (Table 6). Although termite parameters loaded the second factor and explained 25.6% of the variance, none significantly positively correlated with the fractions (Table 6).

Multiple regression analysis confirmed the outcome of factor analysis and indicated that a greater percentage of the variation in the quantity of aggregate and associated SOM fractions, and the C and N contents of whole soil and fractions was accounted for by the first factor that is related to earthworm parameters than the second factor that is related to termite parameters (Table 6).

Table 5. Soil macrofauna (earthworm and termite) diversity and biomass as affected by management in the Kabete field trial, Kenya

			Soil macrofauna group					
			Earthworm parameters			**Termite parameters**		
Treatment	**Organic fertilizer (OF)**	**Mineral fertilizer (MF)**	**Shannon index (H')**	**Abundance (No. m^{-2})**	**Biomass (g m^{-2})**	**Shannon index (H')**	**Abundance (No. m^{-2})**	**Biomass (g m^{-2})**
C−F	None	−	0.00 (0.00)^{c}	272 (98)	3.24 (1.78)^{b}	0.11 (0.05)	384 (149)	1.35 (0.79)
C+F	None	+	0.00 (0.00)^{c}	208 (112)	4.73 (2.43)^{b}	0.21 (0.20)	251 (212)	0.11 (0.11)
R−F	Residue	−	0.00 (0.00)^{c}	75 (14)	0.93 (0.34)^{b}	0.25 (0.02)	341 (70)	1.07 (0.49)
R+F	Residue	+	0.00 (0.00)^{c}	80 (9)	0.98 (0.18)^{b}	0.00 (0.00)	117 (117)	0.17 (0.17)
FYM−F	Manure	−	0.00 (0.00)^{c}	107 (56)	1.08 (0.93)^{b}	0.00 (0.00)	144 (121)	0.09 (0.08)
FYM+F	Manure	+	0.33 (0.16)^{b}	395 (199)	18.99 (11.21)^{a}	0.08 (0.04)	1029 (402)	6.25 (5.94)
NF	na	na	0.74 (0.30)^{a}	363 (118)	7.97 (1.77)^{ab}	0.13 (0.10)	203 (120)	0.75 (0.49)
P-value								
One-way ANOVA			**0.002**	0.247	**0.049**	0.374	0.116	0.529
Two-way ANOVA								
Organic fertilizer (OF)			**0.041**	0.264	0.166	0.460	0.294	0.530
Mineral fertilizer (MF)			**0.041**	0.420	0.149	0.688	0.358	0.522
OF × MF			**0.024**	0.290	0.076	0.134	0.060	0.285

Within columns, means followed by the same lower case letters in superscript are not statistically significantly different at $p < 0.05$. Values in parentheses are standard errors. C-F = control minus fertilizer, C+F = control plus fertilizer, R-F = residue minus fertilizer, R+F = residue plus fertilizer, FYM-F = farm yard manure minus fertilizer, FYM+F = farm yard manure plus fertilizer, NF = natural fallow, n.a = not applicable.

Earthworms affected the relative distribution of the different fractions in the soil as well as their C and N contents and C and N in whole soil, whereas effects of termites were mostly insignificant (Table 6).

Table 6. Correlation matrix and results of factor analysis and regression analysis between soil macrofauna parameters, whole soil C and N, aggregate fractions, and C and N contents of aggregate fractions. Values in bold are significantly different from 0 at $p < 0.05$; values in parentheses are standard errors

	Macrofauna parameters						**Multiple regression analysis**	
Variable	**EH**	**EN**	**EB**	**TH**	**TN**	**TB**	**Factor I**	**Factor II**
Fractions (g 100 g^{-1} total soil)								
TM (> 250 µm)	0.15	**-0.35**	-0.19	-0.05	-0.13	0.07	16.60 (12.30)*	0.00 (13.50)
m (53-250 µm)	-0.12	**0.34**	0.17	0.04	0.11	-0.09	13.70 (9.46)*	0.00 (10.20)
sc (< 53 µm)	-0.22	**0.37**	0.23	0.04	0.16	0.02	23.20 (3.11)**	0.00 (3.61)
mM (53-250 µm)	-0.22	0.27	0.07	0.11	0.04	-0.10	15.80 (0.42)*	0.00 (0.47)
cPOM + sand (> 250 µm)	-0.24	0.29	0.19	0.06	0.10	0.12	16.00 (0.11)*	0.00 (0.12)
scM	-0.11	0.25	0.16	-0.04	0.15	-0.05	4.30 (0.12)	1.60 (0.12)
				Total organic C				
WS C **(g kg^{-1} soil)**	**0.60**	**0.59**	**0.55**	-0.24	0.12	0.11	47.30 (2.44)***	4.10 (3.29)
C content of the fractions (g kg^{-1} fraction)								
TM	**0.68**	**0.54**	**0.53**	-0.20	0.08	0.12	51.60 (2.33)***	0.00 (3.37)
m	**0.62**	**0.60**	**0.54**	-0.17	0.16	0.14	51.10 (2.09)***	1.70 (2.97)
sc	**0.45**	**0.35**	**0.31**	-0.11	0.06	0.17	17.90 (3.36)*	0.00 (3.76)
mM	**0.63**	**0.57**	**0.57**	-0.22	0.02	0.03	49.00 (2.35)***	0.00 (3.31)
cPOM + sand	**0.50**	0.23	0.27	-0.03	0.04	0.12	19.00 (6.23)*	0.00 (0.001)
scM	0.25	0.20	0.15	-0.25	-0.01	0.02	1.20 (7.62)	0.00 (7.68)
				Total organic N				
WS N **(g kg^{-1} soil)**	**0.66**	**0.62**	**0.61**	-0.18	0.09	0.05	56.30 (0.19)***	0.00 (0.29)
N content of the fractions (g kg^{-1} fraction)								
TM	**0.74**	**0.55**	**0.54**	-0.12	0.09	0.05	60.30 (0.17)***	0.00 (0.27)
m	**0.64**	**0.58**	**0.51**	-0.13	0.19	0.11	51.90 (0.17)***	2.20 (0.24)
sc	**0.60**	**0.36**	**0.36**	-0.12	0.08	0.16	33.20 (0.22)***	0.00 (0.28)
mM	**0.67**	**0.60**	**0.60**	-0.15	0.04	-0.02	56.00 (0.18)***	0.00 (0.28)
cPOM + sand	**0.61**	**0.38**	**0.43**	-0.09	-0.04	0.10	35.30 (0.28)***	0.00 (0.36)
scM	0.11	**0.41**	**0.34**	-0.19	-0.10	-0.05	10.22 (0.39)	0.00 (0.42)

				Factor analysis			
Macrofauna parameters	**EH**	**EN**	**EB**	**TH**	**TN**	**TB**	
Factors	**Factor I**			**Factor II**			
R-values	0.465	0.835	0.983	0.336	0.992	0.644	Cumulative variance
Explained variance (%)		31.71			25.61		57.32

WS = whole soil, TM = total macroaggregates, m = microaggregates, sc = silt and clay, mM = microaggregates within macroaggregates, cPOM = coarse particulate organic matter, scM = silt and clay within macroaggregates; EH = earthworm Shannon index; EN = earthworm abundance (individuals m^{-2}), EB = earthworm biomass (g m^{-2}); TH = termite Shannon index; TN = termite abundance (individuals m^{-2}); TB = termite biomass (g m^{-2}). Values in bold and in asterisks are significant at $P < 0.05$.

Discussion

Aggregate stability and C and N stabilization in aggregate fractions

Our study has shown that the application of farm yard manure in combination with mineral fertilizer resulted in an improvement in stable aggregation at 0-15 cm soil depth compared to all other arable treatments, but not to the extent of the fallow, which can be explained by absence of soil disturbance and associated higher accumulations of organic matter in the fallow compared to arable systems. The relatively higher TM in FYM+F plots than in control plots can be attributed to regular addition of organic matter through manure and additional root biomass added to soil due to fertilizer-enhanced plant growth. This results in greater C availability and enhanced microbial and macrofaunal activity which lead to the formation of aggregates (Six et al., 2004). Probably, when manure is incorporated together with mineral fertilizer into the soil, organic matter gradually decomposes to produce humic substances, bacterial biomass, which in turn releases polysaccharides which serve as binding agents, and fungal mycelia which grow into the soil pores, thus binding soil particles into aggregates (Bossuyt et al., 2004; Aoyama et al., 1999). Singh et al. (2007) have similarly shown that addition of animal manure with mineral fertilizers in rice-wheat-cowpea improved the aggregation of soil particles.

Application of manure in combination with mineral fertilizer increased the C content of whole soil and most of the fractions in the 0-15 cm layer. Aggregate-fraction C and N were higher in the silt and clay fractions, especially scM, compared to all other fractions among the treatments. Soils high in clay, and iron and aluminum oxides, such as the Nitisol of our study site, have been shown to respond positively to organic inputs in that they have high C and N stabilization binding capacity in aggregate fractions (Gentile et al., in press). Our results show that application of manure in combination with fertilizer is the best among the treatments tested in this study for enhanced C and N stabilization with dual benefits of improving soil physical and chemical properties. This in general underscores the importance of integrated soil fertility management practices for rehabilitation soils in sub-Saharan Africa.

Role of soil macrofauna in aggregation and SOM dynamics

Both fallow and FYM+F supported higher earthworm diversity compared to all other arable treatments, whereas FYM+F application supported higher earthworm biomass. Organic manure benefits earthworms by providing food sources and mulching effects on the habitat (Tian et al., 1993; Whalen et al., 1998). In addition, organic manure stimulates plant growth and litter return (Curry, 2004). The effects of moderate levels of application of mineral fertilizers on earthworms are positive, but heavy applications of nitrogenous fertilizers may depress earthworm populations (Ma et al., 1990). The endogeic and epigeic species of earthworms were favored under fallow (e.g. high organic matter accumulation and no mechanical disturbances) and by the application of manure in combination with fertilizer. The foraging termites (e.g. Microtermes spp., Odontotermes spp. and Pseudacanthotermes spp.) sampled in our study were not significantly influenced by management practices.

The significant positive correlations between earthworms, aggregation and whole soil and aggregate-associated C and N, and the negative correlations between earthworms and the TM fraction and TM-associated C and N concentrations indicate the possible role of earthworms in these processes. The stronger positive correlations between earthworms and aggregate and soil fraction C and N than between termites and those variables indicates that earthworms are more likely to play an important role in explaining management-induced differences in aggregate formation as well as in C and N stabilization than termites. The results of factor analysis and regression analysis were consistent with this conclusion.

Lavelle et al. (2001) suggested linking soil biodiversity to soil functioning through the diversity of the soil structures produced by ‘ecosystem engineers’ like earthworms and termites. Earthworms ingest soil as they burrow and forage on SOM, thus promoting the formation of stable aggregates rich in soil C and N. The endogeic and epigeic earthworm species sampled in our study feed on SOM and litter respectively, thus incorporated C and N into their casts, resulting in higher C and N in aggregate fractions. Several studies have shown the importance of earthworms in aggregation and SOM stabilization in soil aggregates (Scullion et al., 2000; Pulleman et al., 2005; Bossuyt, et al., 2005; Fonte, et al., 2009). Our study site was dominated by the presence of epigeic worms, while the endogeic species (*Nematogenia lacuum*) was sampled across all treatments. *N. lacuum* is a small endogeic species (ca 0.8-1.2

mm in diameter) that produces small excrements. We suggest that this species also feeds on excrements of other larger epigeic worms, such as *Polytoreutus annulatus* (sampled in our study site) and thus could reduce the mean aggregate size (Csaba Czuzdi, personal communication). Whereas large endogeic and anecic earthworms in tropical soils form compact macroaggregates as excrements, smaller earthworms have been shown to act as decompacting species by fragmenting the excrements of larger earthworms (Blanchart, et al., 2004). Such processes regulate the mineralization of carbon and nutrients occluded in soil biogenic structures (Blanchart, et al., 2004). Bossuyt et al. (2004) and Fonte et al (2009) also showed that earthworms increased the concentration of residue-derived C in macroaggregates and macroaggregate-occluded fractions, and in so doing, they stabilize SOM by slowing the turn-over of newly added C. Fonte et al. (2007) found that in a low-input system based on alternate legume cover crop-mineral fertilizer application, earthworms increased N availability for incorporation and sorption into aggregate fractions by accelerating rates of decomposition and N-mineralization, while simultaneously protecting organic N in their casts.

Termites influence soil aggregation by mixing organic matter with inorganic soil particles, thereby modifying the physical properties of soil (Jungerius et al., 1999). Through their activities they move large amounts of soil and this may result in the breakdown of large macroaggregates into smaller macroaggregates or microaggregates. Lack of significant effect of management on termite indices and lack of significant correlations between termite parameters and aggregation, and C and N dynamics shows that the role of this group in explaining differences in SOM stabilization due to management may be limited. This may be because the termites that were sampled here were not typically soil feeders, but foraging species that feed in the arable fields but nest elsewhere, probably resulting in less of a role of termites in aggregation, C and N stabilization in aggregate fractions. Numerous studies have shown that the role of termites in aggregate stability differs between species, and could depend on the biology of particular trophic groups (Garnier-Sillam, 1989; Garnier-Sillam and Harry, 1995). Humivorous termites that build organic matter-enriched nests are more effective and contribute more to structural stability than fungus-growing termites (Garnier-Sillam and Harry, 1995), but these were absent from our plots.

Conclusions

Application of manure in combination with fertilizer significantly improved aggregate stability and C and N stabilization in arable soil. Furthermore, manure-fertilizer application enhanced earthworm diversity and biomass. Significant correlations between the amount and C and N contents of aggregate fractions and whole soil C and N were observed with earthworm parameters, but not with termite parameters. Factor and regression analyses showed that earthworms had a profound effect on aggregation, C and N stabilization in whole soil and in aggregate fractions, whereas contributions of termites were limited. Overall, our results indicate that long-term application of manure in combination with fertilizer result in higher earthworm Shannon diversity and biomass, which leads to improved soil aggregation and enhanced C and N stabilization within this more stable soil structure. These practices therefore result in the dual benefits of improving soil physical and chemical properties. In contrast, no significant improvements in soil aggregation and C and N stabilization were found when organic inputs were applied in the form of maize stover as compared to the no-input control, irrespective of fertilizer addition. Under the conditions studied, earthworms were more important drivers of aggregate stability and C and N stabilization in aggregate fractions than termites.

Acknowledgements

This study was supported by Science for Global Development/WOTRO through Wageningen University, Norman Borlaug LEAP Fellowship Program through UC-Davis and a research grant from the International Atomic Energy Agency (IAEA) to TSBF-CIAT. We thank our partners, especially the scientists and field technicians of the Tropical Soil Biology and Fertility Institute of the International Centre for Tropical Agriculture (TSBF-CIAT, Kenya), UC-Davis and Kenya Agricultural Research Institute (KARI), who agreed to work with us and have allowed us to use their experimental sites and facilities for this study.

CHAPTER FIVE

Effects of tillage and organic inputs on soil macrofauna-induced biogenic structures in East and West African soils

---

To be submitted as F.O. Ayuke [a*, b], M. Kooistra, L. Brussaard [a], M.M. Pulleman [a]

Abstract

Although belowground biodiversity has been implicated in many studies as important for sustainable management of agricultural soils, the relationships between soil fauna diversity and agroecosystem functioning are not straightforward. There is also general lack of knowledge on how the functional roles played by soil fauna are affected by agricultural management factors such as tillage intensity and crop residue management. A micromorphological approach was used to describe and quantify fauna-induced biogenic structures in undisturbed soil samples from long-term field experiments in East Africa (Nyabeda, Kenya) and West Africa (Saria, Burkina Faso). Management systems differing in tillage intensity and with or without organic amendments (no till vs. hand-hoeing with and without crop residues in Nyabeda; and hand-hoeing vs. tractor plowing with and without manure in Saria) were compared and a natural fallow was used as a relatively undisturbed reference. We used micromorphology to: (i) describe general soil profile characteristics for two soils under contrasting agroecological conditions and differing in soil texture; (ii) describe the effects of different tillage and residue management systems on soil fauna-induced biogenic soil structures and soil physical properties; and (iii) quantify the different biogenic features as affected by management in the two soils. Natural fallow had a high proportion of biogenic features induced by the activities of earthworms, termites and mesofauna, and hence a well developed and porous structure. Natural fallow of Saria fallow, however, had a weakly developed structure due to instability of the soils. Among the arable soils, reduced tillage intensity combined with organic inputs in the form of crop residues (Nyabeda) or manure (Saria) resulted in the highest volume percentage of biogenic soil structural features, most diverse pores sizes and continuous pore systems due to burrowing activities of soil fauna. Influence of soil fauna activities on soil structure following organic matter inputs was, however, dependant on agroecological conditions including soil type. Without organic inputs, the percentage of faunal induced features was low, resulting in highly compact soils prone to slaking with likely negative consequences on crop productivity. Our study has shown that soil management practices such as tillage and addition of organic inputs influence soil fauna activities with a significant impact on soil structure and hence soil physical properties.

Introduction

Agricultural soils in sub-Saharan Africa are often prone to degradation due to continuous cropping and sub-optimal fertilizer use. Among the technologies with potential to increase and sustain soil productivity is the manipulation of the soil environment through reduced tillage and/or organic inputs in the form of crop residue retention or manure application. Both management factors can have a profound effect on soil macrofauna activities, whereas the macrofauna, in turn, has an important role in soil structure formation (including water stable aggregates and biopores), soil organic matter (SOM) and nutrient dynamics (Mando et al., 1997; Jongmans et al., 2001; Brussaard et al., 2007; Fonte et al., 2009). Stable aggregates are important for water infiltration and retention and to reduce soil erosion (Blanchart et al., 2004). In addition, stable aggregates can physically protect occluded SOM against decomposition (Six et al., 1999; Pulleman et al., 2005). The channels created by earthworms (Lavelle et al., 1997; Blanchart et al., 1999; Lavelle et al., 2001; Brown et al., 2004) and termites (Wielemaker, 1984; Kooyman et al., 1987; Asawalam et al., 1999; Mando et al., 1999; Sarr et al., 2001) improve soil structure by increasing macropore volume and connectivity, and thereby aeration, water infiltration, root growth and consequently water and nutrient availability to plants. Pulleman et al. (2003) and Kooistra and Pulleman (in press) pointed out that agricultural soils whose conditions favor soil faunal activities, e.g. fine textured soils of (semi)-humid climates under long-term pasture, can lead to formation of a structure dominated by excrements and channels (biogenic structures). Unfavorable conditions, e.g. systems with conventional tillage or high pesticide use, on the other hand, may promote formation of physicogenic structures (Jongmans et al., 2001; Jongmans et al., 2003).

Fauna initiated processes such as decomposition and redistribution of soil organic matter, the excretion of faecal pellets that contribute to stable aggregation, and the formation of continuous voids have implication for soil functions such as susceptibility to erosion, aeration, leaching of agrochemicals, and nutrient dynamics hence affect the soil environment for plant growth (Carter et al., 1998; Kooistra and Pulleman in press). However, although belowground biodiversity has been implicated in many studies as important for sustainable management of agricultural soils, the relationships between soil fauna diversity and agroecosystem functioning are not straightforward (Giller et al., 1997; Brussaard et al., 2004; Wardle et al., 2004). There is also a general lack of knowledge on the precise functional roles played by many animals in soils (Davidson et al., 2006). Lavelle et al., (1997; 2001) suggested linking soil fauna diversity to soil functioning through the diversity of the biogenic structures produced by 'ecosystem engineers' like earthworms and termites. However, based on macromorphological characteristics it is often difficult to partition between those soil structures (Blanchart et al., 2009; Jouquet et al., 2010). Macromorphological distinction only works for aggregates >2 mm in diameter and the outer sides of the aggregates can be strongly modified due to aging resulting in a large category of aggregates whose origin is unknown (Jouquet et al., 2010; Pulleman et al., 2005). Using micromorphology, it is possible to look at much smaller features as well as their cross sectional view, and the features can be studied in their natural arrangement as they occur in undisturbed soil.

Climate and soil properties are important factors that influence soil macrofauna and their activities as shown by Ayuke et al. (this thesis; chapter 2), who found that earthworms and termites were nearly two times more abundant in clayey soils under sub-humid climates in East Africa, compared to sandy soils under semi-arid climates in West Africa. Moreover, important factors that determine soil fauna composition and activities such as food sources, moisture, pH, temperature and soil disturbance change depending on land use and agricultural management practices (Kooistra and Pulleman, in press). Little is known, however, about how such influences translate to soil structure and soil functioning. Soil micromorphology can be used to study biogenic structures resulting from the activities of different functional groups of soil organisms, in particular of soil macro- and mesofauna and plant roots, and their interactions (Kooistra and Pulleman, in press) and can therefore offer a valuable contribution in elucidating the role of soil fauna diversity and their functions in soils. Faunal activity in thin sections would be evident in excremental features as well as in the nature and distribution of void space (Bullock et al 1985; Kooistra and Pulleman, 2010). Based on their impact on soil structure formation, Kooistra et al. (1989) grouped soil fauna into two categories: the structure-following and structure-forming soil fauna. Structure-followers depend on the existing soil structure and do not participate in their modification, whereas structure-formers form and modify soil pores. Microfauna (size <100 µm in diameter) rarely has a direct impact on soil structure. Mesofauna (size 0.1-2mm) can be both structure-following and structure-forming, whereas macrofauna (size >2mm) is mostly structure-forming (Kooistra et al., 1989).

The aim of this study was to elucidate the linkage between management factors (tillage intensity and organic inputs), soil macrofauna biodiversity, soil structure formation and soil physical properties (soil compaction, aggregation, porosity) in 2 long-term field trials in different agroecological zones in East and West Africa. The specific objectives of the study were to: 1) micromorphologically characterize and quantify the features formed by soil fauna as affected by tillage type and organic inputs under contrasting agroecological conditions, 2) assess how soil structure modification due to soil macrofauna influences soil compaction, aggregation, and porosity and discuss possible impact on soil functioning for crop growth. The working hypotheses are: 1) reduced tillage intensity and use of organic inputs will enhance soil fauna diversity, abundance and activities, thereby resulting in an increased volume and diversity of macrofauna induced biogenic features, 2) as for natural fallow, reduced disturbance and increasing organic matter input can result in a dominant role for soil fauna in soil structure formation with subsequent positive impact on soil physical properties.

Materials and Methods

Study sites

The study was conducted in two long-term agricultural field trials of East (Nyabeda, Western Kenya) and West (Saria III, Burkina Faso) Africa (Table 1). Nyabeda (latitude: 0° 06′ N and longitude: 34° 36′ E, at an altitude of 1420 meters above sea level) falls within the humid agroclimatic zone with a mean annual rainfall of 1800 mm, bimodally distributed (February-July and August-November) and a mean monthly temperature of 23° C (Jaetzold et al., 1982). The soil is Humic Ferralsol with clay texture (9% sand, 21% silt, 70% clay). The soil has the following chemical characteristics at 0-15 cm depth: pH $_{H20}$ (5.0), P (20.7 mg kg^{-1}), Exchangeable K, Mg and Na (0.4, 4.7, 0.2 cmol kg^{-1} soil respectively), CEC (1.6 meq 100 g^{-1} soil) (Terano, 2010). Total organic C ranges between 16 and 28 g kg^{-1} soil, whereas total organic N ranges between 1.6 and 1.9 g kg^{-1} soil, depending on management. The climate at Saria (latitude: 12° 16′ N and longitude: 02° 09′ W, at an altitude of 300 meters above sea level) is a Sudano-Sahelian type characterized by a unimodal rainfall pattern, with a rainy season from May to September. The a mean annual precipitation is 800 mm (Korodjouma et al., 2006), and the mean monthly temperature is 33° C. The soil type is a Ferric Lixisol with low fertility. The clay content increases with depth and the top soil has a loamy sand texture (53% sand, 36% silt, 11% clay) with the following chemical characteristics at 0-15 cm: pH $_{H20}$ (6.4), P (67.3 mg kg^{-1}), Exchangeable K, Mg, Na, Ca (0.1, 0.7, 0, 2.0 cmol kg^{-1} soil respectively). Total soil organic C ranges between 2.2 and 3.3 g kg^{-1} soil, depending on management, whereas total N ranges between 0.12 and 0.18 g kg^{-1} soil.

These on-going long-term trials were established in 2003 and 1990, respectively to test different management options for arable crop production such as different organic inputs and tillage practices. At the Nyabeda field experiment four treatments (plus/minus tillage and plus/minus organic residue retention) under continuous maize cropping were compared. Maize stover (at 2 t ha^{-1}) is applied at the start of every season for those treatments receiving organic inputs. At Saria, the treatments included oxen plough versus hand hoeing with and without manure application under continuous sorghum, and the manure is applied at 10 t ha^{-1} yr^{-1}. At both sites a nearby fallow was included in the analysis as a relatively undisturbed reference. The fallows consisted of grass fallow or shrubland, which may or may not have been used for crop production in the past, but had been undisturbed for at least 7 years at the time of sampling. No insecticides were applied in the fields that were sampled for this study.

Micromorphological studies

Soil thin sections from the two study sites were collected around 8 weeks after planting, in June 2008 (Nyabeda, Kenya) and September 2008 (Saria, Burkina Faso). At each site, five treatments were selected for this study, i.e. +/- tillage and +/- residues and a natural fallow at Nyabeda and handhoeing/oxen plough +/- manure and a natural fallow at Saria. From each of the treatments, undisturbed soil blocks were extracted by inserting metal Kubiena boxes (15 cm × 8 cm × 5 cm) at two successive depths (0-15 and 15-30 cm) vertically into an undisturbed surface of the wall of a soil pit. The upper 30 cm of the soil profile included the cultivated top soil (10-15 cm deep) and the underlying soil layer. These samples were stored in a cooler with ice to minimize further activity of any remaining soil fauna and fungal growth, transported to the Netherlands and air dried. Soil thin sections (25µm thick) were prepared according to the methods described by Fitzpatrick (1970) and Jongerius et al. (1975).

In addition the samples were hardened as soon as possible by gamma radiation to prevent anomalies in reaction with the polyester resin (Bisdom and Schoonderbeek, 1983). Optical examinations were made with a polarization research microscope, using plane polarized light (PPL) and crossed polarized light (XPL) with magnifications up to 200×. In the thin sections, more or less uniform layers and their transitions could be distinguished and were described successively. First the general soil profile characteristics were described for a reference profile (natural fallow) and confirmed using the other thin sections for each site individually. Second, management induced differences in soil structural and other relevant features were described, with a special emphasis on biogenic features and soil physical properties. We combined both qualitative and quantitative methods to characterize the biogenic features in terms of morphology as well as their quantitative importance. The different biogenic structures produced by earthworms, termites, mesofauna and root channels were identified and described morphologically according to the abundance, shape, composition and arrangement of the organo-mineral components (Babel, 1975; Bullock *et al.*, 1985). Thereafter, a systematic quantification of the different biogenic features was made in each layer using transparent paper with a 2 mm X-Y grid placed over the slides. Two windows were counted per homogenous layer per thin section and randomly positioned within the layer. Each window comprised of 25 (5 by 5) 4-mm^2 square grids. Quantitative data were expressed as volume percentages based on the estimated surface area of each of the features per grid cell. The occurrence of each biogenic feature is presented as a volume percentage on a total soil basis.

Results

General soil profile characterization; Nyabeda

The groundmass material consists of reddish brown clay (Figure 1) containing many mineral grains (20-800 µm Ø) and common rock fragments (50-2000 µm Ø). The mineral grains are angular to rounded and mainly composed of quartz, whereas the rock fragments are sub-angular to sub-rounded and are generally strongly weathered. Weathering products, such as iron accumulations and iron nodules are abundant to common. Clay illuviation features or their remnants occur over the entire depth studied. The angular to rounded mineral grains or the angular to subrounded weathered rock fragments indicate that the soil material consists of a deposit of displaced weathered soil materials. On this deposit probably a forest grew, the period during which clay illuviation took place and faunal activity, especially earthworm activity was abundant. The presence of clay illuviation features and remnants of them over the studied depth indicates that the soil profile has been truncated until the more resistant clay illuviation layer. The surface layer therefore starts with the former Bt horizon. Erosion of the top layers can be explained by past agricultural activities as indicated by the presence of burned fragments of organic matter. The presence of burnt fragments of organic material in all layers of all thin sections, especially in the fallow plot and in former tree-root channels indicate that these soils went through several cycles of slash and burn, cultivation, desertion, erosion and revegetation, before the start of the actual management systems studied. The quantity of burnt fragments decreases with depth. In some deeper layers (> 15 cm), fine fragments of burnt organic matter are found in worm excreta. Their presence indicates that worms were active in these soils after a cycle of slash and burn. Slash and burn of forest patches to reclaim land for agricultural use was a common practice in this part of Kenya (Omondi Wicliff, personal communication). All the management treatments in the Nyabeda field experiment are set in the former Bt horizon, which is relatively resistant and fertile because of the high clay content. In general, the soil has a moderate medium subangular blocky to crumb structure at the top (0-15 cm) and a weak medium to coarse angular blocky structure towards the bottom layers (>15 cm) (Table 1).

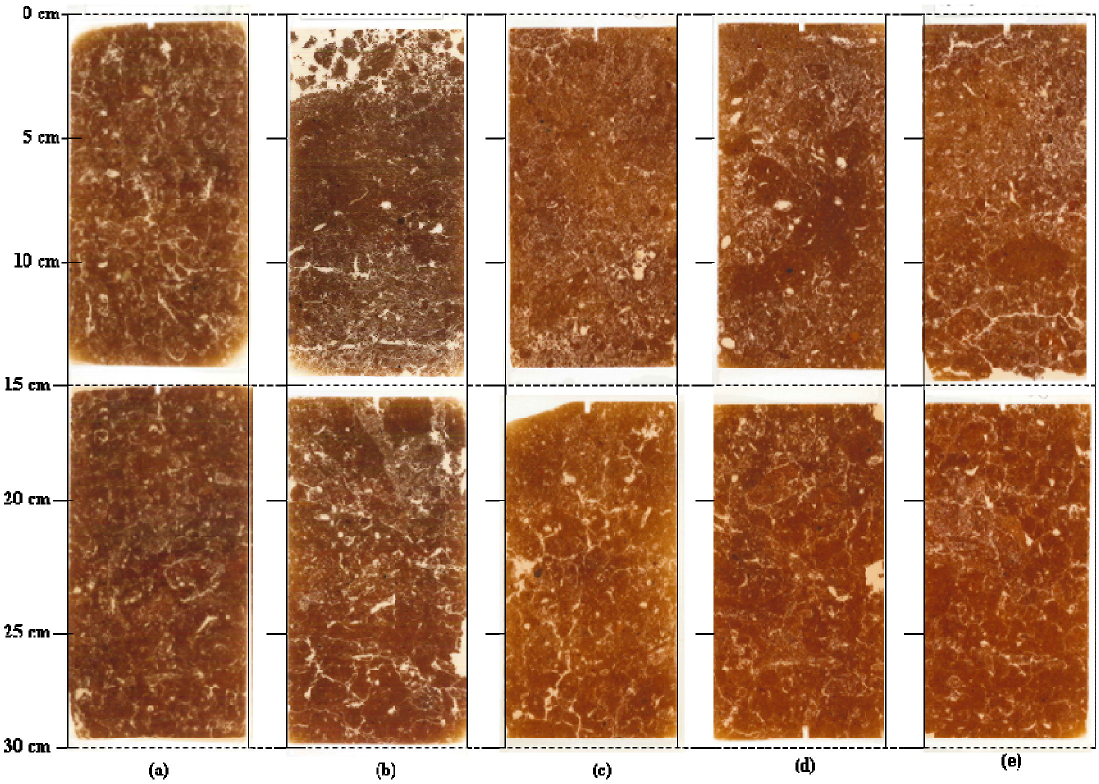

Figure 1. Color scan of thin sections of undisturbed soil samples taken from the different treatments in Nyabeda, Kenya. (a) NF = natural fallow, (b) CT-R = Conventional tillage minus residues, (c) CT+R = Conventional till plus residues, (d) NT-R = No tillage minus residues, (e) NT+R = No tillage plus residues.

Table 1. Microscopic (micromorphological) analysis of the thin sections across different treatments, Nyabeda, Kenya. (a) NF = natural fallow, (b) CT-R = Conventional tillage minus residues, (c) CT+R = Conventional till plus residues, (d) NT-R = No tillage minus residues, (e) NT+R = No tillage plus residues

Treatment	Description
Natural fallow (NF) (0-15 cm): Dark brown	Layer I (0-4.5 cm) • Layer is more or less uniform in structure • Has well developed subangular blocky structure-peds are about 1 cm ∅; peds are very porous; with many faunal & root channels (up to 3 mm ∅); • Has many irregular channels of different faunal species inclusive mesofauna.
	Layer II 4.5-14 cm) • Layer is more or less uniform in structure • Has well developed subangular blocky structure-peds are bigger about 1.5 cm ∅; peds are porous; with many faunal & root channels (up to 3 mm ∅); • Has many irregular channels of different faunal species inclusive mesofauna.
Natural fallow (NF) (15-30 cm) Dark brown	Layer II I (14-24 cm) • Layer is more or less uniform in structure • Has a subangular blocky structure-peds are bigger about 1 cm ∅; peds are porous; with many faunal & root channels (up to 2.5 mm ∅); • Has common, irregular channels of different faunal species inclusive mesofauna.
	Layer IV (>24 cm) • Is more or less uniform in structure • Has a subangular blocky structure-peds are bigger about 1 cm ∅; peds are weakly porous to porous; with common faunal & root channels (up to 3 mm ∅)
216-9: CT-R (0-15 cm) (Darker red brown till the farm implement depth) [Conventional till (hand hoeing) minus residues]	Layer I (0-3.5 cm) • Crumbly structure composed of loosely packed subrounded-to subangular aggregates till 1 cm ∅. • The crumbs are partly composed of broken up slaking crusts that contain vesicles (air bubble holes).
	Layer II (3.5-9 cm) • Compact layer composed weakly developed subrounded-to subangular structure • With few faunal and root channels & irregular packing voids and many excrements (250-400 mµ ∅)
	Layer III (9-15 cm) • Weak sub-angular structure (1.2-1.5 mm); • Very porous composed of many excrements and soil fragments (250-400 mµ ∅); • Faunal and root channels up to 2mm
216-9: CT-R (15-30 cm) Red brown	Layer IV (15-20 cm) • Massive soil fragments embedded in loosely accumulated excrements and soil particles with irregular packing voids; • Common faunal and root channels up to 3 mm ∅. • Lower boundary is at an angle and made by farm implements.
	Layer V (20-24 cm) • Layer is structureless • Common faunal & root channels up to 3 mm ∅.
	Layer VI (> 24 cm) • Well developed subangular blocky structure; weakly porous peds; • Common faunal & root channels up to 2 mm ∅.
336-12: CT+R (0-15 cm): (Darker red brown) [Conventional till plus residues- 2 t ha^{-1} maize stover)	Layer I (0-8 cm) • Very weakly developed subangular blocky structure-peds about 1cm ∅; • Peds are porous and contain aggregated excrements & soil fragments; • Layer has common faunal & root channels (up to 1 mm ∅).
	Layer II (8-15 cm) • Layer has weak sub-angular blocky structure; peds about 1.5 cm. Porosity of the the peds vary from very porous to porous; • Common faunal & root channels (1-4 mm).

Table 1 (Continued). Microscopic (micromorphological) analysis of the thin sections across different treatments, Nyabeda, Kenya. (a) NF = natural fallow, (b) CT-R = Conventional tillage minus residues, (c) CT+R = Conventional till plus residues, (d) NT-R = No tillage minus residues, (e) NT+R = No tillage plus residues

336-12: CT+R (15-30 cm): Red brown	Layer III (15-19 cm) • Well developed subangular blocky structure; peds up to 1.5 cm; porosity of the peds vary from weakly porous to porous; • Common faunal & root channels varying from 0.5-2 mm ∅.
	Layer IV (19-30 cm) • Subangular blocky structure; peds vary from 1- 2 cm ∅; porous peds. • Many faunal & root channels up to 3 mm ∅.
320-3: NT-R (0-15 cm): Darker red brown [Conservation till minus residues]	Layer I (0-1.5/3 cm) • Slaked top layer (0-1.5/3cm depth) is composed of several fluxes of sorted soil materials (excrements & some clusters of mineral materials)
	layer II (3-12 cm) • Half of the groundmass material is massive with very weak subangular blocky structure; the other half is very porous, with many faunal and root channels (up to 3 mm ∅)
320-3: NT-R (15-30 cm): Red brown	Layer III (12-18 cm) • Layer has very weak subangular blocky structure; • Is porous containing excrements and soil fragments; • Common faunal and root channels (3-4 mm)
	Layer IV (18-24 cm) • Well developed subangular blocky structure; peds up to 1.5 cm; porosity of the peds vary from weakly porous to porous; • Common faunal & root channels varying from 0.5-2 mm ∅
	Layer V (24-30 cm) • Weakly developed subangular blocky structure; peds up to 1.5 cm; porosity of the peds vary from weakly porous to very porous; • Common faunal & root channels varying from 0.5-2 mm ∅
312-6: NT+R (0-15 cm): Reddish brown [Conservational till (surface scratching with hoe) plus residues-2 t ha^{-1} maize stover]	Layer I (0-1 cm) • Slaked top layer in 312-6-deposited in 1 flux, composed of sorted excrements & some clusters of mineral materials;
	Layer II (1-8 cm) • Weak subangular blocky structures, with peds about 1cm ∅. • Peds are porous to very porous and are composed of aggregated excrements and soil fragments • Layer has many faunal & root channels (up to 2.5 mm ∅)
	Layer III (8-15 cm) • Has sub-angular blocky structure with peds (up to 1.5-2 mm) • Peds are medium porous and contains a few excrements and some more soil fragments • Has common elongated irregular faunal and root channels up to 2 mm.
312-6: NT+R (15-30 cm): Red brown	Layer IV (15-30 cm) • Well developed subangular blocky structure; weakly porous peds; with a large infilling of 1.5 cm ∅ and 3.5 cm long • Common faunal & root channels; in the top up to 3 mm ∅; decreasing with depth to 1 mm ∅

Soil structure under contrasting management; Nyabeda

In the natural fallow ($NF_{Nyabeda}$), the soil has a more or less uniform structure and slaking features are absent. The soil has a well developed subangular blocky structure with bigger peds, about 1-1.5 cm ∅ (Figure 1a; Table 1). Peds are very porous with many faunal and root channels in the top 24 cm. Below 24 cm depth, peds are smaller (about 1 cm ∅) and are weakly porous. The fallow soil has many irregular channels created by different faunal groups including earthworms, termites and mesofauna (Figure 1a). Root voids and channels are round or elongated, with regular smooth walls and a diameter of up to 3 mm. Many of the clay illuviation features are broken into fragments either due to past tillage or due to fauna activities and are randomly distributed or embedded in the groundmass.

Under conventional till minus residues (CT-R), the top layer I (0-3.5 cm) has a crumbly structure, while lower layers (>3.5 cm) are more compact or massive with weakly developed to well-developed sub-angular blocky structures (Figure 1b; Table 1). The crumbs in the top 3.5 cm are partly composed of slaking crusts (Figure 2a) that are broken up by the tillage and contain vesicles (air bubble holes due to entrapped air indicating sealing of the soil by the surface crusts present before this plowing event) (Figure 2b). In the 0-15 cm layer excrement features are randomly distributed in the groundmass and do not seem to be associated with other features such as channels. Broken pieces of roots are common and randomly embedded in the groundmass. Clay illuviation features (Figure 2c) are few in the top 0-15 cm, whereas they are common and intact below 15 cm depth. The soil has few faunal and root channels (Figure 1b), but has many irregular packing voids filled with faunal excrements (Figure 2d).

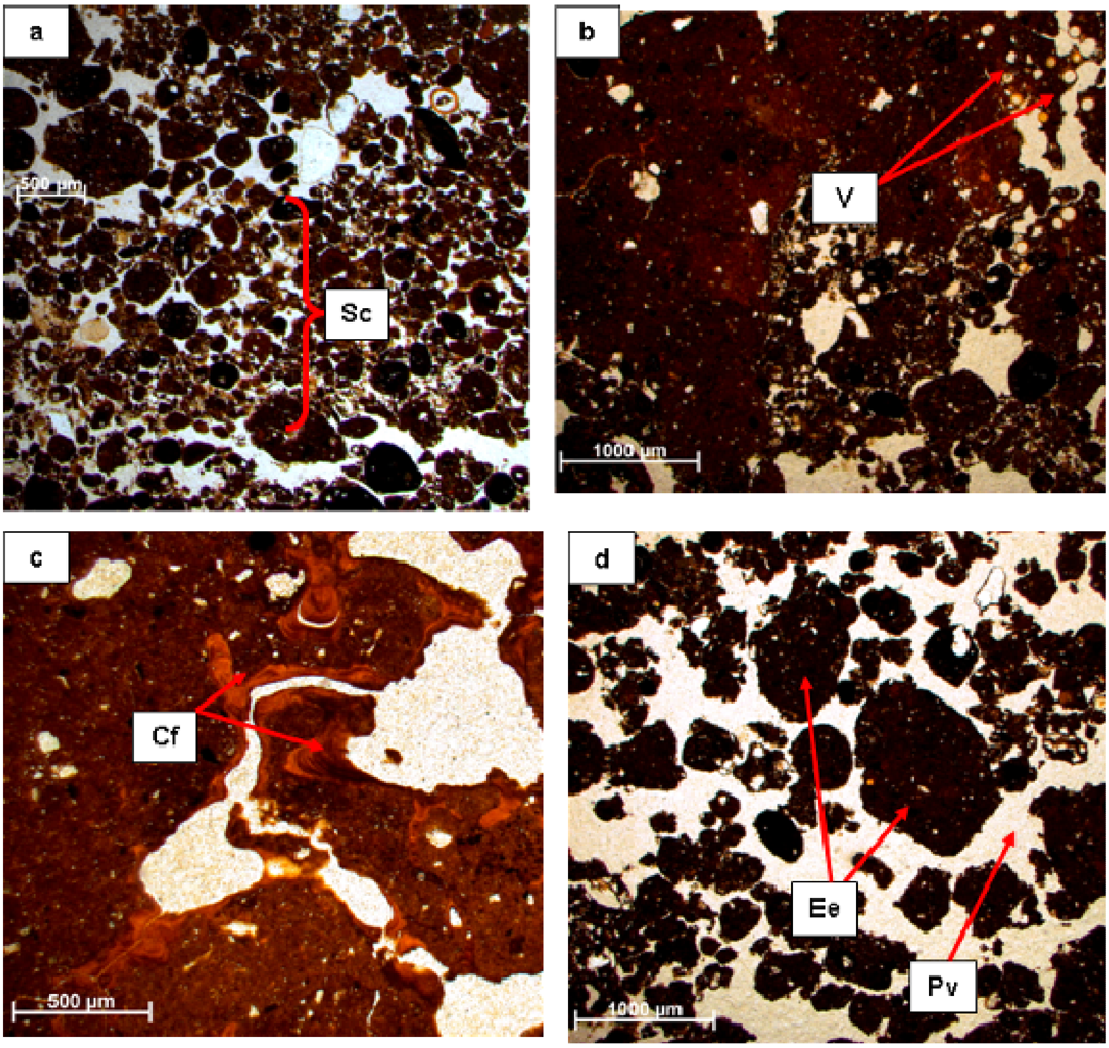

Figure 2. Soil thin section in the Nyabeda field trial. (a) CT-R (0.3.5 cm): Sc = slaking crust, (b) NT-R (0-3.5 cm): V = vesicles (air bubbles), (c) NF (15-30 cm): cf = clay illuviation features, (d) CT+R (0-8 cm): Ec = earthworm excrements, Pv = packing void.

Under conventional till with residue (CT+R), the soil has a very weakly developed subangular blocky structure in the top 15 cm and a well developed structure at 15-30 cm (Table 1). Peds are very porous to porous and become weakly porous towards the lower 15-30 cm depth. The soil has common fauna and root channels (up to 2 mm diameter), but these become many and wider (up to 3 mm diameter) at 15-30 cm depth (Figure 1c and 3c).

Under no till minus residue (NT-R), the soil has a slaking crust at the top (0-1.5/3 cm depth) (Table 1). Between 3 and 12 cm depth, half of the groundmass material is massive with very weak subangular blocky structure; the other half is very porous, with many faunal and root channels (Figure 1d). Between 12 and 18 cm, the soil has a very weak subangular blocky structure. The soil is porous and contains faunal excrements and soil fragments as well as common faunal and root channels. The soil is well developed with sub-angular blocky structure at greater (18-24 cm) depth. Below 24 cm the soil is relatively porous compared to 18-24 cm layer due to fauna (earthworm and termite) activities.

Under no till with residues (NT+R), a slaked top layer has been deposited in one flux, but is shallow (<1 cm) compared to that in NT-R treatment (Table 1). The soil has a weak subangular blocky structure at the top 15 cm and a well developed subangular blocky structure below 15 cm depth. The peds are very porous at the top to weakly porous in the deeper layers (>15 cm). The soil is composed of common to many sorted excrements and the soil has many faunal and root channels (Figure 1e).

Nature and occurrence of faunal features; Nyabeda

Three types of fauna and fauna generated pedofeatures were observed across all treatments in Nyabeda:

1. **Mesofauna features: a)** formed by mites whose organic excrements are ellipsoidal/spheroid (80-90 µm long; 40-50 µm wide) in or around decomposing root fragments (Figure 3a) **b)** formed by enchytraeids whose clay-rich organo-mineral excrements (Figure 3b) occur in small faunal channels measuring (≤100 µm Ø). In most cases the channels are completely infilled with loosely deposited small (25-100 µm) clay-rich organo-mineral excrements. Generally, most of the mesofaunal voids are round and irregularly shaped (<100 µm Ø) or are long, with irregularly shaped rough walls with diameter measuring ≤100 µm Ø.

2. **Earthworm features (a)** small, interconnected, irregular faunal channels (350-500 µm Ø). The channels are largely infilled with organo-mineral excrements (100-400 µm Ø), ellipsoidal/ovoid/spheroid or amalgated and locally excrements contain fine clay or silt grains up to 30 µm Ø (Figure 3c), (b) long elongated channels up to 3 mm wide. The worms also produce bigger organomineral excrements measuring up to 1.5 mm Ø. The excrements occur either in isolation (Figure 2d) or in clusters within the channels and are amalgated (Figure 3c).

3. Termite features, including very irregular interconnected channel systems with smooth surfaces, measuring up to 3 mm Ø. These termite-induced channels typically do not show signs of compaction or pressure on the walls. The channels rarely have excrements (Figure 3d). Infilled irregular channels measure between 1 and 3 mm Ø, and are filled with loosely accumulated mineral grains (40-100 µm Ø), groundmass fragments (600-1300 µm Ø), root fragments (60 µm Ø) and sometimes excrements of other fauna.

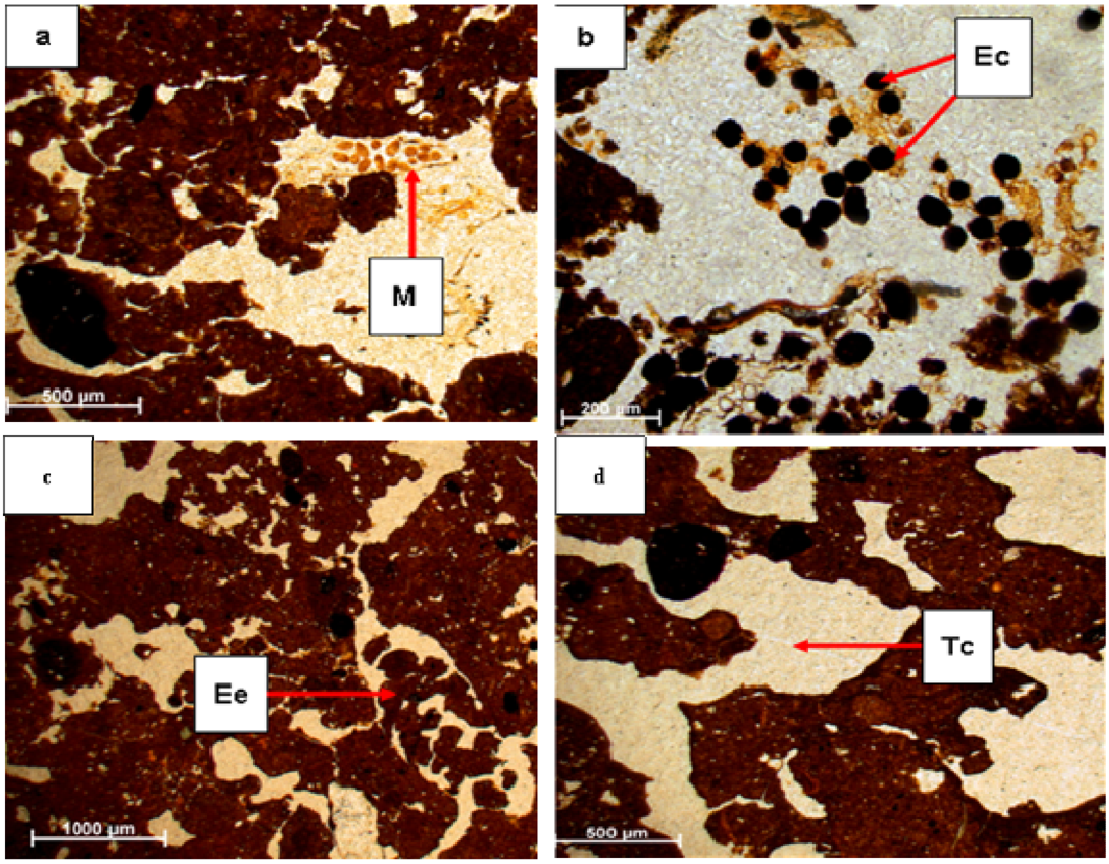

Figure 3. Biogenic features in the Nyabeda field trial. (a) CT+R (12 cm depth): M = mite excrements, (b) NF (8 cm): Ec = enchytraeid excrement, (c) NF (18 cm): Ee = earthworm excrement in a fauna modified channel, (e) NF (24 cm): Tc = termite channel.

Qualitative microscopic analysis of fauna activities; Nyabeda

Faunal activities as indicated by the features described under section 3.3 above varied across the different treatments. In the fallow, features induced by mites are common in the upper 4.5 cm, but are few to rare below 4.5 cm. Features derived from enchytraeids are rare in the upper 14 cm, but common in the lower layers. Earthworm features are many in nearly all the layers in the fallow. The worms have eaten away the materials and in the process enlarged channels and modified their own features as well as the clay illuviation features. Termite induced structures are abundant in the upper 15 cm, but termites have also invaded deeper into the soil profile, where the groundmass is dominated by worm-made features. In the process they have destroyed worm features and replaced them by their own.

Under CT-R, features derived from faunal activities are few, especially in the upper 15 cm. Below 20 cm depth, there are few to common remnants of earthworm features. These are amalgated darkish brown excrements or excrements with dark linings (typical of excrements that have passed through gut), probably from endogeic worms. Worm features have also been ingested/destroyed by enchytraeids (mesofauna). Termite features are few to common below 20 cm depth. In CT+R, faunal features are common. All the three categories (earthworms, termites and mesofauna) of fauna have worked the soil. However, presence of termite and mesofauna features diminishes with depth, while earthworms are many in all depth layers. In NT-R, the soil has very little fauna features and where they occur, it is dominated by those formed by earthworms and termites, the latter being rare at the top but few towards the lower layers >15 cm depth.

In NT+R, the soil is composed of common to many sorted excrements. Faunal activities are dominated by earthworms and mesofauna, giving the soil its porosity. Few termite features were observed in deeper layers. Due to high faunal activity, some of the clay illuviation features are broken. Earthworm induced features are many and some worm excrements are dark, whereas some are light-colored, due to deep burrowing worms bringing materials up. Generally there are less features that indicate termite activities, but mesofauna activities are common to many, with the latter mainly occurring in earthworm excreta, near or in clay illuviation features.

Quantification of different biogenic features across management systems; Nyabeda

The quantity of different fauna-induced features was negatively affected by tillage and positively affected by organic amendments. This was expressed in the higher proportion of biogenic features in NF_n and in NT+R (Table 2). The proportion of biogenic features in the CT treatments was higher in the lower layers (below 15 cm) than in the top layers, whereas a reverse trend was observed under NT. Treatments without residues had relatively lower proportion of biogenic features compared to treatments with residues (Table 2). Proportion of earthworm features ranged from 5-32%. The highest proportion of earthworm biogenic features (32%) was observed in NT+R, whereas the lowest proportion (5%) was observed in NT-R. The proportion of termite features was generally low across treatments, and the highest proportion (11%) was observed in CT+R. Termite features were rarely observed in the upper layers (0-3 cm) of CT-R and NT-R (Table 2). Mesofauna features were higher in NF and in NT+R than in the other treatments and treatments with residues had relatively higher proportions of mesofauna features than treatments without residues. Mesofauna features were generally higher in the upper layers compared to lower layers for all treatments (Table 2).

Root channels were few across treatments, but where they occur, they were more abundant in the top layers, with the highest proportion being observed in the conservational tillage with residue treatment (Table 2).

Table 2. Quantitative distribution of biogenic features across different treatments, Nyabeda, Kenya. NF = natural fallow; CT-R = Conventional tillage minus residues; CT+R = Conventional till plus residues; NT-R = Conservational tillage minus residues; NT+R = Conservational tillage plus residues. <1% = Very few to rare, 1-5 = Few, 6-10 = Common; 11-20 = Many; >20 Very many. In parentheses are the standard errors.

		Earthworms	**Termites**	**Mesofauna**	**Root channels**
Treatment	**Depth (cm)**	**-----------------------(Volume % based on estimate of surface area of feature)----------------------**			
NF	0-4.5	27.5 (4.5)	2.9 (0.2)	14.0 (1.5)	1.2 (0.1)
	4.5-14	23.5 (1.5)	1.6 (1.1)	12.0 (2.1)	0.2 (0.2)
	14-24	14.0 (2.0)	4.0 (2.0)	9.3 (0.1)	0.2 (0.1)
	24-30	13.9 (1.9)	3.6 (0.6)	8.5 (1.3)	0.0 (0.0)
216-9: CT-R	0-3.5	14.1 (4.8)	0.0 (0.0)	6.2 (1.6)	0.0 (0.0)
	3.5-9	8.6 (1.3)	0.1 (0.1)	8.0 (1.5)	2.2 (0.5)
	9-15	8.6 (1.9)	3.5 (1.2)	8.9 (0.3)	1.4 (1.0)
	15-20	11.3 (1.0)	1.5 (0.4)	6.8 (0.1)	1.4 (0.4)
	20-24	12.6 (1.9)	6.2 (1.3)	5.3 (0.8)	0.1 (0.0)
	24-30	13.2 (3.4)	0.5 (0.4)	5.3 (1.3)	0.0 (0.0)
336-12: CT+R	0-8	11.8 (1.7)	3.0 (0.1)	9.2 (1.0)	0.3 (0.2)
	8-15	28.5 (6.3)	10.8 (1.1)	9.8 (2.0)	2.0 (1.0)
	15-19	11.2 (1.0)	0.6 (0.0)	7.3 (0.4)	0.3 (0.1)
	19-30	20.4 (3.1)	1.2 (0.0)	6.4 (1.1)	0.0 (0.0)
320-3: NT-R	0-3	5.3 (0.3)	0.0 (0.0)	7.7 (0.9)	0.9 (0.2)
	3-12	12.3 (2.8)	2.6 (0.71)	4.9 (0.2)	0.0 (0.0)
	12-18	12.9 (1.8)	0.6 (0.14)	6.8 (1.0)	0.7 (0.2)
	18-30	6.7 (0.2)	1.4 (0.00)	4.2 (0.3)	0.3 (0.1)
312-6: NT+R	0-1	32.1 (1.1)	0.0 (0.0)	12.8 (5.3)	1.5 (0.8)
	1-8	17.8 (5.2)	1.3 (0.9)	9.4 (1.9)	2.7 (1.2)
	8-15	23.8 (0.9)	4.2 (2.1)	9.4 (2.8)	0.5 (0.1)
	15-30	16.8 (4.7)	6.7 (0.1)	7.6 (1.3)	0.0 (0.0)

General soil profile characterization; Saria

The Saria soil is yellowish in color and characterized by a sandy cover of ca. 12 cm on top of a former Bt horizon, of which the top layer has been eroded (Figure 4). The Bt horizon is also disappearing due to its consumption by mesofauna. Recently formed clay illuviation features are impure, i.e. mixed with organic material, whereas old ones are pure. Generally, the soil has a very weakly developed subangular blocky structure to loose single grains at the top 0-15 cm, and is mainly composed of coarse sand, and weakly developed, but massive, very friable, firm structure towards the bottom layers (>15 cm) (Table 3; Figure 5a). Rock fragments are ferruginous.

The soil is porous, but most of the soil material easily disintegrates thus blocking the pore spaces. Voids are infilled with loose groundmass material and illuviated fine clay features in large voids. Local compression is from roots, and other biological activities. The soil has been modified through faunal activities, and these depend on management regimes.

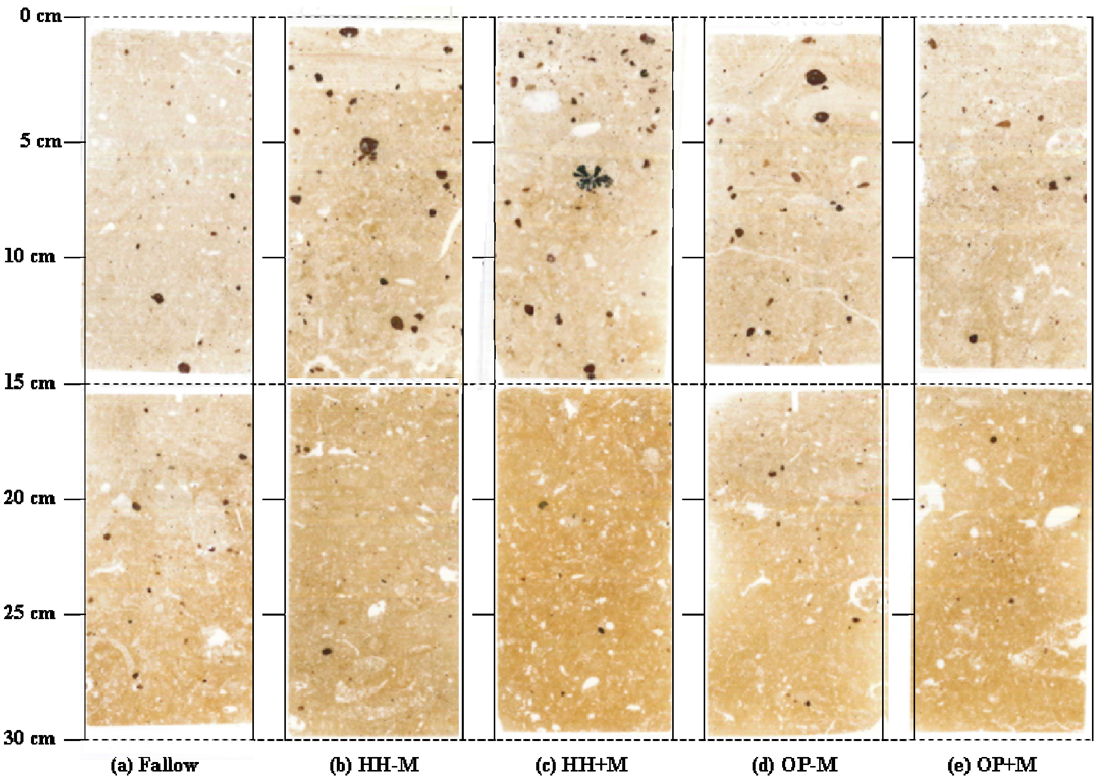

Figure 4. Soil micromorphology of thin sections across different treatments in Saria, Burkina Faso. (a) NF = natural fallow, (b) HH-M = Handhoeing minus manure, (c) Handhoeing plus manure, (d) OP-M = Oxen plough minus manure, (e) OP+M = Oxen plough plus manure.

Soil structure under contrasting management; Saria

Under natural fallow (NF$_{saria}$), the soil material of the 0-15 cm layer is uniform. A thin slaked crust occurs at the top (0-0.5 cm) (Figure 4a) and internal slaking is common in deeper layers (Figure 5b). The layer contains broken vesicles (air bubbles indicating entrapped air). The soil has a very weakly developed structure (near structureless) in the upper 15 cm, but is weakly subangular blocky to single grained at 15-30 cm depth (Table 3). The soil has discontinuous pores. Compared to the arable soils, NF$_{saria}$ soil has more organic matter, and carbon content increases with depth, resulting in a yellowish brown soil color. Voids are very loosely infilled with mineral grain or rock fragments (Figure 5d) and the infilled voids also contain worm excrements (size180 µm ∅). Below 15 cm depth, the clay content is increasing because it is closer to the Bt horizon. There are many roots, remnants of roots, pollen, sporangia. Root channels are nicely shaped, round regular or elongated with smooth walls, and are measuring up to 3 mm Ø. Internal slaking occurs on top of the former Bt horizon. There are many infilled channels in the Bt horizon, and bigger voids contain some materials fallen down from upper layer.

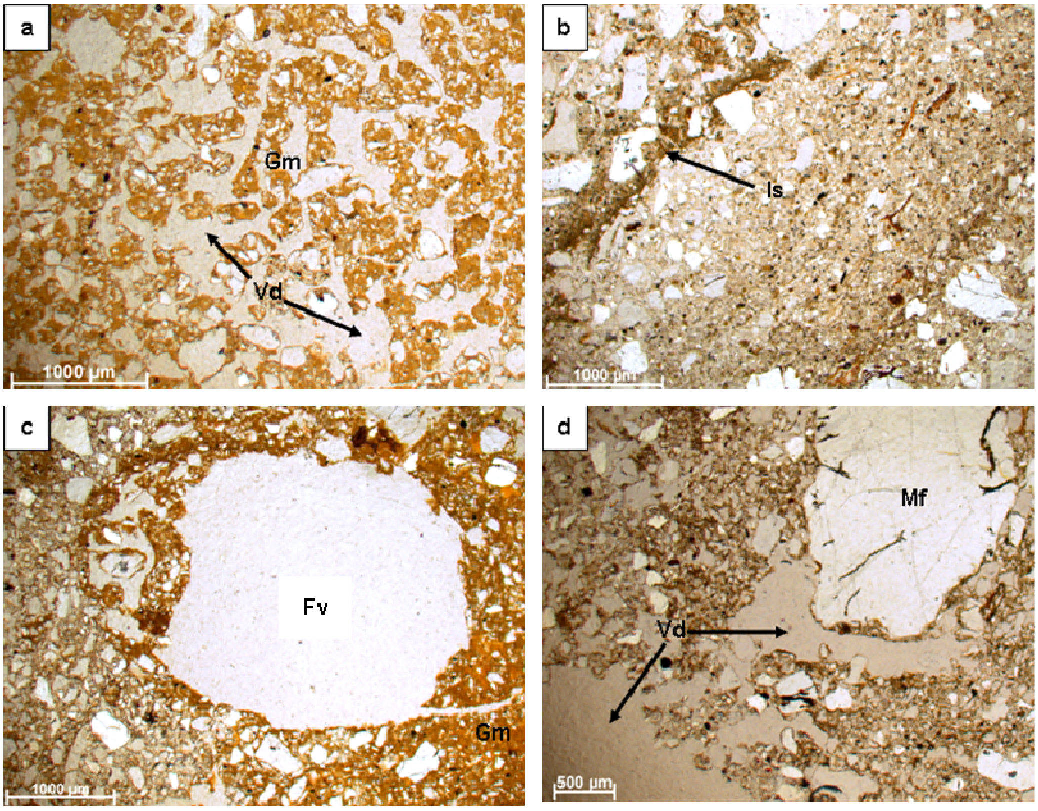

Figure 5. Soil thin section in the Saria field trial. (a) OP-M (28 cm depth): Gm = groundmass, Vd = void, (b) OP-M (3 cm): Is = Internal slaking, (c) NFSaria (10 cm): Fv = Faunal void, (d) HH-M (5 cm): Mf = mineral fragment.

Under handhoeing minus manure (HH-M), a 3 cm thick slaked layer occurred on top and contains many vesicles (air bubbles). The slaking has resulted in disintegration of soil material and deposition of finer and coarser grained materials into separate microlayers (Figure 4a). The small pieces of slaking crust from previous seasons have been incorporated into the soil by hoeing. The soil has a very weakly developed structure that is weakly porous at 0-15 cm and weak subangular to single grain porous structure at 15-30 cm depth (Table 3). Few clay illuviation features occur, and where they occur they have been ingested by fauna. The soil has few faunal and root channels at 0-15 cm depth, but these are common at 15-30 cm depth. Faunal and root channels measure up to 5 mm Ø (Table 3).

Handhoeing plus manure (HH+M) contained no slaking crusts. Below 15 cm depth, the soil is relatively stable, but voids are blocked by soil fragments, hence is less porous compared to the 0-15 cm depth which is very porous (Figure 4c). The soil has a weakly developed structure in both 0-15 cm and 15-30 cm depths, although the peds are slightly compacted at 15-30 cm depth than at the top (0-15 cm depth) (Table 3). The soil has many faunal and root channels measuring up to 5 mm Ø.

Under oxen ploughing minus manure (OP-M), slaking of the groundmass and deposition of the material into a slaking crust typically composed of smaller and coarser grained microlayers occurs at 0-7 cm depth (Figure 4d, 5b). There are pieces of slaking crusts from previous growing seasons or internal slaking ploughed into the soil. The soil has a very weakly developed structure in the top 15 cm and a weak subangular structure to single grains at 15-30 cm depth (Table 3). The soil is weakly porous at 0-15 cm and porous at 15-30 cm depth. The soil has few faunal and root channels in both 0-15 cm and 15-30 cm layers, with some measuring up to 2 mm Ø (Table 3).

Table 3. Microscopic (micromorphological) analysis of the thin sections across different treatments, Saria, Burkina Faso

Treatment	Description
Saria fallow (0-15 cm):	Layer I (0-15 cm) • Layer is light brown; is more or less uniform in structure with slight slaking in top 0-0.5cm, • Has very weakly developed structure (near structureless), composed largely of single loose grains, is porous; • Has very few ferruginous or iron concretions, • Has common faunal & root channels (up to 3 mm ∅)
Saria fallow (15-30 cm):	Layer II (15-19 cm) • Layer has same features as 0-15 cm (is brown, very weakly developed structure with single grains loosely packed, few iron concretions). • Layer has common faunal and root channels up to 3 mm ∅)
	Layer III (>20 cm) • Layer is yellowish brown • Is weakly subangular blocky to single grain, porous • Has few iron concretions, • Has common faunal & root channels (up to 5 mm ∅).
Saria 3 (0-15 cm): **(Hand hoeing minus manure)**	Layer I (0-3 cm)-light brown • Slaked top layer is deposited in several fluxes, • Layer has very weakly developed structure, weakly porous • Is composed of sorted mineral grains (up to 1600 µm ∅) and rock fragments (up to 2 µm ∅) and few iron concretions or nodules (up to 3 mm∅); • Few faunal & root channels
	Layer II (3-15 cm)-brown • Layer has very weakly developed structure; porous • composed of sorted mineral grains (up to 1600 µm ∅) and rock fragments (up to 2 µm ∅) and common iron concretions or nodules (up to 1200 µm ∅); • Common elongated, smooth to round faunal and root channels (up to 3 mm ∅).
Saria 3 (15-30 cm):	Layer III (15-30 cm)-yellowish brown • Colour and features similar to fallow (20-30 cm layer) • Is weakly subangular blocky to single grain, porous • Has very few iron concretions, • Has common faunal & root channels (up to 5 mm ∅).
Saria 3 (0-15 cm): **(Hand hoeing + Manure)**	Layer I (0-6 cm)-light brown • Layer has weakly developed structure to single grains, is very porous • Is composed of sorted mineral grains (up to 1400 µm ∅) and rock fragments (up to 2200 µm ∅) and common iron concretions or nodules (up to 3 mm ∅); • common faunal & root channels (up to 6 mm ∅).
	Layer II (6-15 cm)-is light brown • Layer has weakly developed structure, grains slightly massive than 0-6 cm; layer is porous • Is composed of sorted mineral grains (up to 1400 µm ∅) and rock fragments (up to 2200 µm ∅) and common iron concretions or nodules (up to 3 mm ∅); common faunal & root channels (up to 3 mm ∅).

Table 3 (Continued)**.** Microscopic (micromorphological) analysis of the thin sections across different treatments, Saria, Burkina Faso

Saria 3 (15-30 cm): **(Hand hoeing + Manure)**	Layer I (15-30 cm)-yellowish brown • Layer has weakly developed structure, but more massive than 0-15 cm layers; is porous • Is composed of sorted mineral grains (up to 1400 µm ∅) and rock fragments (up to 2200 µm ∅) and very few iron concretions or nodules (up to 2 mm ∅); • Many faunal & root channels (up to 5 mm ∅)
Saria 3 (0-15 cm) **(Oxen plough minus manure)**	Layer I (0-7 cm)-light brown • Top layer up to 7 cm depth is slaked and in several fluxes • Layer has very weakly developed structure, is porous • Is composed of sorted mineral grains (up to 800 µm ∅) and rock fragments (up to 800 µm ∅) and common iron concretions or nodules (up to 6 mm∅); • Few to common faunal & root channels (up to 3 mm∅).
	Layer II (7-15 cm) • Layer has very weakly developed structure, is porous • Is composed of sorted mineral grains and rock fragments (up to 800 µm ∅) and common iron concretions or nodules (up to 3 mm∅); • Few to common elongated, irregular smooth faunal & root channels (up to 1 mm ∅).
Saria 3 (15-30 cm) **(Oxen plough minus manure)**	Layer III (15-19 cm)-colour same as in layer 7-15 cm; features similar. • Layer has very weakly developed structure, weakly porous • Is composed of sorted mineral grains and rock fragments (up to 800 µm ∅) and few iron concretions or nodules (up to 2 mm∅); • Few to common faunal & root channels (up to 2 mm ∅).
	Layer IV (19-30 cm)-same as fallow >20 cm • Layer is yellowish brown • Is weakly subangular blocky to single grain, porous • Has few iron concretions, • Has common faunal & root channels (up to 5 mm ∅)
Saria 3 (0-15 cm) **(Oxen plough + manure)**	Layer I (0-4 cm)-light brown • Top layer up to 4 cm depth is slaked and in several fluxes • Layer has very weakly developed structure, is weakly porous • Is composed of sorted mineral grains (up to 800 µm ∅) and rock fragments (up to 1500 µm ∅) and few iron concretions or nodules (up to 3 mm∅); • Very few faunal & root channels (up to 3 mm∅).
	Layer II (4-15 cm)-light brown • Layer has weakly developed structure, grains slightly massive; layer is porous • Is composed of sorted mineral grains (up to 1000 µm ∅) and rock fragments (up to 2600 µm ∅) and few iron concretions or nodules (up to 3 mm ∅); • Has common faunal & root channels (up to 3 mm ∅).
Saria 3 (15-30 cm) **(Oxen plough + manure)**	Layer III (15-30 cm)-is yellowish brown • Layer has weakly developed structure-weakly subangular blocky to single grains, but more massive than 0-15 cm layers; is porous • Is composed of sorted mineral grains (up to 1200 µm ∅) and rock fragments (up to 3400 µm ∅) and very few iron concretions or nodules (up to 2 mm ∅); • Many faunal & root channels (up to 10 mm ∅).

Under oxen ploughing plus manure (OP+M), the top layer has a slaking crust of 4 cm deposited in several layers. Internal slaking features were observed in the soil, indicating that the soil is unstable (Table 3). Internal slaking increases with increasing depth. Internal slaking also occurs along biological (root) channels, but the coating thus formed is deformed and the root channels have been infilled. The soil has a very weakly developed structure in the top 0-15 cm and a weak subangular blocky structure at 15-30 cm depth, although the grains are slightly compacted (Table 3). The soil is porous both at 0-15 and 15-30 cm depth. At 15-20 cm depth, infilled channels have been filled with burnt organic materials. The layer is darker in colour because it has been filled with materials from the sandy top layer. Below the infilling clay coatings were observed. The soil contains few faunal and root channels in the top 15 cm, but their abundance increases with depth resulting in many channels at 15-30 cm depth, some measuring up to 10 mm Ø (Table 3).

Nature and occurrence of faunal features; Saria

Three types of fauna and fauna generated pedofeatures were observed across all treatments in Saria:

1. **Mesofauna features: a)** formed by mites whose organic excrements are ellipsoidal/spheroid (80-90 µm long; 40-50 µm wide) in or around decomposing roots and farm yard manure (Figure 6a), b) collembolla with dark round excrements (20 µm ∅) also loosely deposited in roots (Figure 6a), c) enchytraeids whose clay rich organo-mineral excrements occur in small faunal channels (≤100 µm Ø) or in the groundmass (Figure 6b). In most cases the channels are completely infilled with loosely deposited small (25 µm) clay-rich organo-mineral excrements, Generally, most of the mesofaunal voids (≤100 µm Ø) are round and irregularly shaped or are long, with irregularly shaped rough walls with a diameter ≤100 µm.

2. **Earthworm features (a)** small, interconnected, irregular faunal channels (350-500 µm Ø). The channels are largely infilled with organo-mineral excrements (100-400 µm Ø), ellipsoidal/ovoid/spheroid or amalgated and locally excrements contain coarse mineral grains or small rock fragments measuring up to 30 µm Ø (Figure 6c), (b) with long elongated channels up to 3 mm wide. The worms also produce bigger organomineral excrements measuring up to 1.5 mm Ø. The excrements occur either as single mass or in clusters within the channels or are amalgated (Figure 6b, c).

3. Termite features: Irregular interconnected channel systems, measuring up to 3 mm Ø with smooth surface; rarely with excrements and no compaction or pressure on the walls (Figure 6d). Infilled irregular channels measure between 1.1 and 3 mm Ø, and some are filled with loosely accumulated mineral grains (40-100 µm Ø), groundmass fragments (600-1300 µm Ø), root fragments (60 µm Ø) or sometimes excrements of other fauna. (Figure 6d). Due to instability of the Saria soils, they are sometimes difficult to distinguish from other voids.

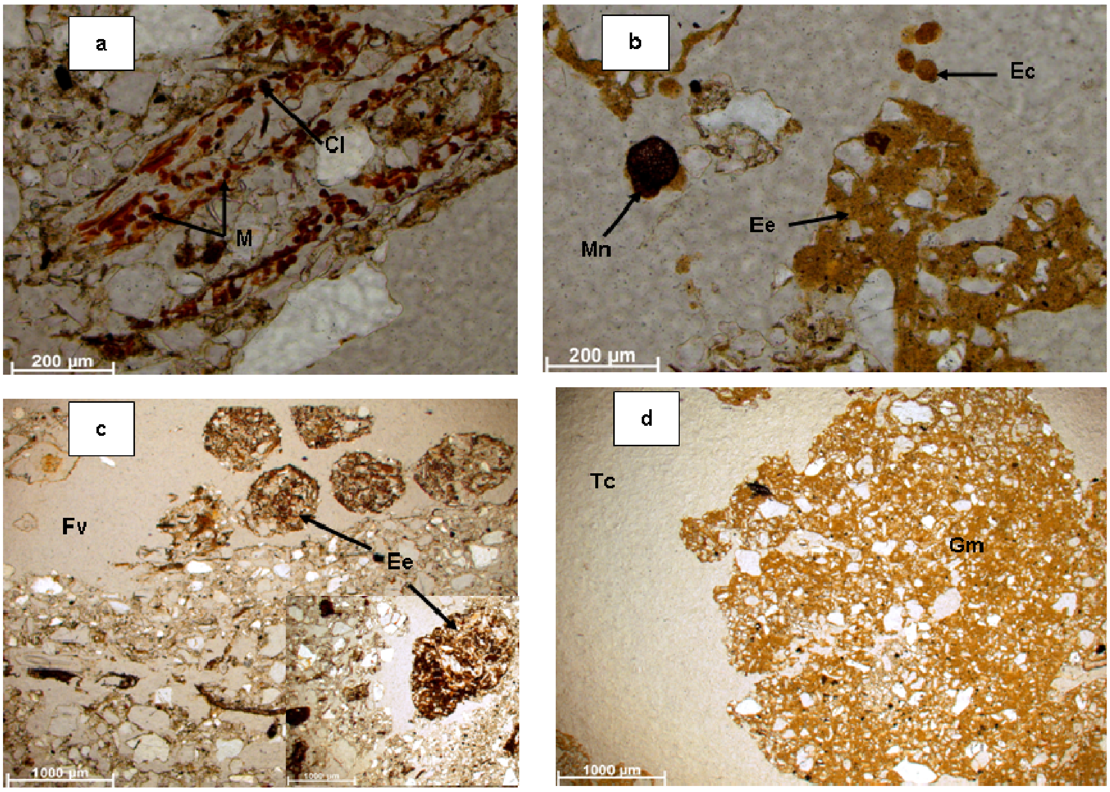

Figure 6. Biogenic features in the Saria field trial. (a) Fallow (0.5 cm depth): M = mite excrements, Cl = collembolla excrements within manure fragment, (b) OP-M (17 cm): Ec = enchytraeid excrement, Ee = earthworm excrement, Mn= farm yard manure, (c) Fallow (0.5 cm): Ee = earthworm excrement, Fv = faunal void, (d) OP-M (24 cm): Tc = termite channel, Gm = groundmass.

Microscopic analysis of faunal features; Saria

Under NF$_s$, earthworm excrements and mesofauna excrements are common. Collembolla and mites are common in the top 0-15 cm layer, whereas enchytraeids are many towards lower layer (15-30 cm), and their excrements (100 µm ∅) are dark because they contain organic materials and loam that has passed through the gut. Earthworm excreta in the bottom layers (>15cm) are composed of relatively coarse mineral grains unlike the top 0-15 cm layer whose worm excrements have fine mineral grains.

Under HH-M, faunal features are very few, although a few earthworm and termite channels occur below 5 cm depth. Under HH+M many faunal features occur. Organic matter has been eaten by mesofauna (e.g. enchytraeids). Earthworm excrements measure up to 1.6 mm and are partly eaten by mesofauna. Deeper in the soil profile (15-30 cm), there are few remnants of manure are few and the mesofauna features occur close to clay illuviation features. Mesofauna features also occur in decaying roots and in root channels (Table 3).

Under OP-M there are hardly any faunal features in the top 0-15 cm layer, but few earthworm channels occur in the 15-30 cm layer (Figure 4d). Under OP+M, faunal features are few in the top 15 cm, but deeper in the soil profile fragments of earthworm excrements occur. Earthworm features are degraded and remnants of farm yard manure are eaten by enchytraeids. Faunal activities occur deeper in the soil profile in the OP+M treatment compared to HH+M. Some faunal features, e.g. earthworm excrements, have been deposited into voids indicating the instability of the soil. In the deeper layer (15-30 cm) mesofauna rework the rotten rocks resulting in yellow feacal pellets of 70-80 µm Ø). Mesofauna have also partly consumed clay illuviation features resulting in the gradual disappearance of these features.

Quantification of different biogenic features across management systems; Saria

A higher proportion of biogenic features was observed in the NF_{Saria} and HH+M treatments than in all other treatments (Table 4). The proportion of biogenic features in the handhoeing treatments, especially in HH+M was higher in the upper layers (0-15 cm) than in the 15-30 cm layer, whereas a reverse trend was observed in oxen ploughed treatments (Table 4). Treatments without manure had lower proportions of biogenic features compared to treatments with manure (Table 4). The proportion of earthworm features ranged from 2-20%. The highest proportion of earthworm biogenic features (20%) was observed in NF, whereas the lowest proportion (2%) was observed in OP-M. The proportion of termite features was generally low across treatments, and the highest proportion (5%) was observed in NF. Except for treatments with manure in which termite features were observed in the upper layers, this was rarely the case for the other treatments including NF (Table 4). Mesofauna features were higher in NF and in HH+M than in the other treatments and treatments with manure had higher proportions of mesofauna features than treatments without manure. Mesofauna features were higher in the upper layers (above 15 cm) compared to lower layers (below 15 cm) for all treatments (Table 4). Root channels were few across treatments (<2%), with the highest proportion being observed in NF (Table 4). Roots were rarely found in the 0-3 cm layer of HH-M and in the 0-7 cm layer of OP-M (Table 4).

Table 4. Quantitative distribution of biogenic features across different treatments, Saria, Bukina Faso. NF = natural fallow; HH-M = Handhoeing minus manure; Handhoeing plus manure; OP-M = Oxen plough minus manure; OP+M = Oxen plough plus manure. <1% = Very few to rare, 1-5 = Few, 6-10 = Common; 11-20 = Many; >20 Very many. In parentheses are the standard errors.

		Earthworms	**Termites**	**Mesofauna**	**Root channels**
Treatment	**Depth (cm)**	------------------Volume % based on estimate of surface area of feature-----------------			
NF	0-6	14.8 (0.7)	0.0 (0.0)	22.9 (1.5)	1.5 (0.4)
NF	6-15	11.7 (3.9)	0.0 (0.0)	18.5 (1.1)	1.0 (0.7)
NF	15-19	15.1 (0.2)	0.0 (0.0)	14.9 (0.4)	0.0 (0.0)
NF	19-30	20.0 (1.9)	5.4 (0.1)	10.8 (0.1)	0.6 (0.4)
HH-M	0-3	5.6 (1.1)	0.8 (0.6)	8.2 (0.3)	0.0 (0.0)
HH-M	3-15	7.9 (0.2)	2.8 (2.0)	8.2 (0.4)	0.7 (0.1)
HH-M	15-30	11.5 (1.1)	3.6 (0.0)	7.0 (0.1)	0.0 (0.0)
HH+M	0-6	19.7 (7.9)	0.8 (0.6)	10.7 (1.0)	0.0 (0.0)
HH+M	6-15	12.7 (1.5)	1.4 (1.0)	12.7 (0.3)	0.2 (0.1)
HH+M	15-30	11.9 (0.5)	0.2 (0.1)	8.0 (1.0)	0.3 (0.2)
OP-M	0-7	2.1 (0.9)	0.0 (0.0)	8.5 (1.2)	0.0 (0.0)
OP-M	7-15	8.9 (0.6)	0.0 (0.0)	9.1 (0.1)	0.0 (0.0)
OP-M	15-19	12.2 (0.5)	1.4 (1.0)	7.7 (0.3)	0.1 (0.1)
OP-M	19-30	10.9 (0.6)	0.0 (0.0)	7.6 (0.3)	0.0 (0.0)
OP+M	0-4	10.4 (2.0)	1.2 (0.9)	12.0 (0.3)	0.2 (0.1)
OP+M	4-15	16.7 (0.6)	0.0 (0.0)	10.8 (2.2)	0.4 (0.3)
OP+M	15-30	16.2 (2.1)	0.6 (0.4)	7.0 (0.4)	0.0 (0.0)

Discussion

Our study has shown that soil tillage practices and addition of organic inputs influence soil fauna activities and hence soil structure and soil physical properties. Natural fallow represents relatively undisturbed conditions with a permanent soil cover, in which mechanical soil disturbance is minimal and organic matter accumulation is high. These conditions are suitable for macrofauna activities and resulted in highly porous soils with well developed structure. In arable systems the impact of soil fauna on soil structure, however, depends on the type and extent (i.e. depth) of tillage (Hulsmann et al., 1998; Fujita et al., 2000). No till plus residue application in the sub-humid climate of Nyabeda and handhoeing plus manure in the semi-arid climate of Saria enhanced soil fauna activities resulting in improved aggregate stability, a well developed soil structure, and highly porous soil. In no till, soil disturbance is minimal and this in addition to organic residue inputs could have favoured soil fauna, whereas addition of manure in handhoeing treatments could have enhanced soil fauna activities. Many studies have shown that reduced soil disturbance enhances soil fauna activities hence improves soil physical properties (Kooistra et al., 1990; Fujita et al., 2000; Bottinellia et al., 2009; Hoogmoed, 2009). Fujita and Fujiyama showed that abundance and diversity of enchytraeids and oribatids were greater under no-till practices because it offered a suitable humid microenvironment for these two groups of mesofauna.

Among the management practices assessed across two agroecological zones, fallowing, conservation tillage plus residue application (in East Africa) and hand-hoeing plus manure (in West Africa) enhanced biogenic soil structure formation, resulting in a well developed soil structure and a continuous pore system through many faunal channels. By contrast, intensive tillage and absence of organic inputs resulted in soil with less biogenic soil structural features and was, therefore, prone to slaking. Handhoeing and oxen-ploughing resulted in many internal slaked crusts in deeper layers. Internal slaking is typical of arable systems of the tropics and is due to low organic matter content and the soils being bare for part of the year (Maja Kooistra, personal communication). Low faunal activities under intensive tillage could be linked to soil disturbances and corresponding lower food supply. Human activity imposes severe and repeated stress on the soil community. Increasing human intervention (ploughing etc) generally destroys the habitat of soil organisms, thereby eliminating natural homeostatic mechanisms and preventing ecosystem self-regulation (Altieri, 1991). Hullsmann and Wolters, 1998 showed that the effect of cultivation on mesofauna such as mites and microarthropods is negative, although different taxa react differently. This was attributed to both disturbance and sudden exposure to adverse conditions.

Our results compare well with earlier studies, in which it was reported that soil physical properties such as aggregate stability, porosity are positively linked to soil fauna activities. In a study conducted across different land use systems in Ibadan, Nigeria, Kooistra et al. (1990) observed that forest pedons had higher faunal activities with evidence of transported fine-grained soil materials, including intact clay illuviation features by soil macrofauna species from the subsoil to the surface. Zero till with residues had a stable layer with worm channels reaching up to the surface. However, in zero-till without mulch cover, the fine-grained materials in the surface layer were eroded following forest clearance and cropping. Such plots showed surface crusting and poor water infiltration during rainstorms. Mechanically-cultivated fields had severe crusting in the unmulched fields and consequently had poor water infiltration. Other studies have also shown the positive influence of soil fauna on soil physical properties with likely positive consequences on crop productivity (Mando, 1997; Blanchart et al., 1999). Mando and Miedema, (1997) showed that mulching enhances termite activities, thus playing an important role in the modification of soil physical structure (e.g. aggregation and porosity) in semi-arid environments. Management practices that enhance termite activities could be an option to consider when improving degraded soils.

The two study sites of Nyabeda and Saria are set under two contrasting agroecological conditions (sub-humid climate in Nyabeda and Semi-arid climate in Saria) which differ in the way they influence soil fauna and soil fauna functioning. Nyabeda climate and clay texture is more favourable and the soil at has a high inherent organic matter content hence had high faunal activities compared to arid conditions and sandy soil of Saria that have low organic matter content. Nyabeda soil also has a clay texture, a well developed and porous soil structure whereas the soil at Saria has a loamy sand texture with a weakly developed structure. Although organic matter addition through manure enhanced soil fauna activities and resulted in little improvement in soil structure, Saria soil is still unstable and has many infilled or collapsed channels and discontinuous pores hence is less porous. The natural fallow of Saria, however, had more roots, remnants of roots, pollen and sporangia compared to Nyabeda fallow.

Conclusions

Our study has shown that tillage and addition of organic inputs influence soil fauna activities with a significant impact on soil structure and hence soil physical properties. Among the management practices assessed across two agroecological zones, fallowing, conservation tillage plus residue application (in East Africa) and hand-hoeing plus manure (in West Africa) enhanced biogenic soil structure formation, resulting in a well developed soil structure and a continuous pore system through many faunal channels. By contrast, intensive tillage and absence of organic inputs resulted in soil with less biogenic soil structural features and was, therefore, prone to slaking.

Acknowledgements

This study was supported by Science for Global Development/WOTRO through Wageningen University and Norman Borlaug LEAP Fellowship Program through UC-Davis. We thank our partners, especially the scientists and field technicians of the Tropical Soil Biology and Fertility Institute of the International Centre for Tropical Agriculture (TSBF-CIAT, Kenya), International Fertilizer Development Centre (IFDC, Burkina Faso), Institute of Natural Environmental and Agricultural Research (INERA, Burkina Faso). We sincerely thank Adama Ouédraogo and Michael Adhaya who helped with field sampling of thin section, the World Soil Reference Centre (ISRIC) in Wageningen, and especially Jan Huting, for facilitating access to microscope and Hans Huisman from the Cultural Heritage Agency in Amersfoort for using the scanning camera.

CHAPTER SIX

Farmers' perception of the presence and role of termites in Western Kenyan farming systems

F.O. Ayuke [a*, b], B. Vanlauwe [b], J. Chianu [b], N.K. Karanja [c], R.G.M. de Goede [a], J. de Graaff [d], M.M. Pulleman [a]

[*a] *Department of Soil Quality, Wageningen University, P.O Box 47, NL-6700 AA Wageningen, The Netherlands*

[b] *Tropical Soil Biology and Fertility (TSBF) Institute of CIAT, P.O Box 30677-00100, Nairobi, Kenya*

[c] *Department of Land Resource Management and Agricultural Technology, University of Nairobi, P.O Box 30197, Nairobi, Kenya*

[d] *Department of Land Degradation and Development, Wageningen University, P.O Box 47, NL-6700 AA Wageningen, The Netherlands*

*Corresponding author: (0317) 486524; Fax: (0317) 419000

Email: fredrick.Ayuke@wur.nl or fredrick.ayuke@yahoo.com*

Submitted to Ecology and Society

Abstract

Termites play an important role in soil structure formation and nutrient cycling in (sub-) tropical ecosystems, but some species are potential pests to crops. Farmers' knowledge and perception of termites and their effects on crop production can enrich scientific understanding of the ecology and sustainable management of termites under different agro-ecological conditions. We studied farmers' knowledge on the occurrence and behavior of termites, their perception of the importance of termites in their cropping systems, and the management of termite activities in their farm fields in Nyabeda, Western Kenya. In total, 104 households from 13 villages were consulted using structured questionnaires and focus group discussions. Relationships between socio-economic factors, farmers' perception variables and termite management practices were explored using Redundancy Analysis. All farmers were aware of the existence of termites and their activities, and had local names for specific termite taxa. About 90% of farmers perceived termites as pests, whereas 10% felt that termites had both harmful and beneficial effects. To control termites, 38% of the farmers used pesticides whereas another 27% combined pesticides with traditional measures, further indicating their low awareness of the beneficial roles ascribed to termites. Farmers rated maize (*Zea mays*) as the most susceptible crop to termite attack, especially during the flowering and tasseling stages, and in particular during wet months. The lowest and highest perceived yield losses of maize due to termite damage were 2% and 86% respectively, but the majority of the households reported losses ranging between 11 and 20%. Redundancy Analysis showed that "geographic location" explained 23% of the variance in farmers' perception and management of termites. Socio-economic variables explained another 5%. Villages that applied diverse termite-control measures reported low yield losses compared with those that applied none, and the location of these villages corresponded with loam soils that farmers associated with prevalent termite damage. This study demonstrates that farmers in Nyabeda viewed termites as pests and use of pesticides and other control measures is widespread. This calls for more scientific studies to assess the trade-offs between positive and negative impacts of termites on crop yields, as well as on the effects of control measures used by farmers on agroecosystem functions. The results also highlight the need for participatory approaches that stimulate farmer-scientist

communication on sustainable termite management, and ensure that research efforts anticipate the factors that enhance or constrain adoption by farmers.

Keys words: Knowledge, perception, termites, crop production

Introduction

Soil biota communities comprise a diversity of organisms that control essential ecosystem functions and services (e.g. organic matter decomposition, biological pest control, soil structure formation and nutrient and water cycling), although some are potential soil-borne pests or diseases for agricultural crops. Termites are considered important ecosystem engineers for their role in soil structure formation and organic matter decomposition (Mando, 1997; Asawalam et al., 1999; Jungerius et al., 1999; Jouquet et al., 2007) and nutrient cycling (Collins, 1981; Martius, 1994; Wood, 1996; Mando and Brussaard, 1999). It has been demonstarted that termite activities can enhance soil fertility and productivity, especially in low-input agricultural systems (Mando, 1997; Roose et al., 1999). In some cropping systems of sub-Saharan Africa, soil from termitaria (termite mounds) is spread onto arable fields to improve soil physical conditions, supply nutrients, and as a consequence, increase crop yields (Nyamapfene, 1986; Logan, 1992). Other farmers leave the mounds intact and plant crops around them (Sileshi et al., 2009). The Zaï traditional soil restoration system practiced in Burkina Faso is based on the use of organic residues which are concentrated in planting basins to, amongst other uses, attract termites which improve water infiltration and availability to crops by creating channels in the soil (Mando, 1997; Roose et al., 1999).

However, despite the potential beneficial role of termites, termite pest problems have been identified as a major constraint to increasing yields of crops such as maize and sorghum, which are the staple foods for millions of people in sub-Saharan Africa (Smale, 1995; Sekamatte et al., 2003; Sileshi et al., 2005). Termite damage has also been a hindrance to afforestation initiatives (Wardell, 1990, Mitchell, 2002). Harvester termites (*Trinervitermes trinervoides*) and *Hodotermes mossambicus* (Hodotermitidae) are major players in the destruction of rangelands in the arid and semi-arid areas. It is therefore not surprising that so far most research on termites in cropping systems is related to crop damage (Sekamatte et al., 2003; Sileshi et al., 2005).Yet only 10% of the more than 2,500 species are considered harmful to crops and trees (Tano and Lepage, 1996; Wood 1996) and out of the 50 termite genera so far recorded from Southern Africa, only 18 have one or more known pest species (Mitchell, 2002). Members of the fungus-growing subfamily Macrotermitinae (Termitidae) are responsible for the majority of crop damage and tree mortality (Mitchell, 2002).

The challenges therefore remain to better understand the interactions between agricultural management practices and soil macrofauna (e.g. termite) effects in order to find ways to enhance soil fertility and crop yields. The design of sustainable crop production systems which are based on management practices that stimulate the beneficial effects of termites and other soil fauna on soil fertility is an important area for scientific research with relevance in rural development in regions practising low-input agriculture. It is against this background that on-going international programmes such as Biodiversity Monitoring Transect Analysis in Africa (BIOTA), the GEF-UNEP programme on the Conservation and Management of BelowGround BioDiversity (CSM-BGBD) and the Dutch WOTRO-funded project “More Crop per Drop, More Cropping per Dropping” were conceived (Bignell et al., 2008). With considerable interest in biodiversity conservation, such studies may help explain the underlying causes of biodiversity changes across different land use systems, and implications for ecosystem services.

Whereas the significant roles of termites in tropical ecosystems are widely expressed in the scientific literature (Collins, 1981; Wood, 1996; Asawalam et al., 1999; Mando et al., 1999; Mitchell, 2002), less is known about farmers’ perception and management of termites in low input cropping systems. Farmers’ perception is based on local experience and indigenous knowledge which can provide valuable insights not presently covered in scientific literature. Scientists can learn from farmers’ knowledge about termites and their behavior and impact on crop production and their management under different agro-ecological conditions. Insights on farmers’ perception may also provide scientists with some understanding on how research could be conducted so as to address the needs and constraints of farmers. Technologies that scientists develop and promote would only have impact if they met farmers’ realities (Van Huis et al., 2007; Tittonell et al., 2008).

Our study was thus aimed at disclosing farmers' knowledge and perception on the roles of termites in Western Kenya, one of the benchmark sites of the Tropical Soil Biology and Fertility Institute of the International Centre for Tropical Agriculture (TSBF-CIAT). Western Kenya, comprises the Nyanza and Western Provinces of Kenya and covers an area of 20, 719 km^{-2}, situated between latitude 1° 8′ N and 1° 24′ N, and between longitude 34° and 35° E (Figure 1).

Western Kenya, the home of over 8 million people is one of Kenya's most densely populated regions. Rural population densities range from 400 to 1300 persons km^{-2}, with the highest densities being in Vihiga and Kakamega districts of Western province (Kenya Ministry of Agriculture and Rural Development, 2001).

The agroecological conditions in Western Kenya are characterized by very gently undulating landscapes with slopes between 2 and 8% to the east and fairly flat areas to the west. The elevation ranges from 1000 to 1600 masl, with a semi-humid climate, bimodal rainfall distribution with two cropping seasons per year. Annual rainfall in western Kenya ranges from less than 1000 mm near the shores of Lake Victoria to 2000 mm away from the lake shores. Temperatures vary with season and altitude; the mean daily maximum is 29° C, whereas the mean daily minimum is 15° C (Jaetzold and Smith, 1982). Soils in this region vary widely, the dominant types being Acrisols, Ferralsols and Nitisols (Jaetzold and Smith, 1982; FAO, 1989; Andriesse and van der Pouw, 1985). These soils are acidic, easily compacted and prone to erosion. In addition, they are poor in organic matter content and have low reserves of nitrogen, phosphorus, potassium and some trace elements. Even the naturally fertile Nitisols still need fertilizer application because once the vegetative cover is removed and land intensely cropped with grain crops, they experience a fast degradation in physical, chemical and biological properties (Sanchez et al., 1997). Population growth has led to gradual depletion of nutrients through crop harvest removal, leaching, and soil erosion, and farmers are unable to compensate for this loss (Shepherd and Soule, 1998). With the liberalization of trade, fertilizer costs have increased to an unaffordable level to small-scale farmers. How to increase and maintain crop yields to meet the needs of the growing population is a major challenge. Thus research efforts that address biophysical and socio-economic factors that are a constraint to improved crop production are of high priority.

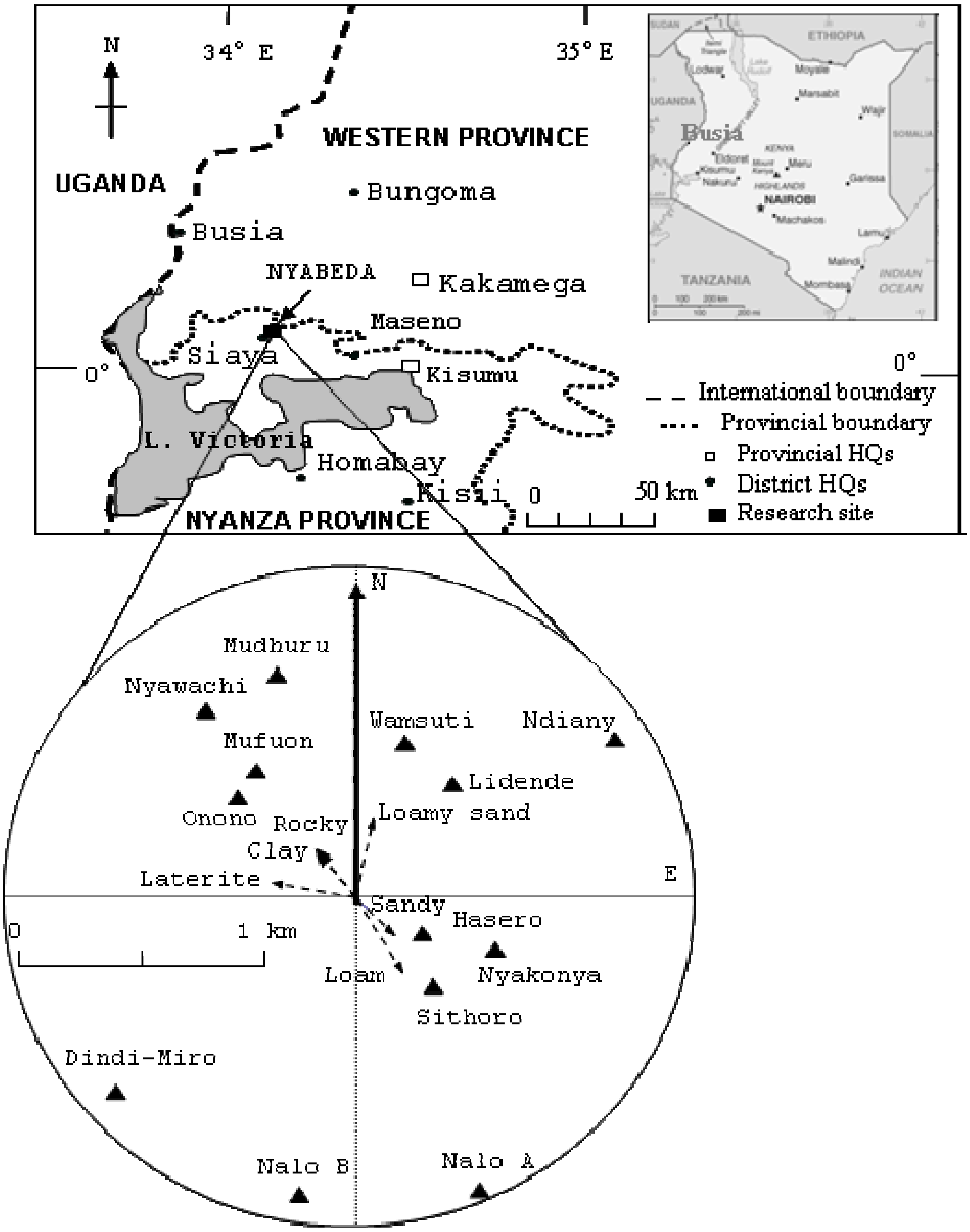

Figure 1. Study site and the distribution of the villages within Nyabeda location. In the cycle are results of RDA analysis with two response variables (coordinates: latitude and longitude, and soil type). Direction (N) is presented as solid arrow. Broken arrows represent corresponding village soils based on farmers' classification.

The dominating ethnic group in western Kenya is the *Luhya* (Bantu speaking tribe), with several sub-tribes showing little differences in language and culture, and with a common agricultural background. Along the shores of Lake Victoria and several km inland the *Luo* are found (a sub group of the River-Lake Nilotes) who were considered earlier as fishermen. On the border with Uganda the Teso people live, who are more broadly represented in Uganda than in Kenya.

The land use systems are fairly diversified and range from subsistence smallholdings in Siaya, Kakamega and Vihiga districts to the more cash-oriented farms in the sugar belt and in the northern regions (Rotich et al., 1999). Due to high population in the subsistence smallholder sector, farm sizes tend to be small, ranging from 0.2 ha to 2.5 ha and the mean household size is 7 persons (Kenya Ministry of Agriculture and Rural Development, 2001). Most households rely on the farm for about 15% of their cash income. The remainder comes from remittances from relatives and small amounts of off-farm income (Tittonell et al., 2005). Incentives for investing capital and labour in farming activities is lacking because expected profits are low. Agriculture in western Kenya is dominated by subsistence farming. Smallholders often intercrop Maize (*Zea mays*) with beans (*Phaseolus vulgaris*), but maize yields are usually low (on average 1 Mg ha^{-1} per season). Banana (*Musa nana*), cowpeas (*Vigna sinensis*), groundnut (*Arachis hypogaea*), cassava (*Manihot esculenta*), sorghum (*Sorghum spp.*) and finger millet (*Eleusine coracana*) are grown on a small scale, but are increasing towards the west. Because the amount of land is limited, livestock numbers are small. Goats and sheep are less common than cattle. The local breeds are usually kept as liquid cash, to sell when necessary, and for beef, milk and manure. Three major farm typologies exist in Western Kenya (Tittonell, 2003): First the few highly endowed types that largely depend on off-farm income. They tend to minimize land and labour limitations by hiring, and to increase their production by intensification (through input use). A few may also be market-oriented. They have the highest variability in land quality and production activities, acquiring labour and input from the market. Second, the relatively large, but moderately endowed type. These are labour-limited subsistence farms. They have the largest grain production under low input selling their surpluses on the market, and often alternative (seasonal) enterprises are observed in these farms (e.g. oxen services, buying and retailing grains at farm gate). A few are, however, not self-sufficient in grain production. Third, the majority which mostly sell their labour to the wealthier farm types. Farm typology is important because it is among the factors that determine crop choice (production activity choice), and can influence decision-making, especially when dealing with resource allocation (Tittonell et al., 2005).

The objectives of the study were to: (i) disclose farmers’ knowledge about the occurrence of termites and their behavior in their farming systems, (ii) describe their perceptions of the beneficial and detrimental effects of termites on food production, (iii) document the practices used for the management of termites in their cropping systems, and (iv) explore the relations between farmers’ perceptions and management of termites, and farmer socio-economic circumstances to identify underlying factors in farmers’ responses.

We hypothesized that farmers would have a positive attitude towards termites, and could play an important role in their management/conservation, if they are sufficiently knowledgeable about their beneficial activities. Variations in the characteristics of the individual farming systems partially arise from resource endowment and family circumstances that constitute the socio-economic and human elements of a system. It was therefore postulated that social attributes would influence the way farmers perceive and manage termites in their cropping systems.

Materials and Methods

Study sites

The study was conducted in Nyabeda, western Kenya, which is situated at latitude: 0° 06′ N and longitude: 34° 36′E, and at an altitude of 1420 meters above sea level. This location was considered representative for typical Western Kenya smallholder conditions. The area falls within the humid agroclimatic zone with a mean annual rainfall of 1800 mm which is bimodally distributed (March-July and August-November), and a mean monthly temperature of 23° C (Jaetzold and Schmidt, 1982). The soils are predominantly Humic Ferralsols with clay texture (Jaetzold and Schmidt, 1982). The principal ethnic community is *Luo,* a subgroup of the River-Lake Nilotes.

Data collection

The survey was carried out between December 2008 and June 2009 in 13 villages at Nyabeda (Figure 1). Data was collected in three steps. First, we collected information about the total number of farm households in each of the 13 villages of Nyabeda from three key informants who were the area chief and two field research assistants who worked for TSBF-CIAT. Sixty farmers randomly chosen were interviewed in a preliminary reconnaissance survey following Participatory Rural Appraisal (Okoba, 2005) that served two purposes: to collect qualitative basic information that was used to design the questionnaires used in step 2, and to train the enumerators on how to conduct the survey and how to interpret and translate the questions. In each village, names of all households were listed and, using lottery, 8 households from each of the 13 villages were drawn for administering of the questionnaires during the second phase.

During the second phase, a structured questionnaire was administered to 104 of the 317 households in the research area, the locations of which were also geo-referenced. The purpose of these structured questionnaires was to collect quantitative data on the socio-economic characteristics of the farm households and the farmers' perception and the management practices used to control or stimulate termite activities in the farm fields. Based on the socio-economic characteristics of the farming systems as obtained from interviews with the key informants and the preliminary survey, farm households were classified into the following resource endowment categories according to Mtambanengwe and Mapfumo (2005): Resource-endowed (High), Intermediate (Moderate) and Resource-constrained (Low) (Table 1). The classification criteria used were not mutually exclusive, but those which fulfilled most of the criteria were assigned to the corresponding endowment category. The interviewees were not informed about the classification on the basis of resource endowment criteria. The third phase of the study consisted of a focus group discussion (FGD) attended by 24 farmers, with the main purpose to validate the responses obtained during the household survey. The farmers who participated in the FDG were selected as follows: The 13 villages were first stratified into four regions: Eastern (Nalo A, Lidende, Ndiany), Western (Nyawachi, Wamsuti, Onono), Nothern (Sithoro, Nalo B, Nyakonya) and Southern (Mufuon, Hasero, Dindi, Muthuru). From each region, 6 farmers (two from each of the 3 resource categories, one male and one female) were randomly selected to attend the meeting.

During the second (detailed survey with structured questionnaires) and third (FGD) phase, the following general issues were addressed:

- Farmers' indigenous knowledge about termites: vernacular names of different termite types, nesting habits, and soil type with the highest termite activities.

- Farmers’ perception about the role of termites: are they useful or harmful, and if so how?
- If harmful, what is the nature or type of damage (type of structures/plants attacked by termites) and ranking based on level/seriousness of attack; which were the most susceptible crops; what were the most susceptible crop parts, the stage when crop is most susceptible, and the weather conditions that favor within-season susceptibility; the plant yield component lost due to termites; the estimated potential yield loss for a maize crop.
- Management of termites in the farmers’ cropping systems: what measures do the farmers use to control or stimulate termite activities?

Table 1. Descriptive criteria (composite index) for classifying farmers in terms of resource endowment at Nyabeda, Kenya. Adapted from Mtambanengwe and Mapfumo (2005).

Farmer category	**Description**
Resource-endowed (High)	•Adequate accommodation with stone/brick under galvanized iron sheets, asbestos or grass thatch •Own farming implements, e.g., plough; ox-drawn cart •High livestock ownership with > 10 cattle and at least 2 oxen •Land holding >3 ha •Regular contact with extension agents and generally employ extension agent recommendations, either through direct training or indirectly by copying other farmers •Often have access to credit facilities •Frequently use hired labour
Intermediate (Moderate)	•Varying resource ownership (e.g., may have a plough, but not enough draught animals) •Cattle ownership ≥ 4 and ≤ 10 •Are limited by resource base (most of the relatively young farming households fall into this category •Seek to enhance their production through enhanced communal social arrangements (e.g., sharing draught animals) and active involvement with extension agencies •Land holding averages 2-3 ha •Limited access to credit •No regular pattern for hiring-in or hiring-out labour
Resource-constrained (Low)	•Major constraints include lack of farming implements; lack of draught power and lack of cash to buy inputs •Cattle ownership 0-3 •Variable farm size (0.5 –2 ha), but those with large landholdings typically utilize small proportions of their total arable land •Unlike other farmer groups, they generally have limited source of income •Usually not members of local social groups •Often sell their labour to the other two groups

For the category of estimated potential yield loss, we selected maize because it is the most important staple food that is widely grown in the study area of Nyabeda. During the interviews we asked farmers about their normal total crop production (grain yield) in case they did not experience any problem due to termite attack, and how much they were likely to get or lose in case of termite infestation on their maize crop. Maize yield production and loss were calculated in kilograms of grain per hectare based on the number of 80-kg bags or 2-kg tins (*gorogoro*) as given by farmers during the interviews. Yield loss (kg ha^{-1}) was expressed as a percentage of total average grain yield production (kg ha^{-1}). Perceived yield loss, therefore, applied to the seasons when termite attack was serious.

Statistical Analysis

Descriptive statistics such as frequency distributions of responses in the household survey data were analyzed using the Statistical Package for Social Sciences (SPSS version 15; Kirkpatrick and Feeney, 2005). P values ≤ 0.05 were regarded as statistically significant.

Multivariate analysis was carried out with the programme CANOCO 3.1 (Ter Braak, 1988). Redundancy Analysis (RDA) was used to investigate the correlative relationships of socio-economic and geographic variables: gender, age, education, resource endowment and village (Table 2) with response variables, i.e. farmers' perception variables and management of termites in farmers' fields. Not all variables collected during interviews were used in the analysis, but only those variables that were thought to be directly linked to the farmers' perception about termites. Response variables included in the analysis and the corresponding ranking of the responses are as listed in Table 2. In the first step, we tested to what extent geographic location (village: Nalo A, Nalo B, Lidende, Ndiany, Nyawachi, Wamsuti, Onono, Sithoro, Nyakonya, Mufuon, Hasero, Dindi-Miro and Mudhuru**)** explained farmers' perception and management of termites. In the second step, we selected villages as co-variable and tested how much the other socio-economic factors (age, gender, education and resource endowment) explained farmers' perception and management of termites, independent of farmers' location. The overall contribution of the socio-economic variables to the description of the variation in farmer perception data was tested by a Monte-Carlo test based on 999 random permutations.

Table 2. Variables used in multivariate analysis as ordinal (O) or nominal (N) explanatory (E) and response (R) variables. Categories are based on the responses to the questionnaires.

Variables	**Data type**	**Category**	**Code/Ranking**
Socio-economic variables (E)			
Gender	N	Male	1
		Female	2
Age	O	15-25	1
		26-35	2
		36-45	3
		46-55	4
		>55	5
Education	N	Informal	1
		Primary	2
		Secondary	3
		Tertiary	4
Resource endowment	O	Low	1
		Moderate	2
		High	3
Village	N	Nalo A, Nalo B, Lidende, Ndiany, Nyawachi, Wamsuti, Onono, Sithoro, Nyakonya, Mufuon, Hasero, Dindi-Miro and Mudhuru	
Perception variables (R)			
Role of termites	N	Beneficial	1
		Harmful	2
		Both	3
Types of termite damage and ranking based on structures/plants identified by farmers	N	Crops	1
		Trees	2
		Building structures	3
		Others	4
Most susceptible crop type	N	Maize	1
		Millet	2
		Bean	3

Table 2. (Continued) Variables used in multivariate analysis as ordinal (O) or norminal (N) explanatory (E) and response (R) variables. Categories are based on the responses to the questionnaires.

Most susceptible crop parts	N	Stem/foliage	1
		Roots	2
		All parts	3
Stage when crop is susceptible	N	Seedling	1
		Flowering/tasseling	2
		Harvest	3
		All stages	4
Susceptible period within season	N	Wet	1
		Dry	2
		Both	3
Plant yield component lost due to termites	N	Grain	1
		stover (stem, foliage)	2
		Both	3
Potential grain yield loss for maize	O	Ranked on classes (1-10)	0-10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, 91-100
Management variables (R)			
Control measures	N	None	1
		Pesticides	2
		Traditional	3
		Both (pesticides/traditional	4

Results

Socio-economic information and farming attributes

Of the respondents, 58% was male and 42% female (Table 3). Age distribution ranged from 24 to 84 years with 48% of the respondents being in the age class > 55 years. The majority (> 70%) of the respondents have attained formal education at least to primary level. Of all respondents, 19% belonged to the relatively wealthy farmer class, whereas 42% belonged to the relatively poor class (Table 3). About 60% of the farmers practiced mixed crop-livestock farming, whereas 40% were arable farmers and 37% of them practiced intercropping. More than 72% of the farmers produced a combination of at least three crops: maize, other cereals, and legumes and only 3% practiced monoculture (Table 3). The most common crops grown in the area were: cereals (maize, sorghum, millet and finger millet) and legumes (common beans, groundnut, soybean and cowpeas). Other crops included: cassava, sweet potato, banana and sugarcane. Most households (88%) grew food crops primarily for own consumption, hence crop production in Nyabeda was largely subsistence in nature.

Table 3. Socio-economic information and farming attributes of surveyed farmers in the study area

Category	**Relative distribution (frequency) of responses (%)**	
Socio-economic information		
Gender	Male	58
	Female	42
Age (years)	15-25	1
	26-35	8
	36-45	19
	46-55	24
	>55	48
Education	Primary	42
	Secondary	18
	Tertiary	10
	Informal	30
Resource endowment	Low	42
	Moderate	39
	High	19
Farming attributes		
Farming system	Mixed crop-livestock	60
	Mixed arable intercropping	37
	Monocropping	1
	Crop rotation	2
Crops grown	Maize/legume/cereal monoculture	3
	Maize-legume	22
	Maize-other cereal	3
	Maize-legume-other cereal	72
Type of crop production	Subsistence	88
	Cash	0
	Subsistence and Cash	12

Farmers' knowledge about termites

All farmers in Nyabeda were aware of the existence of termites and their activities as well as their nesting habits (Table 4).

The majority (80%) of the farmers associated termites predominantly with loamy soils, whereas only 2% associated them with loamy sand or rocky soils. Over 60% of the farmers were able to distinguish between more than two types of termites, based on colour and nesting habits, and identified them using their local names. In total, 10 termite species were identified using vernacular names (Table 5).

Table 4. Farmers' indigenous knowledge about termites and their behavior. In parentheses are farmers classifications of the soil types (in *Luo*)

Category	**Relative distribution (frequency) of responses (%)**	
Occurrence or presence of termites	Yes	100
	No	0
Nesting habits	Soil-underground	49
	Mound	51
Soil type with the highest termites activities	Loam (Lwala)	80
	Sandy (Kwoyo)	5
	Clay (Anywan'g)	6
	Loamy sand (Ongoro)	2
	Laterite (Maram)	5
	Rocky soil (Lwanda)	2
Termite known: number to corresponding termite identified	Only 1	12
	2 types	25
	> 2 types	63

Table 5. Types of termites, their local names (*Luo*), and pest status. *Species identity and pest status based on Nyeko and Olubayo (2005); **Pest status according to Mitchell (2002). In parentheses are farmers' descriptions of identity of some of the termite genera or species

S/N	**Type(s)**	**Local name and farmers identification of the termite genus or species (between brackets)**	**Potential pest species**
1	*Macrotermes herus*	Agoro (Build wide round mounds)	Yes**
2	*Macrotermes* spp.	Riwo (Build sharp-some tall mounds)	Yes**
3	*Amitermes* spp.*	Orudho	Yes**
4	*Pseudacathotermes spiniger*	Oyala/Oyal	Yes**
5	*Pseudacathotermes militaris*	Sisi- small, white in colour, no mounds	Yes**
6	*Cubitermes ugandensis**	Aming (Climb trees-do not make mounds)	No*
7	*Microtermes* spp.	Ogawo (small, mostly feed on foliage/leaves)	Yes**
8	*Trinevitermes oeconomus**	Thuk (small hills)	No*
9	*Odontotermes kibarensis**	Oduwere-grey in colour ; Monge-are black in colour	Yes**
10	*Odontotermes* spp.	Ogwe	Yes**

Farmers' perception of the roles and management of termites in cropping systems

Ninety per cent of the farmers perceived termites as pests (Table 6), whereas 10% felt that termites had both harmful and beneficial roles. Termite worker and soldier castes were a source of food for chickens, while winged termites (*alates*), the termite queen and mushrooms from termite nests were a source of protein for humans. Some farmers also mentioned that soil from termite mounds was good for brick making for use in house constructions. A few of the farmers reported that termites act as decomposers because they "cut, eat or remove weeds/residues". Among the harmful effects caused by termites, damage severity to crops was ranked highest (65%), followed by damage to structures such as buildings (31%) and damage to trees (4%) (Table 6). Based on the results of the household survey, farmers rated maize (*Zea mays*) as the crop that was most susceptible to termite attack (97%), followed by sorghum (3%). According to the responses obtained, common bean was not attacked by termites (Table 6). During the FGD, however, farmers ranked the six most important crops in the following order: maize > beans > sorghum > millet > soybean > sugarcane > finger millet. Most (81%) of the farmers ranked damage to plant roots highly, and they reported that subsequent destruction of other plant parts (e.g. stem/foliage) occurred only after plants had lodged. Farmers reported that damage occurred to crops that were growing in the field, mostly during flowering or tasseling (72%), and also at harvest (11%) (Table 6). About 44% of the farmers believed that damage by termites was more severe during wet months compared to dry months. Most of the losses due to termites were reported to occur to both grains and non-grain plant biomass (stems and foliage) (Table 6).

Table 6. Farmers' perception about the impact and management of termites

Category	Frequency of responses (%)	
Role of termites	Beneficial	0
	Harmful	90
	Both	10
Type of termite damage and ranking based on different structures/plants	Crops	65
	Trees	4
	Building structures	31
	Others (e.g. household items)	0
Most susceptible crop	Maize	97
	Millet	3
	Bean	0
Most susceptible crop parts	Stem/foliage	1
	Roots	81
	All parts	18
Stage when crop is most susceptible	Seedling	6
	Flowering/tasseling	72
	Harvest	11
	All stages	11
Weather conditions that favor within-season susceptibility	Wet	44
	Dry	26
	Both	30
Plant yield components lost due to termites	Grain	28
	Biomass (stem, leaves)	19
	Grain and biomass	53
Termite control measures used	Chemical/pesticide	38
	Traditional	23
	Both chemical and traditional	27
	None	12

The farmers reported measures used to control termites, but none of the farmers reported measures to stimulate termite activities. Termite control measures listed by farmers comprised of both traditional practices and use of pesticides. Sixty-five percent of the farmers applied pesticides such as Pyremix, Gladiator, Diazinol/Diaxonol (mostly against termites) to crops, either as the only measure (38%) or in combination with traditional termite control measures (27%), whereas 23% used only traditional methods. Traditional methods included: application of cow urine, flooding of nests or mounds with rain water, digging of mounds and colonies to get rid of the queen; baiting with sticks, and then feeding the captured termites to chicks; baiting using crop residues to divert termites away from the cropped fields, application of wood ash and second weeding of the crops (as a cultural practice) to reduce organic matter-rich environments that may attract termites, especially around crops. Twelve percent never applied any control measures (Table 6).

Estimated potential maize yield loss due to termite damage ranged from a mere 2% to 86% (Figure 2). However, the largest group of farmers (49%) reported a potential yield loss up to 20%.

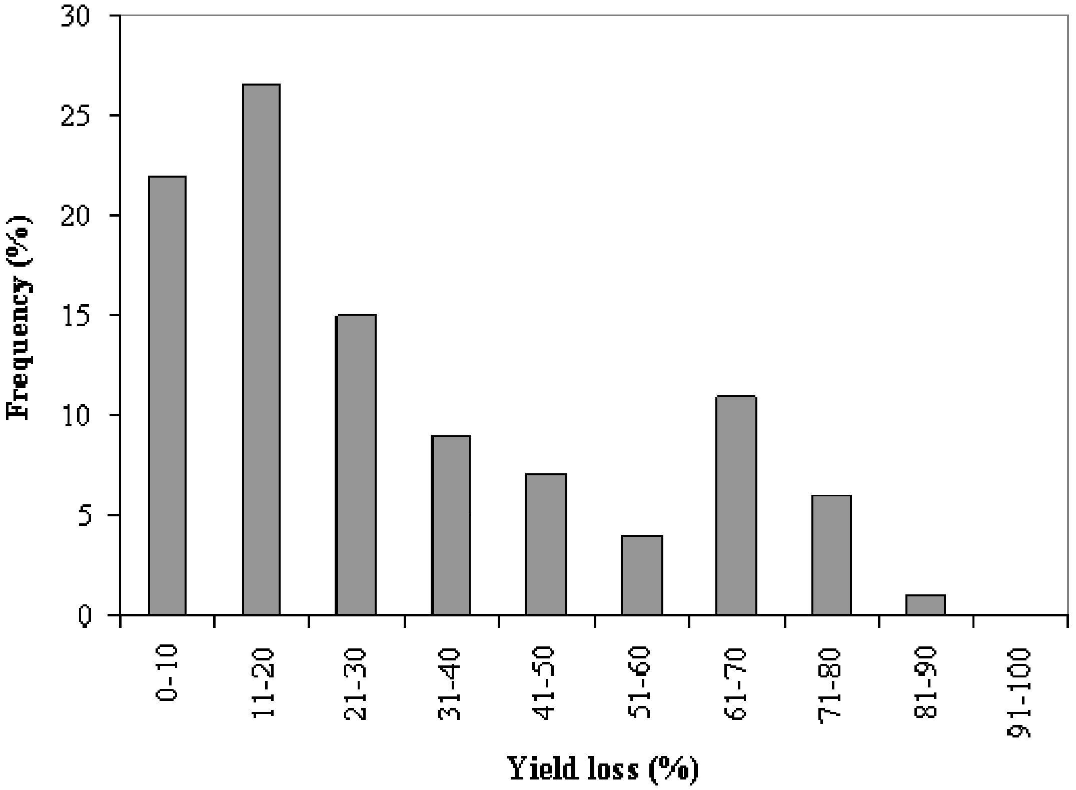

Figure 2. Frequency of occurrence of estimated potential yield loss due to termite damage, as reported by farmers in 13 villages of Nyabeda. Mode and median of yield are 25 and 22%, respectively.

Correlation between socio-economic factors and farmers' perception and management of termites

The sum of all RDA canonical eigenvalues showed that geographic location (village) explained 23% of the total variance in farmers' perception of termites (p = 0.002). Villages such as Nalo A and B perceived higher potential maize yield losses compared to villages such as Nyawachi, Mudhuru, Mufuon and Onono. Many of those villages that perceived lower yield losses, applied more termite control measures compared to villages such as Ndiany, Nalo B, Lidende and Nyakonya (Figure 3). In terms of plant yield components (grain and stover: stem, foliage), farmers reported that they lose both components in case of termites attack. More farmers from Ndiany, Wamsuti, Mudhuru, Lidende and Nyawachi were reported to suffer higher losses compared to Nalo B, Dindi-Miro and Nalo A.

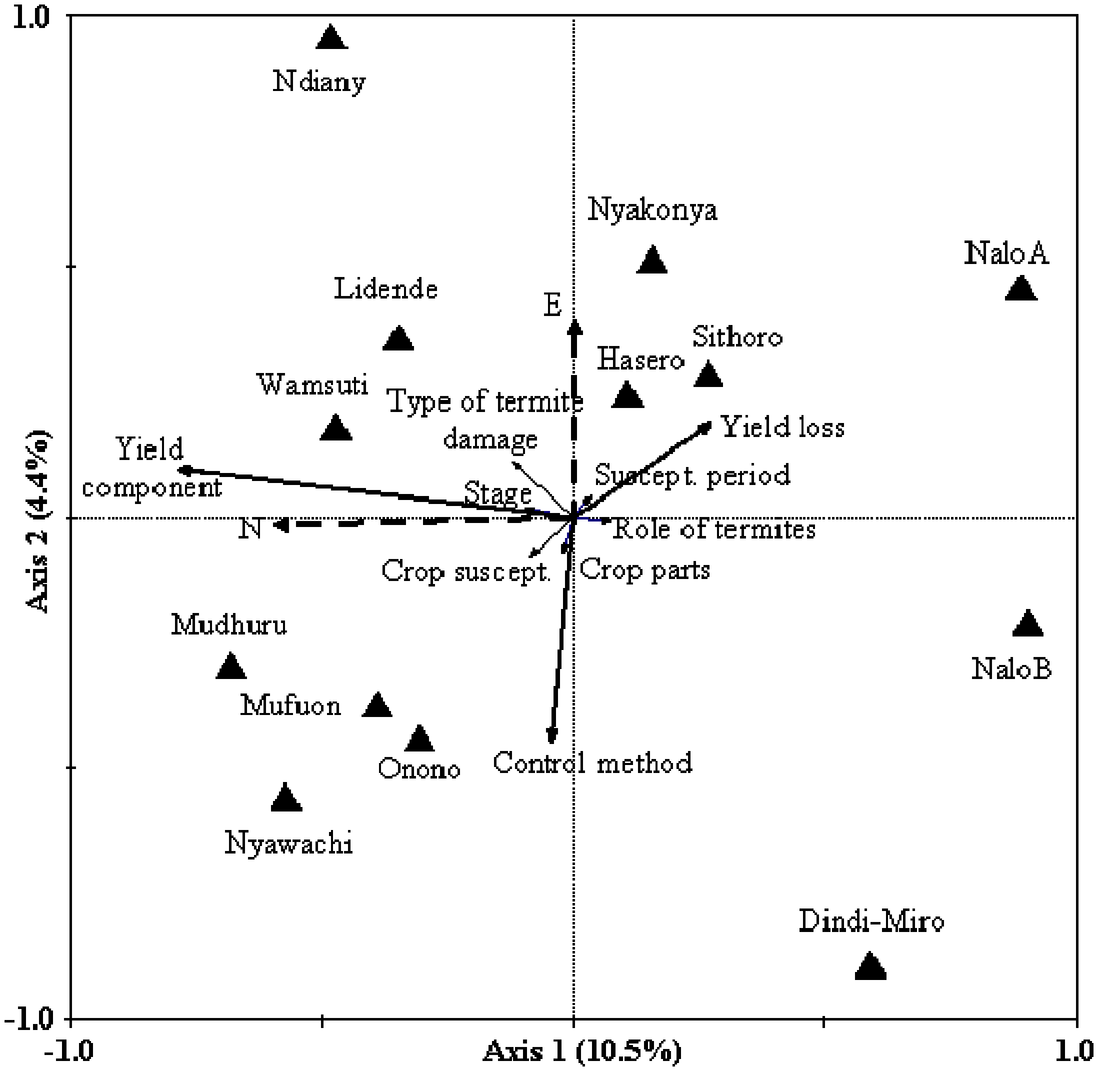

Figure 3. Farmers' perception with regard to termites. Redundancy analysis (RDA) ordination diagram displaying 23% of the variance in the farmers' perception and management, and 65% of the variance fitted in the farmers' perception and management variables. The explanatory variables are indicated by triangles. Directions (N and E), presented as dotted arrows, are supplementary variables. Response variables are indicated by solid arrows. Yield loss = perceived potential grain yield loss; Role of termites (pest, beneficial, both); Suscept. period = weather conditions that favour within season susceptibility (wet, dry or both); Yield component = plant yield portion or parts lost due to termites (grain, stem/leaves or both); Crop suscept. = most susceptible crop; Crop parts = most susceptible crop parts (stem/foliage, roots, all parts); Stage = stage when crop is most susceptible (seedling, flowering/tasseling, harvest), Type of termite damage (crops, trees, structure, others); Control method = termite control method (chemical, non-chemical, both, none).

Besides location, the socio-economic variables age, gender, education and resource endowment explained only 5% ($p = 0.058$) of the variation observed in farmers' perception and management of termites (data not shown). These results confirmed those of Chi-square tests in which we found no significant interactions between farmers' responses and typology (data not shown).

Discussion

Nyabeda represents the regional variablility found in Western Kenya in terms of biophysical, socio-economic and ethnocultural aspects (Tittonell et al. 2005). It has comparable soil types, farming/cropping systems, farm typology, technology and production potential and demography. Nyabeda, just like the other Western Kenya regions supports a high rural population. Nyabeda also exhibits differences in access to output and input markets, to off-farm job opportunities and to high-level education. Soil type and productivity potential, and farm typology are among the factors that determine crop choice (production activity choice), and can affect decision-making to a large extent when dealing with resource allocation (Tittonell et al., 2005). Because of these sources of variability, the farming systems in general and soil fertility management in particular show considerable differences between villages (Vanlauwe et al., 2006). Nyabeda area has high agricultural potential, but this is severely restricted by nutrient depletion (Shepherd et al., 1996) as a consequence of naturally weathered soils and because most farms have been farmed for a long time with little or no inputs (Sanchez et al., 1997). So far, there have been a lot of studies in Western Kenya on smallholder farming systems but none that focused on the role of termites.

Farmers' knowledge and perception of termites

The findings that farmers were aware of termite activities, nesting habits, and also knew local names of different types of termites indicates their interest in this macrofauna group and is in line with results from other areas in East and Southern Africa (Sileshi et al., 2009). Knowledge of farmers, however, was not associated with any of the social characteristics, but only with geographic location. Their classification of termites corresponded with the scientific classification at order or family or sometimes genus level. For instance, termites (order Isoptera) are generally called "biye" in *Luo*. This kind of awareness is similar to the level of resolution in knowledge of the local names of trees and weeds, which are often up to genus level (Kokwaro, 1998). Farmers' indigenous taxonomy, both in terms of the types and number of species of termites was consistent and closely corresponded with those found by Nyeko and Olubayo (2005). The *Luo* names for termite species also correspond to those of *Japadhola* (a sub-group of the River-lake Nilotes to which the *Luo* also belong). As rightly pointed out by Nyeko and Olubayo (2005), such indigenous taxonomic knowledge needs to be documented and promoted to facilitate communication between farmers, extension agents and scientists on sustainable management of termites.

The majority of the farmers perceived termites as pests to crops, though a few farmers reported both positive and negative roles of termites in that they also act as decomposers where they “cut, eat or remove weeds/residues”. Other benefits reported by a small group of farmers were not directly related to crop production. In this study, farmers did not acknowledge the beneficial effects of termites on soil fertility as reported in scientific studies (Mando, 1997; Roose et al., 1999) or as reflected by practices that farmers use in their fields in other parts of Sub Saharan Africa where farmers have been seen to leave the mounds and plant crops around them or spread termite-modified soils on their fields. It could be that the beneficial roles of termites are obscured by negative effects. Farmers demonstrated good understanding of potential pest species as they rated *Macrotermes herus* (Agoro) and *Pseudacanthotermes spiniger* (Oyal) as the species most damaging to crops and building structures such as houses. In contrast, Mitchell (2002) and Nyeko and Olubayo (2005) noted that *P. spiniger* is a minor pest that does not merit control. However, farmers’ perception that termites were pests corresponded with the observation that 8 out of the 10 species they identified were potential agricultural pests (Mitchell, 2002; Uys, 2002; Nyeko and Olubayo, 2005). Three of the pest species (*Macrotermes herus*, *Pseudacanthotermes spiniger*, and *Microtermes* spp.) that the farmers named corresponded with those collected in an agronomic field trial near Nyabeda (Ayuke, unpublished data). However, *Tubeculitermes* spp., the only non-pest species found in the field trial, was not mentioned by farmers.

Farmers’ negative perception about termites needs to be looked into if the beneficial functions of termites were to be exploited and integrated into soil fertility management recommendations. This calls for more scientific studies to assess the trade-offs between positive and negative impacts of termites on crop yields under different agroecological conditions and crop management systems, as well as a better understanding of the effects of control measures used by farmers on agroecosystem functions. Participatory approaches are essential to facilitate knowledge exchange between scientists and farmers and to anticipate the factors that enhance or constrain adoption of sustainable management practices that envisage to stimulate beneficial functions of termites in cropping systems.

Crop susceptibility to termite attack

Farmers ranked maize as the most susceptible crop to termite damage which corroborated with findings by Nyeko and Olubayo (2005) and Obi et al. (2008). Maize (*Zea mays*) is the most important staple food in Kenya. Maize is an exotic crop introduced into the African continent by the Portuguese explorers in 1502 (Miracle, 1965) and has not been exposed to the range of termite life-history strategies of those species occurring in Africa. Sorghum (*Sorghum bicolor)* or millet (*Pennisetum glaucum*), which were reported to be less susceptible compared to maize, are native to Africa (De Wet and Huckabay, 1967; Wilde, 2006) and could be more resistant to termite damage because of co-evolution and selection by farmers over many centuries. In some studies, extracts of sorghum have been demonstrated to have some insecticidal properties such as naphthoquinones which may contribute to plant resistance against termites attack (Osbrink et al., 2005). It is therefore not surprising that very little has been reported about termite damage on sorghum plants, unlike maize for which extensive damage and yield losses have been reported (Wood et al., 1980).

Attack on crops by termites is usually characterized by damage to the roots and above-ground parts, thereby resulting in lodging of mature plants (Wood et al., 1980). Lodging is considered to be the most important damage symptom of termite attack and may result in further attack by rodents and fungi, in post-harvest decay and aflatoxin contamination (Hillocks et al., 1996; Borgemeister et al., 1998). In this study, farmers ranked damage to plant roots highly, and they reported that subsequent destruction of other plant parts (e.g. stem/foliage) occurred only after plants had lodged. Farmers also reported that damage occurs to field crops at the flowering or tasseling stage, and also at harvest. Obi et al (2008) noted that termite infestation is a major production and livelihood constraint destroying crops both in the field and in the store, and those materials that are rich in cellulose or lignin (e.g. paper and wood) are highly susceptible. Farmers' observation is consistent with findings by Wood et al. (1980), who reported higher crop susceptibility near or at crop maturity, but contradicted with Mitchell (2002) who observed that a wide range of crops is attacked at all stages of the plant cycle. Most farmers believed that damage by termites was more severe during wet months compared to dry months which was surprising, given that most studies have shown termite damage to be more severe during dry spells or drought as opposed to wet spells (Malaret and Ngoru, 1989; Van den Berg and Riekert, 2003; Nyeko and Olubayo, 2005; Sileshi et al., 2005). Termites usually cause damage by forming surface soil sheetings around the crops or through stem cutting. Probably during wet periods, moist soils are readily available for the construction of sheetings and farmers perceive this to be high season for termite activities. Pest status is much easier to determine for structural pests because they cause direct damage. In agriculture and forestry, however, it is usually difficult to distinguish consumption of dead tissues from attack of living tissues, thus making damage assessment an uphill task (Constantino, 2002).

Results reported in this study are estimated potential yield losses (used as an indicator of perception), and do not give sufficient quantitative insight on economic losses, because frequency of termite damage and loss was not recorded. Yield loss estimates of 10-20% as reported by most of the farmers were close to those of Maniania et al (2001) and Sekamatte et al (2003) who recorded a yield loss of between 20 and 28% in maize. Higher yield losses were associated with loam soils which farmers reported to be high in termite activity or damage. Villages that reported high grain yield losses had relatively more loam soils, whereas low yield losses corresponded with those villages where clay and lateritic soils or rocky soils were predominant (Fig. 1 and 3). A soil survey was not part of our study, but the findings were linked to the farmers' soil classification system which is based on texture and colour. This system differed from the FAO/UNESCO classification (Jaetzold and Schmidt, 1982; FAO, 1989), which places the soils of Nyabeda as Humic Ferralsol (with clay texture). FAO's classification is neither very detailed nor does it capture the local variations that are captured in the farmers classification (Vanlauwe et al., 2006).

Management of termites in cropping systems

Some of the traditional measures applied for control of termites were mound-digging to remove the queen, flooding of termite nests, and second weeding meant to minimize occurrence of organic matter-rich environments that may attract termites around crops. These were, however, reported to be labour-intensive, whereas methods such as baiting of termites with sticks or crop residue or wood ash application are sometimes ineffective (Maniania et al., 2001). Use of pesticides for termite control was ranked highly and remained the most effective and popular method according to the farmers. It is therefore not surprising that those villages whose households never applied any termite control measures reported higher potential yield losses compared with those villages that used either pesticides or traditional methods against termites. Even though most extension programs encourage pesticides (Abate et al., 2000; Sileshi et al., 2009), there is a general concern because of human toxicity and associated negative environmental consequences and most of these pesticides are restricted in both developed and developing countries (United Nations, 1987). Besides, limited attention has been paid to the conservation of beneficial soil fauna through selection of pesticides that are specific to the target pest, or by adopting appropriate cultural practices to control specific pest groups (Wardell, 1990; Mitchell, 2002). Understanding conditions that control the trade-offs/balance between beneficial and detrimental effects of termites is thus inevitable. This underscores the importance of integrating indigenous and scientific knowledge as both have strengths and weaknesses, but can reinforce one another. Through participatory approaches scientists should work closely with farmers to improve the sustainable management of termites in crop protection systems.

Conclusions

This research has shown that farmers in Nyabeda were aware of the existence of termites, their activities and nesting habits and had local names for termites that they frequently encountered. Geographic location explained 23% of the variance in farmers’ perception and management of termites, whereas socio-economic variables explained only 5%. Ninety percent of the farmers perceived termites as pests and maize was rated as the most susceptible crop to termite attack, especially during the flowering/tasseling stage and in wet periods. More than 88% of the farmers used control measures against termites, further indicating a lack of awareness or appreciation of the beneficial effects often ascribed to termites with respect to soil properties in crop production. There is an urgent need for more research to assess the trade-offs between positive and negative impacts of termites on crop yields, as well as to get an understanding of the effects of different termite control strategies used by farmers on agroecosystem functions.

Acknowledgements

This study was supported by WOTRO Science for Global Development of the Netherlands Organization for Scientific Research (NWO). We thank our partners, especially the scientists and field technicians of TSBF-CIAT, Nairobi, Kenya who have linked us with key informants and field assistants in the study area. Special thanks to Michael Adhaya and Elphas Okonda who helped with data collection. We would like to thank Prof. Lijbert Brussaard for his valuable comments on earlier drafts to this manuscript, and for going through the final draft.

CHAPTER SEVEN

General discussion and conclusions

Soil fertility decline is often cited as a major constraint to crop production in sub-Saharan Africa (SSA). As mineral and organic fertlizers are often limited in quantity and quality, soil fertility research has focused on developing integrated management strategies to address soil fertility decline (Vanlauwe et al., 2009). Soil biota are an essential component of soil health and constitute a major fraction of global terrestrial biodiversity (Moreira et al., 2008). Within the context of Integrated Soil Fertility Management (ISFM), soil biota are responsible for the key ecosystem functions of decomposition and nutrient cycling, soil organic matter synthesis and mineralization, soil structural modification, aggregate stabilization, nitrogen fixation and the biological control of soil-borne pests and diseases (Woomer and Swift, 1994). Understanding of biological processes alongside soil physical and chemical properties creates opportunities for breakthroughs in science related to biotic functions to better serve agriculture. These services accrue through two basic approaches; indirectly as a result of promoting beneficial soil biological processes and ecosystem functions through land management or directly through the introduction of beneficial organisms to the soil (Uphoff et al., 2006). Soil macrofauna, especially earthworms and termites, are important components of the soil ecosystem and as ecosystem engineers, they influence formation and maintenance of soil structure and regulate soil processes such as decomposition and nutrient cycling. Earthworms and termites have different feeding strategies which in turn affect their impact on soil. Because of their sensitivity to disturbance and their importance in redristributing and transforming organic imputs, earthworms and termites represent an important indicator of soil quality. In this thesis I investigated biodiversity of soil macrofauna functional groups (earthworms and termites) and their effects on soil structure, as related to agricultural management practices across agroecological zones of sub-Saharan Africa.

Henceforth, I will discuss findings of my study within the framework of major topics of scientific and societal concern.

Earthworm and termite diversity as affected by agricultural management and agroecological conditions

Current debates on biodiversity issues revolve around the impact of human activities in driving change. Land use conversion, especially for agricultural purposes, is considered to be the strongest driver of change in biodiversity. I took a close look at the effect of agricultural management practices on two soil macrofauna guilds: earthworms and termites. I found (Chapter 2) that earthworm and termite diversity and abundance were low in fallow, high-C and low-C agricultural treatments in 12 long-term trial fields across the sub-humid to semi-arid tropical zones in Eastern and Western Africa. This is in contrast to most typical native or undisturbed forest ecosystems of the tropical zones (Birang et al, 2003). This may suggest that the pool of these two macrofauna groups is getting depleted as a consequence of land degradation through conversion of forests or undisturbed ecosytems for agriculture. Lack of new undescribed species, despite the intensive sampling conducted across different agroecological zones, reinforces this observation. Isolation of ecosystems into pockets of mosaics of different land uses through human actitivities may create conditions leading to loss of original taxa or limit migration of old or new taxa from one ecosystem to another. My data showed a trend for loss in the two macrofauna groups. I demonstrated that continuous crop production has significant negative effects on earthworms, but little effect on termite diversity, as compared to long-term fallow. Agricultural management resulting in high soil C increases earthworm and termite diversity, whereas fewer species of earthworms and termites are favored under agricultural management that leads to lower soil C. It appears that soil disturbance that goes with continuous crop production is more detrimental to earthworms than to termites as compared to fallow. It is therefore imperative to identify and propose management practices that will promote recolonization and conservation of these two groups. My results indicate that earthworms are sensitive to disturbances associated with agriculture and agricultural land use intensity, and that their role can be significantly enhanced by applying management practices that increase soil C in arable systems.

Earthworms sampled in my study were largely comprised of the epigeic, to a smaller extent the endogeic and none of the anecic taxa. Epigeic earthworms, which need organic inputs as mulch, and endogeic species which are capable of utilizing low-quality organic residues as food, will have been favoured by the addition of organic resources as used in many of our sites. Anecic earthworms were lacking across all sites, an indicator of how less resilient they are to management-induced disturbances. They tend to be few in tropical soils in general, due to low litter availability as a result of higher decomposition rates at higher temperatures (Lavelle et al., 1999), and in arable fields in particular because they tend to be more sensitive to disturbance and tillage (Curry, 2004). My results on termites suggest that foraging species sampled in this study are less susceptible to management-induced soil disturbances. Very few typical soil feeders (group IV) were found. Rather, a large proportion of the termites sampled in my study belong to feeding group II and to a smaller extent to feeding groups I and III. These groups are largely foragers of wood, litter, soil, dung/manure and grass. They were probably scavenging for food all over the plots and, hence, were sampled uniformly across treatments. In agreement with my hypothesis, higher termite diversity was recorded in agricultural management that had resulted in high-C than in low-C soils. I suggest that the foraging groups utilizing organic residues as food were favoured by the addition of organic resources characteristic of many of our high-C treatments.

Results of chapter 2 highlighted the importance of climate and soil type in influencing macrofauna diversity as reflected in the highly significant correlations observed between macrofauna taxonomic richness and environmental variables, reflecting the influence of climate and soil type. RDA biplots for earthworms and termites separated the relatively cooler, wetter, more clayey Eastern Africa sites from the warmer, drier, more sandy Western Africa sites. A total of 20 taxa of earthworms and an equal number of termite taxa were sampled across the different ecological zone in my study. Contrary to my hypothesis, more than average earthworm and termite taxa were found under relatively warmer, drier conditions. This is not in line with the observation that earthworm and termite species richness increases with increase in rainfall or soil moisture, as generally found at least in temperate climates (Bohlen et al., 1995; Gathorne-Hardy et al., 2001; Curry, 2004). However, seasonality of rainfall in the tropical regions means rainfall amount per season may be more important than annual total. Lower taxonomic richness among the sites in Eastern Africa is attributed to relatively less favourable conditions arising from high rainfall and low temperatures at higher altitudes. Because correlation studies are indicators of trends and are not causal par se, I propose a detailed site-specific study that will measure effects of individual climatic parameters (e.g rainfall, temperature) on soil macrofauna.

Role of earthworms and termites in ecosystem functioning

The status of soil fauna, especially earthworms and termites in undisturbed and in arable systems, can be monitored through their activities. Through this study (Chapters 3 and 4) I clearly demonstrated that earthworms and termites are an essential component of our ecosystems and are important ecosystem engineers. Through their activities they influence formation and maintenance of soil structure and regulate soil processes such as aggregation and soil organic matter (SOM) stabilization. Based on the fact that tropical soils are very susceptible to rapid losses of SOM and degradation of soil structure under continuous cultivation, conservation of SOM and soil biological processes is very important to improve soil quality and enhance crop production through soil C retention and N availability. An understanding of the effects of soil macrofauna and management practices and their interrelationship with soil aggregation and SOM stabilization processes is important in order to improve the management of infertile soils. Chapters 3 and 4 highlight the important role played by earthworms and termites in aggregation and in SOM allocation. Their degree of influence, however, depends on management intensity. Results of chapters 3 and 4 indicate that fallowing as a management practise resulted in higher faunal abundance compared to arable systems leading to higher soil aggregation. This in turn led to higher SOM allocation in soil fractions in fallow than in arable systems (Chapter 4). Among the soil management practices tested in the long-term field trial of Kabete (chapter 4), long-term application of manure in combination with fertilizer resulted in higher earthworm Shannon diversity and biomass, which leads to improved soil aggregation and enhanced C and N stabilization. Both studies, however, indicate that the role of termites in these processes is minimal compared to that of earthworms. Under the conditions studied, differences in earthworm abundance, biomass and diversity were more important drivers of management-induced changes in aggregate stability and soil C and N pools than differences in termite populations. My results on termites suggest that foraging species sampled in our sites play less of a role in soil aggregation, and C and N stabilization in organo-mineral soil fractions. Studies by Garnier-Sillam (1989) and Ganier-Sillam and Harry (1995) have shown that the role of termites in aggregate stability differs between species, and could depend on the biology of particular trophic groups. Humivorous termites that build organic matter-enriched nests are more effective and contribute more to structural stability than fungus-growing termites (Garnier-Sillam and Harry, 1995), but these were absent from our plots. I suggest a further study in which termites can be solely manipulated in agroecosystems to better understand their role in aggregation and SOM stabilization processes, especially in agroecosystems.

Application of a micromorphological approach to the study of soil ecology

Increasing interest in understanding soil biodiversity and the functional role of soil fauna in soils and ecosystems calls for a more integrated approach to the study of soil fauna and its function in soils (Davidson and Grieve, 2006; Brussaard et al., 2007). In this light, micromorphological studies of soil faunal features can offer a valuable contribution as part of an integrated approach aimed at elucidating the role of soil fauna diversity and their functions. I therefore used a micromorphological approach to describe and quantify macrofauna-induced biogenic structures in undisturbed soil samples (i.e. thin sections) from long-term field experiments in East and West Africa. Management systems differing in tillage intensity and with or without organic amendments (manure/crop residue) were compared. My study (chapter 5) has shown that tillage type and addition of organic inputs influence soil fauna activities and therefore have a significant impact on soil structure and soil physical properties such as aggregate stability and porosity. Among the management practices assessed across the two agroecological zones, fallowing, conservation tillage plus residue application (in East Africa) and hand-hoeing plus manure (in West Africa) enhanced biogenic soil structure formation, resulting in a well developed soil structure and a continuous pore system through many faunal channels. By contrast, intensive tillage and absence of organic inputs resulted in soil with less biogenic soil structural features and was, therefore, prone to slaking.

Agricultural management influences SOM content and soil biota, which have strong interrelationships with soil structure (Jongmans et al., 2001). Fauna-driven activities (e.g. decomposition and redistribution of SOM, the excretion of faecal pellets) contribute to stable aggregation, and the formation of continuous voids and these in turn have important implications for soil functions such as susceptibility to erosion, water infiltration, aeration, root growth, C and N dynamics. Soils with earthworms have been shown to have a higher percentage of macropores, a balance between water- and air-filled pores that is favourable for root growth and microbial activity, and increased aggregate stability (Boersma and Kooistra, 1994).

Use of micromorphology in studies related to soil fauna cannot be without its challenges. Soil biota is taxonomically diverse and the number of individual species so overwhelming, that it becomes difficult to know the exact function of each organism in soil processes (Lavelle, 1996; SP-IPM, 2004; Davidson and Grieve, 2006). This is further complicated by the fact that important factors that determine soil fauna composition and activities (e.g. food sources, moisture, pH, temperature and soil disturbance) can change over time due to changes in land use, land amelioration or tillage (Kooistra and Pulleman, in press). An approach that combines micromorphological methods with other techniques such as field and laboratory isolation of fauna-induced soil structural elements and physical, chemical or biological soil analyses, provides a promising approach to bridge the gap in knowledge about soil fauna and functions in soils (Pulleman, 2002; Kooistra and Pulleman, in press). Using this approach I demonstrated (Chapters 3, 4 and 5) that soil macrofauna play an important role in conducting ecosystem processes and that those management practices that enhanced faunal activities resulted in improved aggregate stability, soil structure and C and N stabilization in soil fractions. Fauna-induced biogenic structures were also high in those management practices with high faunal activities and this resulted in soils with high porosity.

Farmers' perception of termites

Successful approaches to sustainable management of termites call for the involvement of stakeholders, especially farmers. Participatory approaches are essential to facilitate knowledge exchange between scientists and farmers and to anticipate the factors that enhance or constrain adoption of sustainable management practices that stimulates beneficial functions of termites in cropping systems. I considered this in deciding to ask farmers their perception of the importance of termites in their cropping systems, and the management of termite activities in their farm fields. I found (in chapter 6) that farmers were aware of the existence of termites, their activities and nesting habits and had local names for termites that they frequently encountered. However, the majority of the farmers perceived termites as pests and they used control measures against termites, further indicating a lack of awareness or appreciation of the beneficial effects often ascribed to termites with respect to soil properties in crop production. This calls for more research to assess the trade-offs between positive and negative impacts of termites on crop yields, as well as to get an understanding of the effects of different termite control strategies used by farmers on agroecosystem functions.

Conclusions

The knowledge gathered from this study on earthworms and termites and their effect on soil structure and SOM allocation constitutes the baseline information that is important in designing agricultural management systems aimed at increasing long-term soil fertility in sub-Saharan Africa.

Although fallowing is an attractive alternative practice in the conservation of biodiversity for enhanced ecosystem functioning, it may not be practical in many parts of sub-Saharan Africa where land is limiting and fallowing has to be shortened due to increase in population size. Among the management practices tested in my study, long-term application of manure in combination with fertilizer, conservational tillage plus maize stover residue application and hand-hoeing plus manure enhanced faunal activities and contributed positively to soil processes. Given the varied agroecological conditions which differently affect faunal activities, recommendation of these practices should be tailored to meet the circumstances of target farmers.

References

Abate, T., van Huis, A. and Ampofo, J.K.O. (2000). Pest Management Strategies in Traditional Agriculture: An African Perspective. Annual Review in Entomology 45, 631-659.

Abiven, S., Menasseri, S., Chenu, C. (2009). The effects of organic inputs over timeon soil aggregate stability-A literature analysis. Soil Biology and Biochemistry 41, 1-12.

Al-Kaisi, M. M. and Yin, Xinhua. (2005). Tillage and crop residue effect on soil carbon and carbondioxide emission in corn-soybean rotations. Journal of Environmental Quality 34, 437-445.

Altieri, M.A. (1999). The ecological role of biodiversity in agroecosystems. Agriculture,Ecosystems and Environment 74, 19-31.

Amézketa, E. (1999). Soil aggregate stability: A Review Journal of Sustainable Agriculture 14 (2/3), 84-151.

Anderson, J.M. (1988). Invertebrate-mediated transport processes in soils. Agriculture, Ecosystems and Environment 24, 5-19.

Anderson, J.M. (1987). The role of soil fauna in agricultural systems. In: Wilson, J.R.(Ed.), Advances in nitrogen cycling in Agricultural Ecosystems, pp. 89-112. CAB International, Wallingford, UK.

Anderson, J.M. and Wood, T.G. (1984). Mound composition and soil modification bytwo soil-feeding termites (Termitinae, Termitidae) in a riparian Nigerian forest. Pedobiologia 26, 77-82.

Andriesse, W. And Van der Pouw, B.J.A. (1985). Reconnaissance Soil Map of the Lake Basin Development Authority, Western Kenya (Scale 1: 250,000). Netherlands Soil Survey Insitute/Kenya Soil Survey, Wageningen/Nairobi.

Angers, D.A., Caron, J. (1998). Plant-induced changes in soil structure: processes and feedbacks. Biogeochemistry 42, 55-72.

Antil, R. S., Gerzabek, M.H., Haberhauer, G. and Eder, G. (2005). Long-term effects of cropped verus fallow and fertilizer amendments on soil organic matter. Journal of Plant Nutrition and Soil Science 168, 108-116.

Aoyama, M., Angers, D.A., N'Dayegamiye, A. (1999). Particulate and mineral-associated organic matter in water stable aggregates as affected by mineral fertilizer and manure applications. Canadian Journal of Soil Science 79, 295-302.

Asawalam, D.O., Osodeke, V.E., Kamalu, O.J. and Ugwa, I.K. (1999). Effects of Termites on the Physical and Chemical Properties of the Acid Sandy Soils of Southern Nigeria. Communications in Soil Science and Plant Analysis 30 (11 and 12), 1691-1696.

Ayuke, F.O., Rao, M.R., Swift, M.J. and Opondo-Mbai, M.L. (2003) Impact of soil fertility management strategies on diversity and populations of soil macrofauna in agroecosystem. Special Issue: Sustainable use of land resources to alleviate poverty in the new millenium. East African Agricultural and Forestry Journal 69 (1 and 2), 131-137.

Babel, U. (1975). Micromorphology of soil organic matter. In: Gieseking, J.E. (Ed.), Soil Components, vol. 1. Organic Components. Springler, Berlin, pp. 369-473.

Barros, E., Pashanasi, B., Constantino, R. and Lavelle, P. (2002). Effects of land-use System on the soil macrofauna in western Brazilian Amazonia. Biology and Fertility of Soils 35, 338-377.

Beare, M.H., Reddy, M.V., Tian, G. and Scrivasta, S.C. (1997). Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of decomposer biota. Applied Soil Ecology 6, 87-108.

Bignell, D.E. and Eggleton, P. (2000). Termites in ecosystems. In: Abe, T. (Ed.),Termites: Evolution, Society, Symbiosis and Ecology. Kluwer Publishers, Dordrecht, pp. 363-387.

Bignell, D.E., Constantino, R., Csuzdi, C., Karyanto, A., Konate, S., Louzada, J., Susilo, F.X., Tondoh, J.E. and Zanetti, R. (2008). Macrofauna. In: Moreira, F.M.S., Huising, J.E., Bignell, D. (Eds.), A handbook of Tropical Soil Biology: Sampling and characterization of Below-ground Biodiversity. Earthscan, UK, 3, pp. 43-83.

Birang, M., Csuzdi, C., Hauser, S., Zebaze, I., Didden, W.A. and Brussaard, L. (2003). Earthworm community structure along a gradient of land use intensification in the humid forest zone of southern Cameroun. Wageningen University Papers, no. 47, 819-824.

Black, H.I.J. and Okwakol, M.J.N. (1997). Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of termites. Applied Soil Ecology 6, 37-53.

Blair, J.M., Bohlen, P.J. and Freckman, D.W. (1996). Soil invertebrate as indicators of soil quality. In: Doran, J.W. and Jones, A.J. (Eds.), *Methods for assessing soil quality*. Soil Science Society of America, special publication, no. 49, pp. 273-289.

Blanchart, E., Marilleau, N., Chotte, J.L., Drogoul, A., Perrier, E., Ch, C., 2009. SWORM: an agent-based model to simulate the effect of earthworms on soil structure. European Journal of Soil Science 60, 13-21.

Blanchart, E., Albrecht, A., Brown, G., Decaens, T., Duboisset, A., Lavelle, P., Mariani, L., and Roose, E. (2004). Effects of tropical endogeic earthworms on soil erosion. Agriculture, Ecosystems and Environment 104, 303-315.

Blanchart, E., Albretch, A., Alegre, J., Duboisset, A., Gilot, C., Pashanasi, B., Lavelle, P. and Brussaard, L. (1999). Effects of earthworms on soil structure and physical properties. In: Lavelle, P., Brussaard, L. and Hendrix, P. (Eds.), *Earthworm management in Tropical Agroecosystems.* CABI publishing, pp. 149-172.

Blanchart, E., Lavelle, P., Braudeau, E., Le Bissonnais, Y. and Valentin, C. (1997). Regulation of soil structure by geophagous earthworm activities in humid savannas of Cote d'Ivoire. Soil Biology and Biochemistry 29, 431-439.

Blanchart, E., Bruand, A. and Lavelle, P. (1993). The physical structure of casts of *Millsonia anomala* (Oligochaeta: Megascolecidae) in shrub savanna soils (Cote d’Ivoire). Geoderma 56, 119-132.

Boersma, O.H. and Kooistra, M.M. (1994). Differences in soil structure of silt loam typic Fluvaquents under various agricultural management practices. Agriculture, Ecosystems and Environment 51, 21-42.

Bohlen, P.J., Edwards, W.M. and Edwards, C.A. (1995). Earthworm community structure and diversity in experimental agricultural watersheds in Northeastern Ohio. Plant and Soil 170, 233-239.

Boix-Fayos, C., Calvos-Cases, A., Imeson, A.C. and Soriano-Soto, M.D. (2001). Influence of soil properties on the aggregation of some Mediterranean soils and the use of aggregate size and stability as land degradation indicators. Catena 44 (1), 47-67.

Borgemeister, C., Adda, C., Setamou, M., Hell, K., Djomamou, B., Markham, R.H. and Cardwell, K.F. (1998). Timing of harvest in maize: effects on post harvest losses due to insects and fungi in Central Benin, with particular reference to Prostephanus truncatus (Horn) (Coleoptera: Bostrichidae). Agriculture, Ecosystems and Environment 69, 233-242.

Bossuyt, H., Six, J. and Hendrix, P.F. (2005). Protection of soil carbon by microaggregates within earthworm casts. Soil Biology Biochemistry 37, 251-258.

Bossuyt, H., Six, J. and Hendrix, P.F. (2004). Rapid incorporation of carbon from fresh residues into newly formed stable microaggregates within earthworm casts. European Journal of Soil Science 55, 393-399.

Bottinellia, N., Hallairea, V., Menasseri-Aubrya, S., Le Guilloua, C. and Cluzeauc, D.(2009). Abundance and stability of belowground earthworm casts influenced by tillage intensity and depth. Soil and Tillage Research (In Press).

Brauman, A. (2000). Effect of gut transit and mound deposit on soil organic matter transformations in the soil feeding termite: a review. European Journal of Soil Biology 36, 117-125.

Brown, G.G., Edwards, C.A. and Brussaard, L. (2004). How Earthworms Affect Plant Growth: Burrowing into the Mechanisms. In: Edwards, C.A. (Ed.), Earthworm Ecology, 2nd ed. CRC Press, Boca Raton, pp. 13-49.

Brown, G.G., Moreno, A.G. and Lavelle, P. (1996). Soil macrofauna under different Agricultural Systems and native vegetation in four countries of East Africa. Biological Management of Soil Fertility in Small-Scale Farming Systems in Tropical Africa. In: Carter, S (Ed.), Proceedings of the 2nd Project Workshop, held at Kyle View, Masvingo, Zimbabwe, 1996, p. 185-191.

Brussaard, L. and Juma, N.G. (1996). Organisms and humus in soils. In: Piccolo, A. (Ed.), Humic Substances in Terrestrial Ecosystems. Elsevier, Amsterdam, pp. 329-359.

Brussaard, L., Pulleman, M.M., Ou′edraogo, E., Mando, E. and Six, J. (2007). Soil fauna and soil function in the fabric of the food web. Pedobiologia 50, 447-462.

Brussaard, L., Kuyper Th, W., Didden, W.A.M., de Goede, R.G.M. (2004). Biological soil quality from biomass to biodiversity - importance and resilience to management stress and disturbance. In: Schjønning, P S., Emholt, S. and Christensen, B.T. (Eds.), Managing Soil Quality - Challenges in Modern Agriculture. CAB International, Wallingford, UK, pp. 139-161.

Brussaard, L. (1998). Soil fauna, guilds, functional groups and ecosystem processes. Applied Soil Ecology 263, 1-13.

Brussaard, L., Hauser, S. and Tian, G. (1993) Soil fauna activity in relation to the sustainability of agricultural systems in the humid tropics. In: Mulongoy, K. and Merckx, R. (Eds.), Soil Organic Matter Dynamics and Sustainability of Tropical Agriculture. A Wiley-Sayce co-publication, pp. 455-460.

Brust, G.E., Stinner, B.R and McCartney, D.A. (1986). Predation by soil inhabiting arthropods in intercropped and monoculture agroecosystems. Agriculture Ecosystems and Environment 18, 145-54.

Bullock, P., Fedoroff, N., Jongerius, A., Stoops, G., Tursina, T. and Babel, U. (1985). Handbook for Soil thin section Description. Albrighton, Waine, 152p.

Buxton, R.D. (1981). Changes in the composition and activities of termite communities in relation to changing rainfall. Oecologia 51, 371-378.

Cadisch, G. and Giller, K.E. (1997). Driven by nature: Plant residue quality and decomposition. CAB International Wallingford, U.K, 409p.

Cairns, J. (1997). Defining goals and condition for a sustainable world. Environmental Health Perspectives 105, 1164-1170.

Carter, S.P. and Davidson, D.A. (1998). An evaluation of the contribution of soil micromorphology to the study of ancient arable agriculture. Geoarchaeology 13, 535-547.

CBD. (2001). Convention on Biological Diversity: Agricultural biological diversity, soil biodiversity and sustainable agriculture. Food and Agriculture Organization (FAO) paper. UNEP/CBD/SBSSTA/7/INF/11.

Chan, K.Y. (2001). An overview of some tillage impacts on earthworm population abundance and diversity-implications for functioning in soils. Soil Tillage Research 57, 179-191.

Chaney, K. and Swift, R.S. 1984. The influence of organic matter on aggregate stability in some British Soils. Journal of Science 35, 223-230.

Chauvel, A., Grimaldi, M., Barros, E., Blanchart, E., Desjardins, T., Sarrazin, M. and Lavelle, P. 1999. Pasture damage by an Amazonian earthworm. Nature 398, 32-33.

Chikara, I., Takashi, M., Madoka, N. and Yasuhisa, K. (2004). Impacts of tillage practices on hoppers and preatory wolf spiders (Araneae: Lycosidae) in rice paddies. Applied Entomology and Zoology 39(1), 155-162.

Chivenge, P., Vanlauwe, B., Gentile, R., Wangechi, R., Mugendi, D., Van Kessel, C. and Six, J. (2009). Organic and mineral input management to enhance crop productivity in Central Kenya. Agronomy Journal 101, 1266-1275.

Chivenge, P.P., Murwira, H.K., Giller, K.E., Mapfumo, P. and Six, J. (2007). Long-term impact of tillage and residue management on soil carbon stabilization: Implications for conservation agriculture on contrasting soils. Soil and Tillage Research 94, 328-337.

Choo, L.P.D. and Baker, G.H. (1998). Influence of four commonly used pesticides on the survival, growth and reproduction of the earthworm Apporectodea trapezoids (Lumbicidae). Australian Journal of Agricultural Research 49, 1297-1303.

Clapperton, J. (2005). Conservation Biology. Saskatchewan Soil Conservation Association (SSCA), pp. 1-7.

Clergue, B., Amiaud., Pervanchon, F., Lasserre-Joulin, F. and Plantureux, S. (2005). Biodiversity: function and assessment in agricultural areas. A review in Agronomy. Sustainability Development 25, 1-15.

Collins, N.M. (1983). Termite populations and their role in litter removal in Malaysian rainforests. In: Sutton, S.L (Eds.). Tropical Rainforests: Ecology and Management, Blackwell, Oxford.

Collins, N.M. (1981). The role of termites in the decomposition of wood and leaf litter in Guinea Savanna of Nigeria. Oecologia 51, 389-399.

Collins, H.P., Rasmussen, P.E., and Douglas, Jr. C.L. (1992). Crop rotation and residue management effect on sol carbon and microbial dynamics. Soil Science Society of America Journal 56, 783-788.

Constantino, R. (2002). The pest termites of South America: taxonomy, distribution and status. Journal of Applied Entomology 126, 355-365.

Coq, S., Barthes, B.G., Oliver, R., Rabary, B. and Blanchart, E. (2007). Earthworm activity affects soil aggregation and organic matter dynamics according to the quality and localization of crop residues-An experimental study. Soil Biology and Biochemistry 39(8), 2119-2128.

Crossley, D.A., Mueller, B.R. and Perdue, J.C. (1992). Biodiversity of microarthropods in agricultural soils: relations to processes. Agriculture Ecosystems and Environment 40, 37-46.

Curry, J.P. (2004). Factors affecting the abundance of earthworms in soils. In: Edwards, C.A. (Ed.), Earthworm ecology, second edition, CRC Press, Boca Raton, London, New York, pp. 91-111.

Curry, J.P., Byrne, D. and Schmidt, O. (2002). Intensive cultivation can drastically reduce earthworm populations in arable land, European Journal of Soil Biology 38, 127-130.

Dangerfield, J.M. (1993). Characterization of soil fauna communities. In: Rao, M.R. and Scholes, R.J. (Eds.), Report on Characterization of an Experimental Field in KARI farm, Muguga, Kenya, pp. 51-67. ICRAF, Nairobi, Kenya.

Davidson, D.A. and Grieve, I.C. (2006). Relationship between biodiversity and soil structure and function: Evidence from laboratory and field experiments. Applied Soil Ecology 33, 176-185.

De Gryze, S., Bossuyt, H., Six, J., Van Meivenne, M., Govers, G. and Merckx, R. (2007). Factors controlling aggregation in a minimum and a conventionally tilled undulating field. European Journal of Soil Science 58, 1017-1026.

De Gryze, S., Jassogne, L., Bossuyt, H., Six, J. and Merckx, R. (2006). Water repellence and soil aggregate dynamics in a loamy grassland soil as affected by texture. European Journal of Soil Science, 57, 235-246.

De Gryze, S., Six J., Paustian, K., Morris, S.J., Paul, E.A. and Merckx, R. (2004). Soil organic carbon pool changes following land-use conversions. Global Change Biology, 10, 1120-1132.

De Wet, J.M.J. and Huckabay, J.P. (1967). The origin of Sorghum bicolor. II. Distribution and Domestication. Evolution 21 (4), 787-802.

Donovan, S.E., Eggleton, P., Dubbin, W.E., Batchelder, M. and Dibog, L. (2001). The effect of soil-feeding termite, Cubitermes fungi-faber (Isoptera: Termitidae) on soil properties: termites may be an important source of soil microhabitat heterogeneity in tropical forests. Paedobiologia 45, 1-11.

Doran, W.J., Elliot, E.T. and Paustian, K. (1998). Soil microbial activity, nitrogen cycling, and long-term changes in organic carbon pools as related to fallow tillage management. Soil Tillage Research 49, 3-18.

Doube, B.M., Ryder, M.H., Davoren, C.W. and Stephen, P.M. (1994). Enhanced root nodulation of subterranean clover (Trifolium subterraneum) by Rhizobium leguminosarium biovar trifolia in the presence of the earthworm Aporrectodea trapezoides (Lumbricidae). Biology Fertility of Soils 18, 169-174.

Dudal, R. and Deckers, J. (1993). Soil organic matter in relation to soil productivity. In: Mulongoy, K. Merckx, R. (Eds.), Soil Organic Matter Dynamics and Sustainability of Tropical Agriculture. A wiley-Sayce co-publication, pp. 377-388.

Duelli P. and Obrist, M.K. (2003). Biodiversity indicators: the choice of values and Measures. Agriculture, Ecosystems and Environment 98, 87-98.

Edwards, C.A. and Lofty, J.R. (1982). Nitrogenous fertilizers and earthworm populations in agricultural soils. Soil Biology and Biochemistry 14, 515-521.

Eggleton, P., Bignell, D.E., Hauser, S., Dibog, L., Norgrove, L. and Birang, M. (2002). Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. Agriculture Ecosystems and Environment 90, 189-202.

Eggleton, P., Bignell, D.E., Sands, W.A., Mawdsley, N.A., Lawton, J.H., Wood, T.G. and Bignell, N.C. (1996). The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroun. Philosophical Transactions of the Royal Society of London, series B 351, 51-68.

Elliott, E.T. (1986). Aggregate structure and carbon, nitrogen and phosphorus in native and cultivated soils. Soil Science Society of America Journal 50, 627-633.

FAO. (1989). Forestry and food security. FAO forestry paper, FAO (UN) 90, 1-2.

Farrar, F.P. and Crossley, D.A. Jr. (1983). Detection of soil microarthropod aggregations in soybean fields, using a modified Tullgren extractor. Environmental Entomology 12, 1303-1309.

Ferguson, H.J., McPherson, R.M. and Allen, W.A., 1984. Effect of four soy-bean cropping Systems on the abundance of foliage-inhabiting insect predators. Environmental Entomology 13, 1105-1112.

Field, A., 2005. Discovering statistics using SPSS. 2nd edition. SAGE Publication, 779p.

Fitzpatrick, E.A. (1994). An introduction to soil science (2nd edition). ELBS with Longman, 255p.

Fitzpatrick, E.A. (1986). Soils: Their Formation, Classification and Distribution. ELBS/Longman, 353p.

Fitzpatrick, E.A. (1970). A technique for the preparation of large thin sections of soil and unconsolidated materials. In: Osmond, D.A., Bullock, P. (Eds.), Micromorphological Techniques and applications. Technical Monograph 2, Rothamsted Experimental Station, Harpendum, pp. 3-13.

Fonte, S.J., Winsome, T. and Six, J. (2009). Earthworm populations in relation to soil Organic matter dynamics and management in California tomato cropping systems. Applied Soil Ecology 41, 206-214.

Fonte, S.J., Kong, A.Y.Y., van Kessel, C., Hendrix, P.F. and Six, J. (2007). Influence of earthworm activity on aggregate-associated carbon and nitrogen dynamics differs with agroecosystem management. Soil Biology and Biochemistry 39, 1014-1022.

Fragoso, C., Brown., G.G., Patron, J.C., Blanchart, E., Lavelle, P., Senapati, B. and Kumar, T. (1997). Agricultural Intensification, Soil Biodiversity and Agroecosystem Function in the Tropics: The Role of earthworms. Applied Soil Ecology 6, 17-35.

Fujita, M. and Fujiyama, S. (2000). Soil meso-fauna in two microenvironments of a no-tillage farming field. Edaphologia 66, 11-20.

Garnier-Sillam, E. and Harry, M. (1995). Distribution of humic compunds in mounds of some soil-feeding termite species of tropical rainforests: its influence on soil structure stability. Insect Sociobiology 42, 167-185.

Garnier-Sillam, E. (1989). The pedological role of fungus-growing Termites (Termitidae, Macrotermitinae) in tropical environments with special reference to Macrotermes muelleri. Sociobiology, 15, (2), 181-196.

Gathone-Hardy, F.G., Syaukani and Eggleton, P. (2001). The effects of altitude and rainfall on the composition of the termites (Isoptera) of the Leuser Ecosystem (Sumatra, Indonesia). Journal of Tropical Ecology 17, 379-393.

GENSTAT 11.1. (2009). Genstat release, 11th edition. VSN International LTD.

Gentile, R., Vanlauwe, B., Kavoo, A., Chivenge, P. and Six, J. (2009). Residue quality and N fertilizer do not influence aggregate stabilization of C and N in two tropical soils with contrasting texture. Nutrient Cycling in Agroecosystems (In press).

Gentile, R., Vanlauwe, B., Van Kessel, C. and Six, J. (2009). Managing N availability and losses by combining fertilizer-N with different quality residues in Kenya. Agriculture, Ecosystems and Environment 131, 308-314.

Giller, K.E., Cadisch, G., Ehaliotis, C., Sakala, W.D. and Mafongoya, P.L. (1997). Building soil nitrogen capital in Africa. In: Buresh, R.J., Sanchez, P.A. and Calhoun, F. (Eds.), Replenishing Soil Fertility in Africa. SSSA Special publication 51, 151-192.

Gilot-Villenave, C., Lavelle, P., F. and Ganry, F. (1996). Effects of a tropical geophagous earthworm, Millsonia anomala, on some soil characteristics, on maize-residue decomposition and on maize production in Ivory Coast. Applied Soil Ecology 4, 201-211.

Gitay, H., Wilson, J.B. and Lee, W.G. (1996). Species redundancy: a redundant concept? Journal of Ecology 84, 115-118.

Golderberg, S., Kapoor, B.S. and Rhoades, J.D. (1990). Effects of aluminium and iron oxides and organic matter on flocculation and dispersion of arid zone soils. Soil Science 150, 588-593.

Grandy, A.S. and Robertson, G.P. (2006). Aggregation and organic matter protection following tillage of a previously uncultivated soil. Soil Science Society of America Journal 70, 1398-1406.

Hallaire, V., Curmi, P., Duboisset., Lavelle, P. and Pashanasi, B. (2000). Soil structural changes induced by the tropical earthworm Pontoscolex corethrurus and organic inputs in a Peruvian Ultisol. European Journal of Soil Biology 36, 35-55.

Harinikumar, K.M. and Bagyaraj, D.J. (1994). Potential of earthworms, ants, millipedes, termites for dissemination of vesicular-arbuscular mycorrhizal fungi in soil. Biology and Fertility of Soils 18, 115-118.

Haynes, R.J., Swift, R.S. and Stephen, R.C. (1991). Influence of mixed cropping Rotations (pasture-arable) on organic matter content, water stable aggregation and clod porosity in a group of soils. Soil Tillage Research 19, 77-87.

Heal, O.W., Anderson, J.M. and Swift, M.J. (1997). Plant litter quality and decomposition: an historical overview. In: Cadisch, G. and Giller, K.E. (Eds.), Driven by nature: Plant litter quality and decomposition. CAB International, Wallingford, U.K, pp. 107-124.

Hedde, M., Lavelle, P., Joffre, R., Jimenez, J.J. and Decaens, T. (2005). Specific functional signature in soil macro-invertebrate biostructures. Functional Ecology 19, 785-789.

Hoogmoed, M. (2009). Interactive effects of crop residue management and soil macrofauna on soil aggregation and associated C and N dynamics. MSc thesis, Wageningen University.

Hoogmoed, W.B. (1999). Tillage for soil and water conservation in the semi-arid tropics. Tropical resource management papers 24, Wageningen University, 184p.

House, G.J. and Parmele, R.W. (1985). Comparison of soil arthropods and earthworms from conventional, and no-tillage agroecosystems. Soil and Tillage Research 5, 351-360.

Hulugalle, N.R., Rohde, K.W. and Yule, D.F. (2002). Cropping systems and bed width effect on runoff, erosion and soil properties in a rainfed Vertisol. Land Degradation and Development 13, 363-374.

Hulsmann, A. and Wolters, V., 1998. The effects of different tillage practices on soil mites, with particular reference to Oribatida. Applied Soil Ecology 9, 327-332.

ICIPE. (1997). International Centre for Insect Physiology and ecology. Annual Report Highlights, pp. 2, Nairobi, Kenya.

Jaetzold, R. and Helmut, S. (1982). Farm Management Handbook of Kenya. Volume II: Natural Conditions and Farm Management Information Ministry of Agriculture, Kenya, pp. 225-525.

Jannette, M.D. (2002). Termites as pests of crops, forestry, rangeland and structures inSouthern Africa and their control. Termite Crops 40 (1), 47-69.

Jastrow, J.D. (1996). Soil aggregate formation and the accrual of particulate and mineralassociated organic matter. Soil Biology and Biochemistry 28, 656-676.

Jimenez, J.J. and Thomas, R.J. (2001) Nature's Plow: Soil Macroinvertebrate Communities in the Neotropical Savannas of Colombia CIAT, Cali, 389p.

Jones, D.T. and Eggleton, P. (2000). Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. Journal of Applied Ecology 37, 191-203.

Jones, C.G., Lawton, J.H. and Schachak, M. (1994). Organisms as ecosystems engineers. Oikos 69, 373-386.

Jongerius, A. and Heintzberger, G. (1975). Methods in soil micromorphology: a technique for the preparation of large thin sections. Soil Survey Papers 10, Soil Survey Institute, Wageningen, The Netherlands.

Jongmans, A.G., Pulleman, M.M., Balabane, M., van Oort, F. and Marinissen, J.C.Y. (2003). Soil structure and characteristics of organic matter in tow orchards differing in earthworm activity. Applied Soil Ecology 24, 219-232.

Jongmans, A.G., Pulleman, M.M. and Marinissen, J.C.Y. (2001). Soil structure and earthworm activity in a marine silt loam under pasture versus arable land. Biology Fertility of Soils 33, 279-285.

Jouquet, P., Zangerlie, A., Rumpel, C., Brunet, D., Bottinelli, N. and Tran Duc, T. (2010). Relevance and limitations of biogenic and physicogenic classification: a comparison of approaches for differentiating the origin of soil aggregates. European Journal of Soil Science 60, 1117-1125.

Jouquet. P., Podwojewski, P., Bottinelli, N., Mathieu, J., Ricoy, M. and Orange, D. (2008). Above-ground earthworm casts affect water runoff and soil erosion in Northern Vietnam. Catena 74, 13-21.

Jouquet, P., Bottinelli, N., Lata, J.P., Mora, P. and Caquineau, S. (2007). Role of the fungus-growing termite Pseudacanthotermes spiniger (Isoptera, Macrotermitinae) in the dynamic of clay and soil organic matter content. An experimental analysis. Geoderma 139, 127-133.

Jouquet, P., Dauber, J., Lagerlof, J., Lavelle, P. and Lepage, M. (2006). Soil invertebrate as ecosystem engineers: Intended and accidental effects on soil and feedback loops. Applied Soil Ecology 32, 153-164.

Jouquet, P., Mamou, L., Lepage, M. and Velde, B. (2002). Effect of termites on clay minerals in tropical soils: fungus-growing termites as weathering agents. European Journal of Soil Science 53, 521-527.

Jungerius, P.D., van den Ancker, J.A.M., and Mücher, H.J. (1999). The contribution of termites to the microgranular structure of soils on the Uasin Gishu Plateau, Kenya. Catena 34, 349-363.

Kapkiyai, J.J., Karanja, N.K., Qureshi, J.N., Smithson, P.C. and Woomer, P.L. (1999). Soil organic matter and nutrient dynamics in a Kenyan nitisol under long-term fertilizer and organic input management. Soil Biology and Biochemistry 31, 1773-1782.

Kamoni, P.T., Gicheru, P.T., Wokabi, S.M., Easter, M., Milne, E., Coleman, K., Falloon, P., Paustian, K., Killian, K. and Kihanda, F.M. (2007). Evaluation of two soil carbon models using two Kenyan long term experimental datasets. Agriculture, Ecosystems and Environment 122, 95-104.

Karanja, N.K., Ayuke, F. O. and Swift, M.J. 2006. Organic resources quality and Soil fauna: Their role on the microbial biomass, decomposition and nutrient release patterns in Kenyan soils. Journal of Tropical and Subtropical Agroecosystems 6, 73-86.

Kenya Ministry of Agriculture and Rural Development. (2001). Annual Reports for Vihiga, Kakamega and Teso districts: Surveys on population and Agricultural Production 2001.

Ketterings, Q.M., Blair, J.M. and Marinissen, J.C.Y. (1997). Effects of earthworms on Soil aggregate and carbon and nitrogen storage in a legume cover crop agroecosytem. Soil Biology and Biochemistry 29 (3/4), 4101-4108.

Kirkpatrick, L.A. and Feeney, B.C. (2005). A simple guide to SPSS for windows, for Version 12.0. Thomson Wadsworth.

Kladivko, E. J. (2001). Tillage systems and soil ecology. Soil and Tillage Research 61, 61-76.

Kokwaro, J.O. (1988). Conservation status of the Kakamega Forest in Kenya: The esternmost relic of the equatorial rainforests of Africa. Monograph of Systematic. Botany. Missouri Botanical Garden 25, 471-481.

Kooistra, M.J., Juo, A.S.R. and Schoonderbeek, D. (1990). Soil degradation in cultivated Alfisols under different management systems in Southwestern Nigeria. In: Douglas, L.A (Ed.), Soil Micromorphology. Elsevier Science Publishers B.V., Amsterdam, pp. 61-69.

Kooistra, M.J., Lebbink, G. and Brussaard, L. (1989). The Dutch programme on soil ecology of arable farming systems. 2. Geogenesis, agricultural history, field site characteristics and present farming systems at Lovinkhoeve experimental farm. Agriculture, Ecosystems and Environment 27, 361-387.

Kooistra, M.J. and Pulleman, M.M. (2010). Features related to faunal activity in soils and regoliths. In Stoops, G. (Ed.), Micromorphological features of soils and regoliths. Elsevier, Amsterdam (In press).

Kooyman, C. and Onck, R.F.M. (1987). The interaction between termite activity, agricultural practices and soil characteristics in Kisii district, Kenya. Wageningen Agicultural University Papers, 87-3, 120p.

Korodjouma, O., Badiori, O., Ayemou, A. and Sedogo, P.M. (2006). Long-term effect of ploughing, and organic matter input on soil moisture characteristics of a Ferric Lixisol in Burkina Faso. Soil and Tillage Research 88, 217-224.

KRC. (1998) Crop rotation. Kansas Rural Centre (KRC) Sustainable agriculture management guide. MG2A.1.

Kurt, G., Steiner, G.T.Z. and Twomlow, S. (2003). Weed management in conservation tillage systems. African conservation tillage network (ACT) information series no. 8.

Kushwaha, C.P., Tripathi, S.K. and Singh, K.P. (2001). Soil organic matter and water-stable aggregates under different tillage and residue conditions in a tropical dryland agroecosystem. Applied Soil Ecology 16, 229-241.

Lal, R. (1988). Effects of macrofauna on soil properties in tropical agroecosystems. Agriculture, Ecosystems and Environment 24, 101-116.

Lampurlanes, J. and Cantero-Matinez, C. (2003). Tillage: soil bulk density and penetrometer resistance under different tillage and crop management systems and their relationship with barley root growth. Agronomy Journal 95, 526-536.

Lavelle, P. (1999). Key functional groups of soil biota: Macrofauna. Managing soil biota for sustainable agriculture. International workshop of Tropical Soil Biology: Opportunities and challenges for an African Agriculture, March, 16-19, 1999, Nairobi, Kenya.

Lavelle, P. (1996). Diversity of soil fauna and ecosystem function. The convention on Biological Diversity, Diversitas and a new focus on Soil Biodiversity: Biology International No. 33, July, 1996.

Lavelle, P. (1988). Assessing the abundance and role of invertebrate communities in tropical soils: Aims and methods, Journal of African Zoology 102, 275-283.

Lavelle, P., Barros, E., Blanchart, E., Brown, G., Desjardins, T., Mariani, L. and Rossi, J.P. (2001). SOM management in the tropics: Why feeding the soil macrofauna? Nutrient Cycling in Agroecosystems 61, 53-61.

Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W. and Dhillion, S. (1997). Soil function in a changing world: the role of invertebrate ecosystem engineers. European Journal of Soil Biology 33, 159-193.

Lavelle, P., Brussaard, L. and Hendrix, P. (1999). Earthworm management in tropical agroecosystems CABI, Wallingford, 300p.

Lavelle, P., Dangerfield, M., Fragoso, C., Eschnebrenner, V., Hernadez, D.L., Pashanasi, B. and Brussaard, L. (1994a). The relationship between soil macrofauna and tropical soil fertility. In: Woomer, P.L. and Swift, M.J. (Eds.), The Biological Management of Tropical Soil Fertility. A Wiley- Sayce publication, pp. 136-169.

Lavelle, P., Gilot, C., Fragoso, C. and Pashanasi, B. (1994b). Soil fauna and sustainable land use in the humid tropics. In: Greenland, G.A. and Szalbolcs, I. (Eds.), Soil Resilience and Sustainable Land use. CAB International, Wallingford, pp. 291-307.

Lavelle, P., Blanchart, E., Martins, S., Martin, A., Barios, S., Toutin, F., Spain, A. and Schaefer, R. (1993). A hierarchical model for decomposition in terrestrial ecosystem. Application to soils in the humid tropics. Biotropica 25 (2), 130-150.

Le Bissonais, Y. (1996). Aggregate stability and assessement of soil crustability and erodibility: I. Theory and methodology. European Journal Soil Science 47, 425-437.

Lobry de Bruyn, L.A. and Conacher, A.J. (1990). The role of termites and ants in soil modification: a review. Australian Journal of Soil Research 28, 55-93.

Logan, J.W.M. (1992). Termites (Isoptera)- a pest or resource for small scale farmers in Africa. Tropical Science 32, 71-79.

Lopez-Hernandez, D. (2001). Nutrient dynamics (C, N and P) in termite mounds of Nasutitermes ephratae from savannas of the Orinoco Llanos (Venezuela). Soil Biology and Chemistry 33, 747-753.

Ma, W.-C., Brussaard, L. and de Ridder, J.A. (1990). Long-term effects of nitrogenous fertilizers on grassland earthworms Oligochaeta: Lumbricidae: their relation to acidification, Agriculture Ecosystems and Environment 30, 71-80.

Mackay, A.D., and E. J. Kladivko, E.J. (1985). Earthworms and rate of breakdown of soybean and maize residues in soil. Soil Biology and Biochemistry 17, 851-857.

Mafongoya, P.L., Giller, K.E. and Palm, C.A. (1998). Decomposition and nitrogen release patterns of tree prunings and litter. Agroforestry systems 38, 77-97.

Magurran, A.E. (1988). Ecological diversity and its measurements. Cambridge University Press, Great Britain, 179p.

Mainoo, N.K., Whalen, J.K. and Barrington, S. (2008). Earthworm abundance related to soil physicochemical and microbial properties in Accra, Ghana. African Journal of Agricultural Research 3(3), 186-194.

Malaret, L. and Ngoru, F.N. (1989). Ethno-ecology: a tool for community based

management farmer knowledge of termites in Machakos district, Kenya. Sociobiology 15, 197-211.

Mando, A. (1998). Soil-dwelling termites and mulches improve nutrient release and crop performance on Sahelian crusted soil. Arid Soil Research and Rehabilitation 12, 153-164.

Mando, A. (1997a). Effect of termites and mulch on the physical rehabilitation of structurally crusted soils in the Sahel. Land Degradation and Development 8, 269-278.

Mando, A. (1997b). The impact of termites and mulch on the water balance of crusted Sahelian soil. Soil Technology, 11, 121-138.

Mando, A. and Brussaard, L. (1999). Contribution of termites to the breakdown of straw under Sahelian conditions. Biology and Fertility of Soils 29, 332-334.

Mando, A. and Miedema, R. (1997). Termite-induced change in soil structure after mulching degraded (crusted) soil in the Sahel. Applied Soil Ecology 6, 241-249.

Mando, A., Brussaard, L. and Stroosnijder, L. (1999). Termite- and mulch-mediated rehabilitation of vegetation on crusted soil in West Africa. Restoration Ecology 7, 33-41.

Mando, A., Stroosnijder, L. and Brussaard, L. (1996). Effects of termites on infiltration into crusted soil. Geoderma 74, 107-113.

Maniania, N.K., Ekesi, S. and Songa, J.M. (2001). Managing termites in maize with the entomopathogenic fungus Metarhizium anisopliae. Insect Science and its Applications 22 (1), 41-46.

Marinissen, J.C.Y. and Hillenaar, S.I. (1997). Earthworm-induced distribution of organic matter in macroaggregates from differentially managed fields. Soil Biology and Biochemistry 29, 391-395.

Martius, C. (1994). Diversity and ecology of termites in Amazonian forests. Pedobiologia 38, 407-428.

Mbagwu, J.S.C. and Piccolo, A. (1989). Changes in soil aggregate stability induced by amendment with humic substances. Soil Technology 2, 49-57.

McVay, K.A., Budde, J.A., Fabrizzi, K., Mikha, M.M., Rice, C.W., Schlegel, A.J., Peterson, D.E., Sweeney, D.W. and Thompson, C. (2006). Management effect on soil physical properties in long-term tillage studies in Kansas. Soil Science Society of American Journal 70, 434-438.

Melillo, J.M., Aber., J.D. and Muratore, J.F. (1982). Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621-626.

Mikha, M.M. and Rice, C.W., 2004. Tillage and manure effects on soil aggregate associated carbon and nitrogen. Soil Science Society of America Journal 68, 809-816.

Miracle, M.P. (1965). The introduction and spread of maize in Africa. The Journal of African History 6(1), 39-55.

Mitchell, J.D. (2002). Termites as pests of crops, forestry, rangeland and structures in Southern Africa and their control. Sociobiology 40(1), 47-69.

Moore, J.C., Snider, R.J. and Robertson, L.S. (1984). Effects of different management systems o collembolan and Acarina I corn production systems. Pedobiologia 26, 143-152.

Mora, P., Seuge, C., Chotte, J.L. and Rouland, C. (2003). Physico-chemical typology of the biogenic structures of termites and earthworms: a comparative analysis. Biology and Fertility of Soils 37, 245-249.

Moreira, F.M.S., Huising, J.E. and Bignell, D. (2008), A handbook of Tropical Soil Biology: Sampling and characterization of Below-ground Biodiversity. Earthscan, Publishers, UK.

Mrabet, R., Ibno-Namr, K., Bessam, F. and Saber, N. (2001). Soil chemical changes and implications for fertilizer management after 11 years of no-tillage wheat production systems in semi-arid Morocco. Land Degradation and Development 12, 505-517.

Mtambanengwe, F. and Mapfumo, P. (2005). Organic matter management as an underlying cause for soil fertility gradients on smallholder farms in Zimbabwe. Nutrient Cycling in Agroecosystems 73, 227-243.

Naeem, S. (1998). Species redundancy and ecosystem reliability. Conservation Biology 12 (1), 39-45.

Nakamura, Y. (1988). The effect of soil management on the soil faunal makeup of a cropped Andosol in Central Japan. Soil Tillage Research 12, 177-186.

Newman, J. (1988). Soil fauna other than protozoa. In: Wild, A. (Ed.), Russell’s Soil Conditions and Plant Growth (11th edition). Longman and Scientific Technical, Co-publication, John Wiley and Sons, New York, pp. 500-525.

Nyamapfene, K.W. (1986). The use of termite mounds in Zimbabwe peasant agriculture. Tropical Agriculture 63, 191-192.

Nyeko, N. and Olubayo, F.M. (2005). Participatory assessment of farmers’ experiences of termite problems in agroforestry in Tororo district, Uganda. Agricultural Research and Extension Network Paper No. 143, Overseas Development Institute, London, UK.

Obi, J.C., Ogunkunle, A.O. and Meludu, N.T. (2008). Effect of termite infestation on the farming system characteristics of an endemic area in the Guinea Savanna region of Nigeria. American-Eurasian Journal of Scientific Research 3 (1), 1-6.

Ohiagu, C.E. (1979). Nest and soil populations of Trinevitermes spp. with particular reference to T. germinatus (Wasmann), Isoptera) in Southern Guinea Savanna near Mokwa, Nigeria. Oecologia 40, 169-178.

Okoba B.O. (2005). Farmers' indicators for soil erosion mapping and crop yield estimation in central highlands of Kenya. Tropical Resource Management papers 64, Wageningen University, 143p.

Okwakol, M.J.N., 2000 Changes in termite (Isoptera) communities due to the clearance and cultivation of the tropical forest in Uganda. African Journal of Ecology 38, 1-7.

Osbrink, W.L.A., Tellez, M,R., Kobaisy, M. and Lax, A.R. (2005). Assessment of Natural Products for Control of Formosan Subterranean Termites. American Chemical Society 6, 73-87.

Osler, G.H.R., Harrison, L., Kanashiro, D.K. and Clapperton, M.J. (2008). Soil microarthropod assemblages under different arable crop rotations in Alberta, Canada. Applied Soil Ecology 38, 71-78.

Ou'edraogo, E., Mando, A. and Brussaard, L. (2006). Soil macrofauna affect crop nitrogen and water use efficiencies in semi-arid West Africa. European Journal of Soil Biology 42, 275-277.

Ou'edraogo, E. (2004). Soil quality improvement for crop production in semi-arid West Africa. Tropical resource management Papers 51, Wageningen University, 193p.

Ou'edraogo, E., Mando, A. and Zombie, N.P. (2001). Use of compost to improve soil properties and crop productivity under low-input agricultural system in West Africa. Agriculture Ecosystem and Environment 84, 259-266.

Ouédraogo, E., Mando, A. and Zombie, N.P. (2001). Use of compost to improve soil properties and crop productivity under low-input agricultural system in West Africa. Agriculture, Ecosystems and Environment 84, 259-266.

Palm, C.A. (1995). Contribution of agroforestry trees to nutrient requirements in intercropped plants. Agroforestry Systems 30, 105-124.

Palm, C.A., Gachengo, C.N., Delve, R.J. Cadisch, G and Giller, K. (2001). Organic inputs for soil fertility management in tropical agroecosystems: application of an organic resource database. Agriculture, Ecosystems and Environment 83, 27-42.

Palm, C.A., Myers, R.J.K. and Nandwa, S.M. (1997). Combined use of organic and inorganic nutrient sources for soil fertility maintenance and replenishment. In: Buresh, R.J., Sanchez, P.A. and Calhoun, F. (Eds.). Replenishing Soil Fertility in Africa. SSSA Special publication Number 51, pp. 193-217.

Paoletti, M.G., Pimentel, D., Stinner, B.R. and Stinner, D. (1992). Agroecosystem biodiversity: matching production and conservation biology. Agriculture Ecosystems and Environment 40, 3-23.

Pedro, L.O, Machado, de A. and Silva, A. (2001). Soil management under no tillage systems in the tropics with special reference to Brazil. Nutrient Cycling in Agroecosystems 61, 119-130.

Pikul Jr, J.L., Chilom, G, Rice, J., Eynard, A., Schumacher, T.E., Nichols, K., Johnson, J.M.F., Wright, S., Caesar, T. and Ellsbury, M. (2009). Organic matter and water stability of field aggregate affected by tillage in South Dakota, Soil Science Society of America Journal 73 (1), 197-206.

Puget, P., Chenu, C. and Balesdent, J. (1995). Total and young organic matter distributions in aggregates of silty cultivated soil. European Journal of Soil Science 46, 449-459.

Pulleman, M. (2002). Interactions between soil organic matter dynamics and soil structure as affected by farm management. Thesis Wageningen University, The Netherlands, 146p.

Pulleman, M.M., Six, J., van Breemen, N. and Jongmans, A.G. (2005a). Soil organic Matter distribution as affected by agricultural management and earthworm activity. European Journal of Soil Science 56, 453-467.

Pulleman, M.M., Six, J., Uyl, A., Marinissen, J.C.Y. and Jongman, A.G. (2005b). Earthworms and management affect organic matter incorporation and microaggregate formation in agricultural soils. Applied Soil Ecology 29, 1-15.

Pulleman, M.M., Six, J., van Breemen, N. and Jongman, A.G. (2004). Soil organic matter distribution and microaggregate characteristics as affected by agricultural management and earthworm activity. European Journal of Soil Science 10, 1-15.

Pulleman, M.M., Six, J., Jongman, A.G., Marinissen, J. and Bouma, J. (2003). Effects of organic versus conventional arable farming on soil structure and organic matter dynamics in a marine loam in the Netherlands. Soil Use and Management 19, 157-165.

Ramani R., Ramachandra P., Ramgopal G., Ranganathaiah C., Sardar Z., Fernandes, E.C.M., Motavalli, P.P., Castilla, C. and Mukurumbira L. (1997). Management control of soil organic matter dynamics in tropical land use systems. Geoderma 79, 49-67.

Roper, M.M. and Gupta, V.V.S.R. (1995). Management practices and soil biota. Australian Journal of Soil Research 33, 321-339.

Roose, E., Kabore, V. and Guenat, C. (1999). Zai Practice: A West African Traditional Rehabilitation System for Semi-arid Degraded Lands, a case study in Burkina Faso. Arid Land Research Management 13 (4), 343-355.

Rotich, D.K., Ogaro, V.N., Wabuile, E., Mulamula, H.H.A., Wanjala, C.M.M. and Defoer, T., 1999. Participatory characterization and on-farm testing in Mutsulio village, Kakamgea district. Pilot project on Soil Fertility Replenishment and Recapitalisation in Western Kenya, report No 11. Kenya Agricultural Research Insitute, Kakamega, Kenya.

Rouland, C., Lepage, M., Chotte, J.L., Diouf, M., Ndiaye, S., Seuge, C. and Brauman, A. (2003). Experimental manipulation of termites (Isoptera, Macrotermitinae) foraging patterns in a Sahelo-Sudanese savanna: effect of litter quality. Insect Society 50, 309-316.

Sanchez, P.A. (2002). Soil fertility and hunger in Africa. Science 295, 2019-20.

Sanchez, P.A and Jama, B. (2002). Soil fertility replenishment takes off in East and

Southern Africa. In: Vanlauwe, B., Diels, J., Sanginga, N. and Merckx, R. (Eds.), Integrated plant nutrient management in sub-Saharan Africa: from concept to practice. CABI, Wallingford, pp. 23-46.

Sanchez, P.A., C.A Palm, L.T. Szott, E. Cuevas, and R. Lal. 1989. “Organic input management in tropical agroecosystems” In: Coleman, D.C., Oades, J.M. and Uehara, G. (Eds.), Dynamics of Soil Organic Matter in Tropical Ecosystems, NifTAL Project, University of Hawaii, Honolulu, HI, pp. 125-152. Sanchez, P.A., Shepherd, K.D., Soule, M.J., Place, F.M., Buresh, R.J., Anne-Marie, N.I.,

Mokwunye, A.U., Kwesiga, F.R., Ndiritu, C.G. and Woomer, P.L. (1997). Soil fertility replenishment: An investment in Natural Resource Capital. In: Buresh, R.J., Sanchez, P.A. and Calhoun, F. (Eds.), Replenishing Soil Fertility in Africa. Soil Science Society of America (SSSA). Special publication No 51, USA.

Sarr, M., Agbogba, C., Russell-Smith, A. and Masse, D. (2001). Effect of soil faunal activity and woody shrubs on water infiltration rates in a semi-arid fallow of Senegal. Applied Soil Ecology 16, 283-290.

SAS INSTITUTE LIBRARY. (1995). Factor analysis using SAS PROC FACTOR. The University of Texas at Austin Statistical services.

Scullion, J. and Malik, A. (2000). Earthworm activity affecting organic matter, aggregation and microbial activity in soils after opencast mining for coal. Soil Biology and Biochemistry 32, 119-126.

Sekamatte, B.M., Ogenga-Latigo, M. and Russell-Smith, A. (2003). Effects of maize-legume intercrops on termite damage to maize, activity of predatory ants and maize yield in Uganda. Crop production 22, 87-93.

Shepherd, K.D. and Soule, M.J. (1998). Soil fertility management in west Kenya: dynamic simulation of productivity, profitability and sustainability at different resource endowment levels. Agriculture, Ecosystems and Environment 71, 131-145.

Shepherd, K.D., Ohlsson, E., Okalebo, J.R. and Ndufa, J.K. (1996). Potential impact of agroforestry on soil nutrient balances at the farm scale in the East African Highlands. Fertility Research 44, 97-99.

Shiran, H., Hajabbasi, M.A., Afyuni, M. and Hemmat, A. (2002). Effects of farmyard manure and tillage systems on soil physical properties and corn yield in Central Iran. Soil Tillage Research 68, 101-108.

Sodhi, G.P.S., Beri, V. and Benbi, D.K. (2009). Soil aggregation and distribution of carbon and nitrogen in different fractions under long-term application of compost in rice-wheat system. Soil Tillage Research 103, 412-418.

SP-IPM. (2004). Soil Biota and Sustainable Agriculture: Challenges and Opportunities. IPM Research Brief No. 2. SP-IPM Secretariate, International Institute of Tropical Agriculture (IITA), Cotonou, Benin.

Siderius, W. and Muchena, F.N. (1977). Soils and Environmental Conditions of Agricultural stations in Kenya, pp. 53-55.

Sileshi, G. and Mafongoya, P.L. (2006). Long-term effects of improved legume fallows on soil invertebrate macrofauna and maize yields in Eastern Zambia. Agriculture, Ecosystems and Environment 115, 69-78.

Sileshi, G. W., Nyeko, P., Nkunika, P. O. Y., Sekematte, B.M., Akinnifesi, F.K. and Ajayi, O.C. (2009). Integrating ethno-ecological and scientific knowledge of termites for sustainable termite management and human welfare in Africa. Ecology and Society 14 (1), 48.

Sileshi, G., Mafonoya, P.L., Kwesiga, F. and Nkunika, P. (2005). Termite damage to maize grown in agroforestry systems, traditional fallows and monoculture on nitrogen-limited soil in eastern Zambia. Agricultural and Forest Entomology 7, 61-69.

Singh, G., Jalota, S.K. and Singh, Y. (2007). Manuring and residue management effects on physical properties of a soil under the rice-wheat system in Punjab, India. Soil Tillage Research 94, 229-238.

Six, J., Bossuyt, H., Degryze, S. and Denef, K. (2004). A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics. Soil Tillage Research 79, 7-31.

Six, J., Feller, C., Denef, K., Ogle, M., de Morei sa, J.C. and Albretch, A. (2002). Soil organic matter, biota and aggregation in temperate and tropical soils-Effects of no-tillage. Agronomie 22, 755-775.

Six, J., Elliot, E.T. and Paustian, K. (2000). Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage systems. Soil Biology and Biochemistry 32, 2099-2103.

Six, J., Elliot, E.T. and Paustian, K. (1999). Aggregate and soil organic matter dynamics under conventional and no-tillage systems. Soil Science Society of American Journal 63, 1350-1358.

Six, J., Elliott, E.T., Paustian, K. and Doran, J. (1998). Aggregation and Soil Organic Matter Accumulation in Cultivated and Native Grassland Soils. Soil Science Society of America Journal 62, 1367-1377.

Smale, M. (1995). ‘Maize is life’: Malawi’s delayed green revolution. World Development 23, 819-831.

Smith, A.W., Hammond, R.B. and Stinner, B.R. (1988). Influence of rye-cover crop management on soybean foliage arthropods. Environmental Entomology 17, 109-114.

Smith, I. (2001). Conservation or conventional tillage? A report on alternative crop management practices under high rainfall. Vol. 4 (2). Natural Resource Management, pp. 9-15.

Smith, A.W., Hammond, R.B. and Stinner, B.R. (1988). Influence of rye-cover crop management on soybean foliage arthropods. Environmental Entomology 17, 109-114.

Steiner, K. (2002). Conservation tillage-Gateway to food security and sustainable rural development: impact of conservation tillage on soil quality. African Conservation tillage (ACT) network, information series no. 4. GTZ.

Stinner, B.R. and House, G.J. (1990). Arthropods and other invertebrates in conservation tillage agriculture. Annual Review of Entomology 35, 299-318.

Su, Y.Z., Wang, F., Suo, D.R., Zhang, Z.H. and Du, M.W. (2006). Long-term effect of fertilizer and manure application on soil-carbon sequestration and soil fertility under the wheat-wheat-maize cropping system in northwest China. Nutrient Cycling in Agroecosystems 75, 285-295.

Swift, M.J. (1999). Management of decomposition process: Managing the soil biota for sustainable agriculture. International workshop of Tropical Soil Biology: Opportunities and challenges for African agriculture, Nairobi, March 16th-19, 1999.

Swift, M.J. and Bignell, D. (2001). Standard methods for assessment of soil biodiversity and land use practice. ASB Lecture Note 6B, Bogor, Indonesia.

Swift, M.J. and Woomer, P. (1992). Organic matter and the sustainability of agricultural systems: definition and measurement. In: Merckx, R., Mulongoy, K. (Eds.), Dynamics of Soil Organic Matter in Relation to the Sustainability of Agricultural Systems. John Wiley, Chichester, pp. 3-18.

Swift, M.J., Vandermeer, J., Ramakrishnan, P.S., Anderson, J.M., Ong, C.K. and Hawkins, B.A. (1996). Biodiversity and Agroecosystem Function. In: Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E. and Schulze, E.D. (Eds.), Functional Roles of Biodiversity: A Global Perspective, John Wiley and Sons Ltd, pp. 261-298.

Swift, M.J., Dvorak, K.A, Mulongoy, K., Musoko, M., Sanginga, N. and Tian, G. (1994). The role of soil organisms in the sustainability of tropical cropping systems. In: Syers, J.K. and Rimmer, D.L. (Eds.), Soil Science and Sustainable Land Management in the Tropics. CABI/British Society of soil science, pp. 155-172.

Swift, M.J., Frost, P.G.H., Campbell, B.M., Hatton, J.C. and Wilson, K.B. (1989). Nitrogen cycling in farming systems derived from savanna: Perspectives and challenges. In: Clarholm, M. and Bergstrom, L. (Eds.), Ecology of Arable Land, Kluwer: Dordrecht, Netherlands.

Swift, M.J., Heal, O.W. and Anderson, J.M., (1979). Decomposition in Terrestrial Ecosystems. Blackwell Scientific Publications, Oxford, 372p.

Szczech, M., Rondomanski, W., Brzeski, M.W., Smolinska, U. and Kotowski, J.F. (1993). Suppresive effect of a commercial earthworm compost on some root infecting pathogens of cabbage and tomato. Biological Agriculture and Horticulture 10, 47-52.

Tafera, A.T. (1997). A report for on-going farm evaluation of agroforestry technologies and their adoption in Machakos, Kenya, ICRAF, 78p.

Tano, Y. and Lepage, M. (1996). Soil biota: termites as crop pests of maize in a humid savanna of Cote de′ Ivoire. In: Swift, M.J. (Ed.), Report of the Tropical soil Biology and fertility Programme (TSBF), Nairobi, Kenya, 52p.

Ter Braak, C.J.F. (1990). Update notes: Canoco version 3.10. Agricultural Mathematics Group, Wageningen, The Netherlands.

Ter Braak, C.J.F. (1988). CANOCO- A FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis and redundancy analysis (version 2.1). Report LWA-88-02. Agricultural Mathematics Group, Wageningen.

Ter Braak, C.J.F. and Verdonschot, P.F.M. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sci. 57, 255-289.

Ter Braak, C.J.F. and Smilauer, P. (1998). CANOCO Reference manual and User's Guide to Canoco for windows: Software for Caonical Community Ordination (Version 4). Microcomputer Power, Ithaca, NY, USA, 352p.

Terano, Y. (2010). Effect of soil macrofauna exclusion on termite activity and crop yield in conventional and conservation tillage system in western Kenya. MSc thesis,Wageningen University.

Tian, G., Kang, B.T., Brussaard, L. and Swift, M.J. (1997a). Soil fauna mediated decomposition of plant residues under constrained environmental and residue quality and conditions. In: Cadisch, G. and Giller, K.E. (Eds.), Driven by nature: Plant litter quality and decomposition. CAB International Wallingford, U.K, pp. 125-134.

Tian, G., Kang, B.T. and Brussaard, L. (1997b). Effect of mulch quality on earthworm activity and nutrient supply in the humid tropics**.** Soil Biology and Biochemistry 29, 369-373

Tian, G., Kang, B.T. and Brussaard, L. (1995). An index for assessing the quality of plant residues and evaluating their effects on soil and crop in the sub-humid tropics. Applied Soil Ecology 2, 25-32.

Tian, G., Kang, B.T. and Brussaard, L. (1992). Biological effects of plant residues with contrasting chemical characteristics (composition) on plant and soil under humid tropical conditions- decomposition and nutrient release: Soil Biology Biochemistry 23: 1051-1061.

Tinzara, W. and Tukahirwa, E.M. (1995). The effects of soil macrofauna on soil properties in a banana cropping system, Masaka District, Uganda, TSBF, Afnet V Report, pp. 23.

Tisdall, J.M. and Oades, J.M. (1982). Organic matter and water-stable aggregates in soils. Journal of Soil Science 33, 141-163.

TSBF. (2001). Integrating Soils, Systems and Society Strategic directions for TropicalSoil Biology and Fertility (TSBF). TSBF's contribution to integrated natural resource management research, 2001-2005, TSBF Programme, Nairobi, Kenya.

Tittonell, P. (2003). Soil fertility gradients in smallholder farms of western Kenya: their origin, magnitude and importance. MSc thesis. Wageningen University, The Netherlands, 233p.

Tittonell, P., Misiko, M. and Ekise, I. (2008). Talking soil science with farmers. Leisa Magazine 24.2, 9-11.

Tittonell, P., Vanlauwe, B., Leffelaar, P.A., Rowe, E.C. and Giller, K.E. (2005). Exploring diversity in soil fertility management of smallholder farms in western Kenya. I. Heterogeneity at regional and farm scale. Agriculture, Ecosystems and Environment 110, 149-165.

Uphoff, N., Ball, A., Fernandez, E., Herren, H., Husson, O., Laing, M., Palm, C., Pretty, J. and Sanchez, P. (2006). Biological Approaches to Sustainable Soil Systems. CRC Press, Boca Raton, USA. 784p.

UN. (1987). Consolidated list of products where consumption and/or sale have been banned, withdrawn, severely restricted or not approved by governments. New York, United Nations (United Nations Publication, ST/ESA/192.

Uys, V. (2002). A guide to the termite genera of southern Africa. Plant Protection Research Institute Handbook no 15. Agricultural Research Council, South Africa, pp. 116.

Van den Berg, J. and Riekert, H.F. (2003). Effect of planting and harvesting dates on fungus-growing termite infestation in maize. Suid-Afrikaase Tydskrift Plant Grond, 20, 76-80.

Vandermeer, J. and Perfecto, I. (1997). The agroecosystems: a need for the conservation biologist’s lens. Conservation Biology 11, 591-592.

Van Huis, A., Jiggins, J., Kossou, D., Leeuwis, C., Roling, N., Sakyi-Dawson, O., Struik, P.C. and Tossou, R.C. (2007). Can convergence of agricultural sciences support innovation by resource-poor farmers in Africa? The cases of Benin and Ghana. International Journal of Agricultural Sustainability 5 (2 and 3), 91-108.

Vanlauwe, B., Bationo, A., Chianu, J., Giller, K.E., Merckx, R., Mokwunye, U., Ohiokpehai, O., Pypers, P., Tabo, R., Shepherd, K., Smaling, E., Woomer, P.L. and Sanginga, N. (2009). Integrated Soil Fertility Management: Operational definition and consequences for implementation and dissemination. Outlook on Agric. (In Press).

Vanlauwe, B., Tittonell, P. and Mukalama, J. (2006). Within-farm soil fertility gradients affect response of maize to fertilizer application in western Kenya. Nutrient Cycling in Agroecosystems 76, 171-182.

Vanlauwe, B., Aihou, K., Tossah, B.K., Diels, J., Sanginga, N. and Merckx, R. (2005). Senna siamea trees recycle Ca from a Ca-rich subsoil and increase the top soil pH in agroforestry systems in the West African derived Savanna zone. Plant and Soil 269, 285-296.

Vanlauwe, B., Palm, C.A., Murwira, H.K. and Merckx, R. (2002). Organic resource management in sub-Saharan Africa: validation of a residue quality-driven decision support system. Agronomie 22, 839-846.

Vanlauwe, B., Sanginga, N. and Merckx, R (1998) Soil organic matter dynamic after addition of nitrogen-15-labeled Leucaena and Dactyladenia residues. Soil Science Society of America Journal 62, 461-466. Vikram, R.M. (1994). Earthworm and termite abundance and activity in relation to soil fertility and productivity in semi-arid tropical agroecosystems. TSBF, pp. 1-6.

Walker, A.P., Mutuo, P.K., van Noordwijk, M., Albretch, A. and Cadisch, G. (2007). Modelling of planted fallows in Western Kenya using WaNuLCAS (I) Model calibration and validation. Agroforestry Systems 70, 197-209.

Wander, M.M. and Young, X. (2000). Influence of tillage on the dynamics of loose- and occluded-particulate and humified organic matter fractions. Soil Biology and Biochemistry 32, 1151-1160.

Wardell, D.A. (1990). The African termite: peaceful co-existence or total war? Agroforestry Today 2(3), 4-5.

Wardle, D.A. and Lavelle, P. (1997). Linkages between soil biota, plant litter quality and decomposition. In: Cadisch, G. and Giller, K.E. (Eds.), Driven by nature: Plant litter quality and decomposition. CAB International, Wallingford, U.K, pp. 107-124.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H. and van der Putten, W.H. (2004). Ecological linkages between aboveground and belowground biota. Science 304, 1629-1633.

Wartenkin, B.P. (2001). The tillage effect in sustaining soil functions. Journal of Plant Nutrition and Soil Science 164, 345-350.

Whallen, J.K., Parmelee, R.W. and Edwards, C.A. (1998). Population dynamics of earthworm communities in corn agroecosystems receiving organic or inorganic fertilizer amendments, Biology and Fertility of Soils 27, 400-407.

Wielemaker, W.G. (1984). Soil formation by termites, a study in the Kisii area, Kenya, Wageningen University, Wageningen.

Wilde, G.E. (2006). Sorghum insects: Ecology and Control. Encyclopedia of Pest Management 1, 1-5.

Wood, T.G. (1996). The agricultural importance of termites in the tropics. Agricultural Zoology Reviews 7, 117-155.

Wood, T.G. (1978). Food and feeding habits of termites. In: Brian, M.V. (Ed.), Production ecology of ants and termites. University Press Cambridge, pp. 55-80.

Wood, T.G., Johnson, R.A. and Ohiagu, C.E. (1980) Termite damage and crop loss studies in Nigeria: review of termite (Isoptera) damage, loss in yield and termite (Microtermes) abundance at Mokwa. Tropical Pest Management, 26, 241-253.

Woomer, P.L. and Swift, M.J. (1994). The Biological Management of Tropical Soil Fertility. John Wiley and Sons, Chichester, West Sussex, UK. 243p.

Wu, T., Schoenau, J.J., Li., Qian, P., Mahli, S.S. and Shi, Y. (2003). Effect of tillage and rotation on organic carbon forms of chernozemic soils. Journal of Plant Nutrition and Soil Science, 166, 328-335.

XLSTAT PRO. (2009). Factor analysis. Kovach Computing Services.

Zehnder, G.W. and Linduska, J.J. (1987). Influence of conservation tillage practices on populations of Colorado potato beetle (Coleoptera: Chrysomelidae) in rotated and non-rotated tomato fields. Entomology 16, 135-139.

Summary

Soil macrofauna, especially earthworms and termites are important components of the soil ecosystem and, as ecosystem engineers, they influence formation and maintenance of the soil structure and regulate soil processes. Despite advances made in understanding the links between soil macrofauna and agricultural productivity, this component of biodiversity is still very much a “black box”. In this thesis, I proposed to link soil biodiversity to soil functioning through the diversity of the soil structures produced by ‘ecosystem engineers’ like earthworms and termites, i.e. organisms, which physically modify and create habitats for other soil organisms and plant roots. This study aimed at providing an understanding of the link between soil macrofauna and crop management practices with soil aggregation and soil organic matter (SOM) dynamics as this is key to the improvement and management of infertile or degrading soils.

The methodological approach used in this study involved assessment of:

1. How agricultural management affects earthworm and termite diversity across sub-humid to semi-arid tropical zones.

2. The influence of soil macrofauna on soil aggregation and SOM dynamics in agro-ecosystems of Sub-Saharan Africa as influenced by management practices.

3. How management practices (e.g. tillage and use of organic inputs) influence macrofauna-induced biogenic structures in East and West African soils.

4. Disclosing farmers’ knowledge and perception on the roles of termites in Western Kenya.

In chapter 2, I examined how agricultural management affects earthworm and termite diversity across sub-humid to semi-arid tropical zones. This study, conducted in 12 long-term agricultural field trials of Eastern and Western Africa, provides new insights on diversity of earthworms and termites in SSA, since it is the first time that a study like this is done on this scale. In each trial, treatments with high and low soil organic C were chosen to represent contrasts in long-term soil management effects, including tillage intensity, organic matter and nutrient management and crop rotations. High soil C was considered to reflect relatively favorable conditions, and

low soil C less favourable conditions for soil macrofauna. For each trial, a fallow representing a relatively undisturbed reference was also sampled.

I have shown that earthworm and termite diversity and abundance were low in fallow, high-C and low-C agricultural treatments in 12 long-term trial fields across the sub-humid to semi-arid tropical zones in Eastern and Western Africa. This is in contrast to most typical native or undisturbed forest ecosystems of the tropical zones. Environmental variables contributed 42% and 25% of variation observed in the abundance of earthworm and termite taxa, respectively. Earthworm and termite taxa were less abundant in the relatively cooler, wetter and more clayey sites characteristic of Eastern Africa, compared to the warmer, drier and more sandy sites in West Africa. Continuous crop production has significant negative effects on earthworm-, but little effect on termite diversity, as compared to long-term fallow, and agricultural management resulting in high soil C increases earthworm and termite diversity as compared to low-C soil. I conclude that fewer species of earthworms and termites are favored under agricultural management that leads to lower soil C. Results indicate that soil disturbance that goes with continuous crop production is more detrimental to earthworms than to termites as compared to fallow.

In **chapter 3**, a broad regional study was conducted to examine how management intensity affects soil macrofauna, and how macrofauna in turn influence soil aggregation in agro-ecosystems of Sub-Saharan Africa.

My study has shown that macrofauna, especially earthworms, and to a smaller extent termites, are important drivers of stable soil aggregation, in conjunction with climate, soil organic C content and soil texture in Sub-Saharan agroecosystems. However, the beneficial impact of earthworms and termites on soil aggregation is reduced with increasing management intensity and associated soil disturbance due to cultivation. I suggest that this knowledge is important in designing agricultural management systems aimed at increasing long-term soil fertility in Sub-Saharan Africa.

In **chapter 4**, a long-term trial at Kabete, Kenya was selected to examine in detail the interactive effects of organic and inorganic fertilizers on soil macrofauna diversity and soil aggregation and SOM dynamics in arable cropping systems.

Differently managed arable systems were compared to a long-term green fallow system representing a relatively undisturbed reference.

Application of manure in combination with fertilizer significantly improved aggregate stability and C and N stabilization in arable soil. Furthermore, manure-fertilizer application enhanced earthworm diversity and biomass. Significant correlations between the amount and C and N contents of aggregate fractions and whole soil C and N were observed with earthworm parameters (Shannon diversity index, abundance and biomass), but not with termite parameters. Factor and regression analyses showed that earthworms had a profound effect on aggregation, C and N stabilization in whole soil and in aggregate fractions, whereas contributions of termites were limited. Therefore, my results indicate that long-term application of manure in combination with fertilizer results in higher earthworm Shannon diversity and biomass, which leads to improved soil aggregation and enhanced C and N stabilization within this more stable soil structure. These practices therefore result in the dual benefits of improving soil physical and chemical properties. In contrast, no significant improvements in soil aggregation and C and N stabilization were found when organic inputs were applied in the form of maize stover as compared to the no-input control, irrespective of fertilizer addition. Under the conditions studied, earthworms were important drivers of aggregate stability and C and N stabilization in aggregate fractions, but termites less so.

In **chapter 5,** a micromorphological approach was used to describe and quantify macrofauna-induced biogenic structures in undisturbed soil samples (i.e. thin sections) from long-term field experiments in East and West Africa. Management systems differing in tillage intensity and with or without organic amendments (manure/crop residue) were compared.

My study has shown that soil management practices, tillage type and addition of organic inputs influence soil fauna activities with a significant impact on soil structure and, hence, soil physical properties. Among the management practices assessed across two agroecological zones, fallowing, conservation tillage plus residue application (in East Africa) and hand-hoeing plus manure (in West Africa) enhanced biogenic soil structure formation, resulting in a well developed soil structure and a continuous pore system characterized by many faunal channels. By contrast, intensive tillage and absence of organic inputs resulted in soil with less biogenic soil structural features which was, therefore, prone to slaking.

Chapter 6 describes farmers' knowledge on the occurrence and behavior of termites, their perception of the importance of termites in their cropping systems and the management of termite activities in their farm fields in Nyabeda, Western Kenya. Being the main actors in environmental conservation or degradation, farmers' knowledge and perception can enrich scientific understanding of the ecology and sustainable management of termites under different agroecological conditions.

My research has shown that farmers in Nyabeda were aware of the existence of termites, their activities and nesting habits and had local names for termites that they frequently encountered. Geographic location explained 23% of the variance in farmers' perception and management of termites, whereas socio-economic variables explained only 5%. Ninety percent of the farmers perceived termites as pests and maize was rated as the most susceptible crop to termite attack, especially during the flowering/tasseling stage and in wet periods. More than 88% of the farmers used control measures against termites, further indicating a lack of awareness or appreciation of the beneficial effects often ascribed to termites with respect to soil properties in crop production. There is an urgent need for more research to assess the trade-offs between positive and negative impacts of termites on crop yields, as well as to get an understanding of the effects of different termite control strategies used by farmers on agroecosystem functions.

Samenvatting

De bodemmacrofauna is een belangrijke component van het bodemecosysteem. Vooral regenwormen en termieten, als het ware de ‘graafmachines’ van het bodemecosysteem, beïnvloeden de vorming en het behoud van de bodemstructuur, en reguleren bodemvormende processen. Hoewel we de relatie tussen bodemmacrofauna en gewasopbrengst steeds beter begrijpen, is de component biodiversiteit nog steeds een ‘black box’. In mijn onderzoek heb ik bodembiodiversiteit in verband gebracht met het functioneren van de bodem door het bestuderen van de diversiteit van bodemstructuren, die gevormd worden door regenwormen en termieten, die daarmee habitats creëren voor andere bodemorganismen en plantenwortels. Deze studie richt zich op een beter begrip van de relatie tussen bodemmacrofauna en agrarisch management en het effect van deze relatie op aggregaatvorming en de bodemorganische stofdynamiek, omdat deze elementen de sleutel vormen voor een verbetering van het management van onvruchtbare en degraderende bodems.

De methodologische aanpak van dit onderzoek omvat een beoordeling van:

1. Hoe agrarisch management de regenwormen- en termietendiversiteit beïnvloedt in de subhumide en semi-aride tropische klimaatszones.
2. De invloed van de bodemmacrofauna op aggregaatvorming en bodemorganische stofdynamiek in agro-ecosystemen in sub-Sahara Africa (SSA) onder invloed van managementpraktijken.
3. Hoe managementpraktijken (zoals ploegen en gebruik van organische toevoegingen) de door de macrofauna geïnduceerde biogene structuren beïnvloeden in Oost- en West-Afrikaanse bodems.
4. Een uiteenzetting van boerenkennis en -perceptie omtrent de rol van termieten in West-Kenia.

Hoofdstuk 2 is een onderzoek naar effecten van agrarisch management op regenwormen- en termietendiversiteit in subhumide en semi-aride tropische klimaatszones. Deze studie is uitgevoerd in 12 landbouwkundige lange

termijnproeven in Oost- en West-Afrika en geeft nieuwe inzichten in de diversiteit van regenwormen en termieten in SSA. Het is de eerste keer dat een studie als deze op zo’n grote schaal is verricht. In ieder experiment werden behandelingen met een hoog en laag bodemorganisch koolstofgehalte gekozen om de contrasten tussen effecten van bodemmanagement op de lange termijn weer te geven, waaronder effecten van ploegintensiteit, organische stof- en nutriëntenmanagement en gewasrotaties. Aangenomen is dat een hoog koolstofgehalte relatief gunstige omstandigheden weerspiegelde voor de bodemmacrofauna, en een laag koolstofgehalte minder gunstige omstandigheden. In ieder proefveld is bovendien een braakliggend stuk grond bemonsterd dat als onverstoorde referentie diende.

Ik heb laten zien dat regenwormen- en termietendiversiteit en -aantallen laag waren in de onverstoorde referentie, alsook in de behandelingen met hoge en lage koolstofgehaltes in alle 12 velden van de lange termijnproeven in de subhumide en semi-aride tropische klimaatszones in Oost- en West-Afrika. Dit staat in contrast met de oorspronkelijke, onverstoorde bosecosystemen in tropische klimaatszones. Omgevingsvariabelen droegen respectievelijk 42% en 25% bij aan de waargenomen variatie in aantallen van regenwormen en termieten. Regenwormen- en termietentaxa waren minder talrijk in de relatief koele, natte en meer kleiïge locaties die karakteristiek zijn voor Oost Afrika, dan in de warmere, drogere en meer zandige locaties in West Afrika. Continuteelt had significant negatieve effecten op de regenwormendiversiteit, maar slechts gering effect op de termietendiversiteit in vergelijking tot langdurig braakliggend land. Agrarisch management dat leidde tot een hoog bodemorganisch koolstofgehalte verhoogde de regenwormen- en termietendiversiteit in vergelijking tot een laag bodemorganisch koolstofgehalte. Ik concludeer hieruit dat er minder regenwormen- en termietensoorten voorkomen onder agrarisch management dat leidt tot een lager bodemorganisch koolstofgehalte. De resultaten geven aan dat de bodemverstoring die samengaat met continuteelt schadelijker is voor regenwormen dan voor termieten met braakliggend land als referentie.

Hoofdstuk 3 is een regionale studie naar de effecten van managementintensiteit op de bodemmacrofauna, en hoe deze macrofauna de aggregaatvorming in de bodem beïnvloedt in agro-ecosystemen in sub-Sahara Africa.

Mijn studie heeft laten zien dat, tezamen met klimaat, bodemorganisch koolstofgehalte en bodemtextuur, de macrofauna (in het bijzonder regenwormen en in mindere mate termieten) belangrijk zijn voor de vorming van stabiele aggregaten in agro-ecosystemen beneden de Sahara. De positieve invloed van regenwormen en termieten op aggregaatvorming is echter verminderd met een toenemende managementintensiteit en de daarmee verbonden bodemverstoring door grondbewerking. Ik suggereer dat deze kennis belangrijk is bij het ontwerpen van agrarische managementsystemen die tot doel hebben bodemvruchtbaarheid in SSA op de lange termijn te verbeteren.

Hoofdstuk 4 betreft een lange-termijn proef in Kabete, Kenia, waarbij gedetailleerd is gekeken naar de interactieve effecten van organische en anorganische meststoffen op de diversiteit van de bodemmacrofauna, bodemaggregaatvorming en organische stofdynamiek in akkerbouwsystemen. Verschillend beheerde agrarische systemen zijn vergeleken met een systeem dat reeds lange tijd onder groene braak lag en dat als relatief onverstoorde referentie diende.

Het aanwenden van dierlijke mest in combinatie met kunstmest verbeterde de aggregaatstabiliteit en koolstof- en stikstofstabilisatie in het bouwland significant. Bovendien versterkte de aanwending van dierlijke mest en kunstmest in combinatie de regenwormendiversiteit en -biomassa. Er werden significante correlaties gevonden tussen de hoeveelheid koolstof (C) en stikstof (N) in aggregaatfracties en de totale hoeveelheid C en N in de bodem met regenwormenparameters (Shannon diversiteitsindex, aantallen en biomassa), maar niet met termietenparameters. Factor- en regressieanalyse lieten zien dat regenwormen een sterk effect hadden op aggregaatvorming, koolstof- en stikstofstabilisatie in de gehele bodem en in aggregaatfracties, terwijl de effecten van termieten minimaal waren. Mijn resultaten geven daarom aan dat het langdurig aanwenden van dierlijke mest in combinatie met kunstmest resulteert in een hogere Shannon diversiteitsindex en regenwormenbiomassa, leidende tot een verbeterde bodemaggregaatvorming en versterkte koolstof- en stikstofstabilisatie binnen een stabielere bodemstructuur. Deze managementpraktijken resulteren zodoende in een dubbel voordeel: ze verbeteren zowel fysische als chemische bodemeigenschappen. In vergelijking met de referentie zonder organische toevoegingen werden daarentegen geen significante verbeteringen gevonden in bodemaggregaatvorming en koolstof- en stikstofstabilisatie, wanneer organische toevoegingen werden aangewend in de vorm van maïsresiduen, ongeacht de toediening van kunstmest. Onder de bestudeerde omstandigheden waren regenwormen belangrijker voor bevordering van de aggregaatstabiliteit en koolstof- en stikstofstabilisatie in aggregaatfracties dan termieten.

Hoofdstuk 5 beschrijft en kwantificeert, met behulp van een micromorfologische bestudering van slijpplaten, de door de macrofauna geïnduceerde biogene structuren in ongestoorde bodemmonsters, afkomstig uit lange-termijn proeven in Oost- en West-Afrika. In dit hoofdstuk zijn managementsystemen met verschillende grondbewerkingsintensiteit en met en zonder organische toevoegingen (mest/plantenresten) vergeleken.

Mijn studie heeft laten zien dat bodemmanagementpraktijken, type grondbewerking en organische toevoegingen effect hebben op de activiteiten van de bodemfauna met een significante invloed op de bodemstuctuur en daarmee op bodemfysische eigenschappen. Van de geëvalueerde managementpraktijken die twee agro-ecologische zones omspannen, versterkten braaklegging, conserveringslandbouw met toevoeging van plantenresten (in Oost-Afrika) en handgewied bouwland met toevoeging van mest (in West-Afrika) de vorming van biogene bodemstructuren. Dit resulteerde in een goed ontwikkelde bodemstructuur en een continu poriënsysteem gevormd door de vele door de fauna gemaakte gangen. Intensieve grondbewerking en onthouding van organische toevoegingen resulteerde daarentegen in bodems met minder biogene structuren die daardoor gevoelig waren voor verslemping.

Hoofdstuk 6 beschrijft de kennis van boeren over het vóórkomen en gedrag van termieten, hun perceptie van het belang van termieten in hun gewassystemen en het management van termietenactiviteit op hun velden in Nyabeda, West-Kenia. Aangezien zij de voornaamste actoren in behoud of degradatie van hun omgeving zijn, kan de kennis en perceptie van boeren het wetenschappelijk inzicht in de ecologie en het duurzaam beheer van termieten onder verschillende agro-ecologische omstandigheden verrijken.

Mijn onderzoek heeft laten zien dat de boeren in Nyabeda zich bewust zijn van het bestaan van termieten, hun activiteiten en hun nestgewoonten, en dat ze lokale namen hadden voor termieten die ze vaak tegenkomen. Geografische locatie verklaarde 23% van de variantie in de boerenperceptie en het termietenmanagement, terwijl socio-economische variabelen slechts 5% verklaarden. Negentig procent van de boeren ziet termieten als ongedierte en maïs wordt gezien als het meest kwetsbare gewas voor termietenschade, vooral tijdens de bloei en in natte perioden. Meer dan 88% van de boeren paste bestrijdingsmaatregelen toe tegen termieten, wat een verder gebrek aan bewustzijn of waardering aangeeft van de gunstige effecten met betrekking tot bodemeigenschappen in de gewasproductie, die vaak aan termieten worden toegeschreven.

Er is dringend behoefte aan meer onderzoek naar een evaluatie van trade-offs tussen positieve en negatieve invloeden van termieten op gewasopbrengsten. Bovendien is er meer inzicht nodig in de effecten van verschillende beheersmaatregelen tegen termieten die door de boeren in agro-ecosystemen worden gebruikt.

ACKNOWLEDGEMENTS

'n Bouwvakker is niet van steen

This study was supported by Science for Global Development/WOTRO through Wageningen University, The Netherlands; Norman Borlaug LEAP Fellowship Program through UC-Davis, USA; and International Atomic Energy Agency (IAEA) grant to TSBF-CIAT, Nairobi, Kenya. Financial support for printing of this thesis was obtained from the Dr. Judith Zwartz Foundation, Wageningen, The Netherlands. I thank my colleagues, especially the scientists and field technicians of the Tropical Soil Biology and Fertility Institute of the International Centre for Tropical Agriculture (TSBF-CIAT, Kenya), Kenya Agricultural Research Institute (KARI), Kenya Forestry Research Institute (KEFRI), Kenyatta University, Kenya, International Institute of Tropical Agriculture (IITA, Nigeria), International Fertilizer Development Centre (IFDC, Burkina Faso), Institute of Natural Environmental and Agricultural Research (INERA, Burkina Faso), Savanna Agricultural Research Institute (SARI, Ghana), Chitedze Agricultural Research Station (Malawi), International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, Niger) and Natural History Museums (Hungary), who agreed to work with me and have allowed me to use their experimental sites for this study.

To all those whom I cannot name here but contributed in one way or the other to the success of this work, I wish to convey that your efforts did not go to waste.

Special thanks are due to my promoters. You gave me hope and lifted me at a time when I was down. I am grateful that you were all very accommodative and I do not recall any incidence in which I had divergent opinion. I look back with nostalgia on the day of the interview, the 10th of October 2005. You made the moment as friendly as possible, making me feel at ease. At the end of it all, I felt as if we had known each other for a long time. I would like in a very special way to thank **Prof. Lijbert Brussaard** for giving me the opportunity to pursue this noble goal and for sending me off on the long journey. In the words of Prof. Mike J. Swift, I can attest "he is an excellent scientist and a nice man". His many encouragements are a pillar and a fundamental base for this research. The two times that you led the entire WOTRO team and visited our study sites both in Kenya and Burkina Faso greatly boosted my spirits and my resolve not to disappoint. Thanks go to him for his constructive criticism, thoroughness and patience while marking rough drafts of this

work. Thanks are due to him for finding time to discuss each of my manuscripts as many times as needed. I also thank him for guiding me well through my training and supervision plan (TSP). I would like to thank **Dr Mirjam Pulleman** for providing daily supervision, both in the field and in the laboratory. I cannot forget the countless times I knocked into her office without notice, and she would readily be available to discuss my work. I truly enjoyed all the moments I spent with you and looked forward to each and every occasion to be able to discuss anything. I also thank **Dr**. **Bernard Vanlauwe** of TSBF-CIAT who led my supervision while in Kenya. His broad smile after my interview for the PhD position in October 2005 was a lot reassuring. Special thanks go to him for: coordinating my field research expenses, administrative and logistics support, and regular guidance during the course of field study and preparation of the draft manuscripts. Thanks are due to **Prof. Johan Six** of UC Davis for accepting to co-supervise the work. I am most grateful for his encouragement during my application for co-funding from Norman-Borlaug Fellowship and ultimate invitation to UC-Davis for a short visit to his ISOTOPE laboratory. I cannot forget his many humorous encouragements that I should go for it. Thanks are due to him for taking time off his busy schedule to look at my draft manuscripts. To **Dr. David Odee**, be blessed for taking me up in your arms when issues were really challenging. Your closeness, visits and encouragement was most soothing. Special thanks to **Dr. Maja Kooistra** for accepting to guide me through the micromorphological work. Your advice to me, that I should start thinking like soil fauna made the otherwise challenging chapter on micromorphology lovely. Thanks for taking time off your busy schedule to accommodate me and for finding time to look at rough drafts of my work. Thanks are due to **Dr. Csaba Csudzi** for introducing me to the world of earthworms, and for inviting me to the Museums of Natural History in Hungary for a training programme in earthworm taxonomy and ultimately for assisting in identification of the collected earthworm specimens.

Many thanks to the BGBD global and Kenya team for providing the linkage that bore this idea. To Dr. Jeroen Huising: that evening phone call to me, has made a big difference in my life, and has completely changed my fortune. Special thanks to Prof. Mike J. Swift, Prof. Nancy K. Karanja, Dr. Sheila Okoth and you (Jeroen) for encouraging me to take up this challenge.

I am also grateful to the entire TSBF-CIAT staff, especially the Finance and Administrative, and Research team of Caleb Mulogoli, Oscar Omutende, Mary Mureithi, Alice Kereri, Juliet Ogolla, Rosemary Meyo, John Mukalama, Elly Owino and Henry Agalo, for providing logistical support and a cosy environment in which to work. To the Finance Department, thanks for speeding up payments even at short notices.

Thanks are due to my great colleague, Zida Zacharie with whom I worked under WOTRO/NWO programme for facilitating field activities in Burkina Faso and the other West African sites; Musombi Kiberenge, Reuben Mwakodi and John Karanja of the National Museums of Kenya, Nairobi for offering me a suitable environment during taxonomic identification of the soil fauna samples collected. I thank the Director, Dr. Pram Bindraban and Jan Huting and the entire staff of World Soil Reference Centre (ISRIC) for offering me their facilities during soil thin section analysis. I also thank Hans Huisman from the Cultural Heritage Agency in Amersfoort for camera for scanning my soil thin sections.

During my first six and last months in Wageningen, I had diverse people in the Department of Soil Quality who helped me in different ways. Special thanks to Dr. Ron de Goede who introduced me to CANOCO statistical programme during early times in my work and for standing by me to ensure its completion. Many thanks to Odair Alberton for showing me around Wageningen; Caroline Witlink, Winnie van Vark, Esther van der Brug, Anita Kok, and the entire administrative and financial unit for providing all that I needed to make my stay as comfortable as possible.

“No play makes Jack a dull boy”. Although a sandwich PhD Programme makes it difficult to have long-time friends, the many rib-cracking jokes and laughter I shared with colleagues during coffee or lunch breaks is worth mentioning. Helton de Souza, Steve Crittenden, Roland Klefoth, Ingrid Lubbers, Maria-Luz Cayuela, Qin Wei, Rolland Yemadje, Dennis Ochieno, Cecilia Onyango, Benjamin Kibor, Samwel Guto, Alfred Nyambane, George Sidimbah, Stanley “Livondo” and all the Kenyan brothers and sisters in Wageningen, thanks for making a small home away from home.

Post humously, I thank the late **Matilda Night** and **Dr. Elly A. Ochola** who in a great way contributed in influencing some of my decisions and encouraged me to follow this path, and my parents **Meshack Elly A. Ongoro** and **Monica Adhiambo** who introduced me to a new environment, gave me all the support, but passed on before I could express my gratitude to them in a special way. May you all rest in peace now that you are in print.

Thanks also go to Sister **Lucy** and **Moses** for giving my daughters **Monica and Regina parental love** in my absence**;** and the **family members** whose love and continued support are pillars on which this work stands. In a special way, I am thanking my loving wife **Irene Adhiambo** whose timely love provided a niche for me to lay my head during the hard times and whose continued support and patience has seen me this far. Your love and the joyous bundles of **HOPE** and **GIFT** that you have given me is a lot inspiring. Thanks for being a great mother and father, all in one. Thanks for being strong, and for enduring my long absence, especially when I had to leave you only hours after giving me a worthy birthday present (on the 22nd of August 2008) to travel to Burkina Faso for a Project Progress Review meeting and field work, and in January 2009 when I had to come back to the Netherlands to walk the last miles. Your skills in convincing the children, that my absence is just but short lived, and is for a worthy cause was most humbling.

"The roots of education are bitter, but the fruits are sweet"

May God bless you all and I thank you once again for being special to me in life.

CURRICULUM VITAE

Frederick Ouma Ayuke

Fredrick O. Ayuke was born on the 22nd of August, 1969 in Omoya Village of Karading (Central Kabuoch Location), Homa Bay District, Nyanza Province, Kenya. In 1977, he started his primary education where he joined Kongowea Primary School, Mombasa, but transferred to Okota Primary School, Homabay in 1981. He later transferred to Magina Primary School where he obtained his Certificate of Primary Education (CPE) in 1983. He then proceeded to Obera Mixed Secondary School where in 1987 he obtained his Kenya Certificate of Education (KCE). In 1988, he proceeded to Rapogi Boys High School where he obtained his Kenya Advanced Certificate of Education (KACE) in 1989. In 1990, he joined Moi University, Eldoret, Kenya for his undergraduate training, and in 1994, he graduated with Bachelor of Science degree in Forestry. After his bachelors training, he worked as a teacher under Board of Governors at Rarage Secondary school, Homa Bay between January 1994 and August 1995. In September 1995, he joined Blanket Industries, Mombasa as a Production Supervisor. In October 1996, he was awarded a Partial Scholarship to pursue his Postgraduate studies at Moi University, Eldoret. In June 1997, he was awarded both African Education Research in Agroforestry (ANAFE) Postgraduate and Programme Research Fellowships by World Agrofrestry Centre (formerly ICRAF) to co-fund his research activities. In December 2000, he graduated with a Master of Philosophy degree in Forestry, specializing in Applied Soil Biology/Ecology. Between May 2000 and February 2002, he worked as a temporary Research Assistant with Tropical Soil Biology and Fertility (TSBF-UNESCO), where he assisted in reviewing University Student (MSc/M.Phil) proposals and developed a work plan to fit within the African Research Network (AfNet) and TSBF framework of activities thereby assisting in coordination/supervision of the students' field activities. As a research assistant, between February 2002 and March 2003, he planned and carried out the Global Litter Invertebrate Experiment (GLIDE) at the designated site of Kakamega Forest, western Kenya. This was a global project of International Biodiversity Observation year (IBOY) involving over 23 countries. Between September 2002 and September 2003, he worked as a research assistant for TSBF-CIAT, where he planned and carried out work focused on production of a Concept note for a study in the Global Environmental Facility (GEF) Project site in Embu and Taita Hills, Kenya that is consistent with the objectives and outputs of the GEF project. This is a United Nations Environmental Programme (UNEP) initiative being coordinated by TSBF-CIAT on Below-ground Biodiversity (BGBD) research involving 7 countries around the globe: Kenya, Uganda, Indonesia, Mexico, Brazil, India and Cote de' Ivoire. In September 2003, he joined Kenya Methodist University as an Assistant Lecturer, where he taught Soil Microbiology and Environmental Sciences (Introduction to Environmental Science, Applied Ecology, and Evolutionary Biology). He was also the Departmental Examinations coordinator. In September 2005, he was promoted to the position of Lecturer and continued with his duties as designated. In August 2005, he applied for a PhD position at the Department of Soil Quality, Wageningen University and emerged successful after an interview conducted on the 10th October 2005 at TSBF-CIAT Nairobi. He was subsequently awarded a Sandwich PhD position beginning January 2006. For his PhD, he conducted work on: *biodiversity of soil macrofauna functional groups and their effects on soil structure in East and West African cropping systems, as related to organic resource management, crop rotation and tillage.* His work covered 12 long-term field trials across the sub-humid to semi-arid tropical zones of Eastern Africa (Embu, Kabete, Impala and Nyabeda in Kenya and Chitala in Malawi) and Western Africa (Tamale in Ghana, Ibadan in Nigeria, Sadore in Niger and Farakoba, Saria I, II and III in Burkina Faso). Upon completion of his PhD studies, he will take a position at the Department of Land Resource Management and Agricultural Technology (Faculty of Agriculture), of University of Nairobi, Kenya. He is married to Irene Adhiambo and they have four children (Monica Adhiambo, Regina Akinyi, Hope-Claris and Gift-Knight). He can be reached on: Fredrick.ayuke@yahoo.com.

PUBLICATIONS

Refereed Journals

Ayuke, F.O., Karanja, N.K., Muya, E.M., Musombi, B.K., Mungatu, J. and Nyamasyo, G.H.N. (2009). Macrofauna diversity and abundance across different land use systems in Embu, Kenya. **Journal of Tropical and Subtropical Agroecosystems, 11 (2): 371-384.**

Karanja, N.K., **Ayuke, F.O.**, Muya, E.M., Musombi, B.K., and Nyamasyo, G.H.N. (2009). Soil macrofauna community structure across land use systems of Taita, Kenya. **Journal of Tropical and Subtropical Agroecosystems, 11 (2): 385-396.**

Wall, D.H., Bradford, M.A., John, M.G.ST., Trofymows, J.A., Behan-Pelletier, V., Bignell, D.E, Dangerfield, J.M., Parton, W.M., Rusek, J., Voight, W., Wolters, V., Gardel, H.Z., **Ayuke, F.O.**, Bashford, R., Beljakova, O.I., Bohlen, P.J., Brauman, A., Flemming, S., Henschel, J.R., Johnson, D.L., Jones, T.F., Kovarova, M., Kranabetter, J.M., Kutny, L., Kuo-Chuan, L., Maryati, M., Masse, D., Pokarzhevskii, A., Rahman, H., Sabara, M.G., Joerg-Alfred, S., Swift, M.J., Varela, A., Vasconcelos, H.L., White, D. and Zou, X. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate dependent. **Global Change Biology, 14: 2661-2677.**

Karanja, N.K., **Ayuke, F.O**. and Swift, M.J. (2006). Organic Resource Quality and Soil Fauna: Their role on the microbial Biomass, Decomposition and nutrient release patterns in Kenya Soils. **Journal of Tropical and Subtropical Agroecosystems, 6: 73-83.**

Ayuke, F.O., M.R. Rao, M.J. Swift and M.L. Opondo-Mbai. (2003). Impact of soil fertility management strategies on diversity and populations of soil macrofauna in agroecosystem. Special Issue: Sustainable use of land resources to alleviate poverty in the new millenium. **East African Agricultural and Forestry Journal, 69 (1,2): 131-137.**

Book Chapters

Ayuke, F.O., Karanja, N.K., Bunyasi, S.W. (2007). Evaluating effect of mixtures of organic resources on nutrient release patterns and uptake by maize. *In:* Bationo, A., Waswa B., Kihara, J., Kimetu, J. (Eds). *Advances in Integrated Soil Fertility Research in sub-Saharan Africa: Challenges and Opportunities, 79: 833-844*. Springer publishers.

Ayuke, F. O., Opondo-Mbai, M.L, M.R. Rao. and Swift, M.J. (2004). Effect of Organic and Inorganic Sources of Nutrients on Soil Mineral Nitrogen and Maize Yields in western Kenya. In Bationo, A (Ed), *Managing Nutrient Cycles to Sustain Soil Fertility in sub-Saharan Africa, 4: 65-76.* Academy of Sciences Publishers, Nairobi Kenya.

Ayuke, F. O., Opondo-Mbai, M.L, M.R. Rao. and Swift, M.J. (2004). An assessment of Biomass Transfer from Green Manure to Soil Macrofauna in Agroecosystems-Soil Macrofauna Biomass. In Bationo, A (Ed), *Managing Nutrient Cycles to Sustain Soil Fertility in sub-Saharan Africa, 4: 65-76.* Academy of Sciences Publishers, Nairobi Kenya.

Conference Proceedings and Reports

Ayuke, F.O., Karanja, N.K., Wickama, J, Awiti, A. and Hella, J. (2007). Soil fauna community structure across land management systems of Kenya and Tanzania. *In:* Njeru, R.W., Kagabo, D.M., Ndabamenye, T., Kayiranga, D., Ragama, P., Sallah, P.Y.K., Nkerabahizi, D., Ndayiragije, A., Ndiramiye, L., Night, G., Akinyemi, S.O.S and Kanuya, N. (eds), *Sustainable agriculture productivity livelihoods. Proceedings* of National Conference on Agricultural Research Outputs, 26-27 March, Kigali, Rwanda, pp. 396-406.

Ayuke, F. O., Karanja, N.K., Swift, M.J, (2003). Global Litter Decomposition Experiment (GLIDE) in Kenya: A Kenyan contribution to the International Biodiversity Observation Year (IBOY). Report of Tropical Soil Biology and Fertility (TSBF) Institute of CIAT, 2003, 22p.

Ayuke, F.O., Opondo-Mbai, M.L, M.R. Rao. and Swift, M.J, (2001). Agricultural intensification, soil fertility management strategies in agroecosystems and implication on belowground biodiversity-Soil Macrofauna diversity and populations. Proceedings of Soil Science Society of East Africa (SSSEA) conference at Mombasa, Kenya: 4th-8th Dec 2000).

Ayuke, F. O., Opondo-Mbai, M.L, M.R. Rao. and Swift, M.J. (2001). An assessment of Soil Fertility Management strategies in Agroecosystems (biomass transfer technology) on Belowground Biodiversity-Soil macrofauna biomass (A paper submitted and approved for presentation to the proceedings of the 8th Tropical Soil Biology and Fertility and Programme Afiican Network meeting, Arusha, Tanzania: 7th –l0th May 2001).

Ayuke, F. O., Opondo-Mbai, M.L, M.R. Rao. and Swift, MJ. (2001). Effect of organic and inorganic sources of nutrients on soil mineral nitrogen (ammonium and nitrate N) and maize yields in western Kenya (A paper submitted and approved for presentation to the proceedings of the 8th Tropical Soil Biology and Fertility and Programme African Network meeting, Arusha, Tanzania: 7th-10th May 2001).

Ayuke, F.O. (2000). Diversity, abundance and function of soil invertebrate fauna in relation in relation to quality of organic residues. M. Phil thesis of Moi University, Eldoret, Kenya.

Ayuke, F. O., Opondo-Mbai, M.L, M.R. Rao. and Swift, M.J. (1999). Diversity, abundance and function fauna in relation in relation to quality of organic residues. Part of this research work was presented in both Soil Science Society of East Africa (SSSEA) and African Research Network (AfNet) workshops in Kampala, Uganda (6th-17th Sept 1999).

PEandRC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PEandRC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of Literature (5.6 ECTS)

- Biodiversity of soil macrofauna groups and their effects on soil structure in West and East African cropping systems, as related to organic resource management, crop rotation and tillage (2006)

Laboratory Training and Working Visits (8.4 ECTS)

- Earthworm taxonomy; Natural Museums, Budapest, Hungary (2006)
- Soil micromorphology analysis; ISRIC World Soil Information (2006/09)
- Soil fractionation, aggregate wet sieving and isotope labelling; UC-Davis, USA (2008)

Post-Graduate Courses (3 ECTS)

- Multivariate analysis; PEandRC (2006)
- Soil ecology; PEandRC (2006)

Deficiency, Refresh, Brush-up Courses (2.7 ECTS)

- Information literacy; CENTA (2006)
- Introduction to biodiversity-R statistical program; BGBD/TSBF-CIAT (2006)

Competence Strengthening / Skills Courses (4 ECTS)

- Project and time management; WGS (2006)
- Presentation skills; WGS (2009)
- Techniques for writing and presenting scientific papers; WGS (2009)

Discussion Groups / Local Seminars and Other Scientific Meetings (4.2 ECTS)

- Students’monthly meeting in Kenya for discussion of research projects, progress and sharing of experiences (2006/08)
- Soil Quality chair group meetings / seminars (2006/09)
- Forest and Conservation Ecology (2009)

PEandRC Annual Meetings, Seminars and the PEandRC Weekend (3 ECTS)

- Mini symposium “Soil fractionation: limits and potential”; Alterra (2006)
- Symposium “The rights-based approach to food”; WICC, Wageningen (2006)
- PEandRC Weekend (2006)
- 91st Dies Natalis; Wageningen University (2009)
- Seminar: “Soils in Spectroscopy , Spectroscopy in Soils”; WUR (2009)
- PEandRC Day (2009)
- Seminar: “Towards a sampling protocol for soil biota in the humid tropics”; WUR

International Symposia, Workshops and Conferences (6.6 ECTS)

- World Soil Issues and Sustainable Development; ISRIC (2006)
- International Conference on Biodiversity: “Biodiversity, People and Agriculture”; Kampala, Uganda ; oral presentation (2006)
- Netherland Ecology Research Network Annual Meeting; poster (2009)
- Diversitas Conference; South Africa; poster (2009)

Co-supervision of MSc Students (3 Students; 40 Days)

- Effects of soil fertility management practices on soil aggregation, carbon and nitrogen dynamics in a long-term experiment; NARL, Kabete, Kenya (David Lelei, MSc University of Nairobi)
- Interactive effects of crop residue management and soil macrofauna on soil aggregation and associated C and N dynamics in field trials in Western Kenya (Marianne Hoegmood, MSc Wageningen University)
- Effect of soil macrofauna exclusion on termite activity and crop yield in conventional and conservation tillage system in Western Kenya (Yusuke Terano, MSc Wageningen University)

The research described in this thesis was supported by Science for Global Development/WOTRO through Wageningen University, Norman Borlaug LEAP Fellowship Program through UC-Davis and a research grant from the International Atomic Energy Agency (IAEA) to TSBF-CIAT.

Financial support for printing this thesis was obtained from the Dr Judith Zwartz Foundation, Wageningen, The Netherlands