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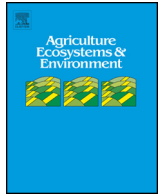


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Highlights

Exclusion of soil macrofauna did not affect soil quality but increased crop yields in a sub-humid tropical maize-based system

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B.K. Paul^{c,*}, B. Vanlauwe^d, M. Hoogmoed¹, T.T. Hurisso^{c,2}, T. Ndabamenye^{c,3}, Y. Terano^c, J. Six, F.O. Ayuke⁴, M.M. Pulleman^c

- Termites were dominant soil macrofauna irrespective of tillage and residue management.
- Termite diversity was low and grass/residue feeding species were dominant.
- Soil macrofauna did not affect soil C content nor soil aggregate stability.
- Maize and soybean yields were higher when soil macrofauna were excluded.

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Exclusion of soil macrofauna did not affect soil quality but increased crop yields in a sub-humid tropical maize-based system

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ABSTRACT

Soil macrofauna such as earthworms and termites are involved in key ecosystem functions and thus considered important for sustainable intensification of crop production. However, their contribution to tropical soil and crop performance, as well as relations with agricultural management (e.g., Conservation Agriculture), are not well understood. This study aimed to quantify soil macrofauna and its impact on soil aggregation, soil carbon and crop yields in a maize–soybean system under tropical sub-humid conditions. A field trial was established in Western Kenya in 2003 with tillage and residue retention as independent factors. A macrofauna exclusion experiment was superimposed in 2005 through regular insecticide applications, and measurements were taken from 2005 to 2012. Termites were the most abundant macrofauna group comprising 61% of total macrofauna numbers followed by ants (20%), while few earthworms were present (5%). Insecticide application significantly reduced termites (by 86 and 62%) and earthworms (by 100 and 88%) at 0–15 and 15–30 cm soil depth respectively. Termite diversity was low, with all species belonging to the family of Macrotermitinae which feed on wood, leaf litter and dead/dry grass. Seven years of macrofauna exclusion did not affect soil aggregation or carbon contents, which might be explained by the low residue retention and the nesting and feeding behavior of the dominant termites present. Macrofauna exclusion resulted in 34% higher maize grain yield and 22% higher soybean grain yield, indicating that pest damage – probably including termites – overruled any potentially beneficial impact of soil macrofauna. Results contrast with previous studies on the effects of termites on plant growth, which were mostly conducted in (semi-) arid regions. Future research should contribute to sustainable management strategies that reduce detrimental impact due to dominance of potential pest species while conserving soil macrofauna diversity and their beneficial functions in agroecosystems.

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1. Introduction

Feeding a rapidly growing human population while preserving environmental sustainability results in unprecedented challenges for agriculture and natural resources. Sustainable intensification is especially urgent in Sub-Saharan Africa where soil degradation and food insecurity are most pressing, and smallholder farmers are challenged by scarcity of resources including organic and inorganic fertilizers (Godfray et al., 2010; Garnett et al., 2013). It is of crucial importance that management of agricultural soils enhances and sustains soil fertility and resource use efficiency, based on a better understanding of ecosystem services (Beare et al., 1997; Brussaard et al., 2010). Management practices involving minimum soil disturbance, organic soil cover and crop diversification –

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collectively known as Conservation Agriculture (CA) – are widely promoted in Sub-Saharan Africa. CA has been shown to stimulate soil macrofauna, which, in turn, can lead to enhanced soil aggregation and therefore C storage, reduced runoff and erosion, improved nutrient and water use efficiency, and ultimately stable crop yields. These potential impacts however vary with specific agro-ecologies (Erenstein, 2003; Hobbs, 2007; Palm et al., 2014; Brouder and Gomez-Macpherson, 2014; Corbeels et al., 2014).

A wide range of different soil macrofauna provide ecosystem services including soil organic matter turnover, nutrient cycling, soil structure formation and pest and disease control (Lavelle et al., 1997; Beare et al., 1997; Brussaard, 2012). Of key interest are soil ecosystem engineers such as earthworms, termites and, to lesser extent ants. Through bioturbation they incorporate plant litter and crop residues into the soil, thereby modifying biological, chemical and physical soil processes that affect the flow of energy and material, and modify the habitat of other soil biota (Jones et al., 1994; Lavelle et al., 1997; Pulleman et al., 2012). The impact of soil ecosystem engineers on soil quality is partly mediated through their effects on soil organic matter incorporation and soil aggregation (Six et al., 2004). Stable soil aggregates can physically protect soil organic matter against rapid decomposition (Six et al., 2000) and reduce soil erosion (Barthes and Roose, 2002). It has been shown that the biogenic structures produced by earthworms and termites, such as casts and sheetings, can differ from bulk soil in organo-physical composition and be enriched in carbon and nutrients, suggesting protection of organic matter against rapid mineralization (Fall et al., 2001; Mora et al., 2003; Pulleman et al., 2005; Bossuyt et al., 2005). The capacity of earthworms to incorporate organic matter into the soil and improve soil aggregation has been widely investigated (Lee, 1985; Lavelle et al., 1997; Six et al., 2004), although effects on C mineralization versus C stabilization are still a matter of debate (Lubbers et al., 2013). It has also been shown that earthworm abundance is generally higher in no-tillage systems due to the lack of mechanical soil disturbance (Chan, 2001; Shuster and Edwards, 2003; Castellanos-Navarrete et al., 2012).

Termites are considered the dominant soil ecosystem engineers in tropical (semi)-arid areas, whereas earthworms occur widely in (semi-) humid climates, both tropical and temperate (Lal, 1988; Lobry de Bruyn and Conacher, 1990). Termites are well known for their role in organic matter breakdown and modification of soil properties. They construct a variety of organo-mineral structures that result from intestinal transit (casts) or are mixed and impregnated with saliva and are used to construct mounds, nests, galleries and surface sheetings (Lobry de Bruyn and Conacher, 1990; Fall et al., 2001; Mora et al., 2003). Termites can mold up to 1300 kg ha⁻¹ of soil annually (Kooyman and Onck, 1987) and it has been suggested that their biogenic structures constitute microsites that protect organic C against rapid mineralization (Mora et al., 2003). Termites are classified on the basis of their food choice, feeding habits and nesting behavior, ranging from soil feeders that occur in the soil profile and feed on organic matter associated with mineral soil, wood feeders that feed on wood and excavate galleries in larger items of wood litter, and litter feeders that forage for leaf litter, dry standing grass stems and small woody items (Swift and Bignell, 2001; Eggleton and Bignell, 1995; Wood, 1996). Similarly, ants modify the soil through foraging and nest building although their impact on soil properties is generally less important compared with earthworms and termites (Jungerius et al., 1999; Lobry de Bruyn and Conacher, 1990).

A number of studies focusing on natural Savanna ecosystems in Australia and West Africa have reported beneficial effect of termites on soil porosity, water infiltration, nutrient uptake and plant cover or biomass, demonstrating their capacity to rehabilitate degraded and crusted soils (Sarr et al., 2001; Dawes, 2010;

Mando and Brussaard, 1999; Ouedraogo et al., 2004). In Kenya, the role of termites and ants in the formation of the microgranular structure of Ferralsols was studied by Jungerius et al. (1999), whereas Fall et al. (2001) compared the effects of different termite feeding groups on soil organic matter and aggregate fractions in West African semi-arid Savanna. Few studies exist, however, that have evaluated the effects of termites or ants on agricultural soils (Kooyman and Onck, 1987; Lobry de Bruyn and Conacher, 1990; Evans et al., 2011), as research on termites in agricultural systems has historically focused on their pest role (Wood and Cowie, 1988; Black and Okwakol, 1997; Bignell, 2006). Positive effects of tropical soil macrofauna on crop yields have been demonstrated experimentally in a limited number of studies, again in (semi-) arid climates in West Africa (Ouedraogo et al., 2006, 2007) and West Australia (Evans et al., 2011), where low rainfall and poor surface structure strongly constrain crop production. The impact of soil macrofauna on soil structural properties, soil C and crop performance in (sub) humid climates, as well as their response to soil tillage and crop residue management in CA systems is largely unclear (Giller et al., 2009).

The overall aim of our study was to quantify the contribution of soil macrofauna (earthworms, termites, and ants) to soil aggregation, soil C and crop productivity as a function of different tillage and residue management under sub-humid climatic conditions. The hypotheses tested were:

- (i) Soil tillage and residue removal negatively affect the abundance of soil macrofauna;
- (ii) Soil macrofauna increase stable soil aggregation and soil C;
- (iii) Soil macrofauna increase crop yields through positive effects on soil quality.

2. Materials and methods

2.1. Site description

This study was conducted in an existing long-term conservation tillage trial in Nyabeda, Siaya district, Nyanza province in Western Kenya. The site is located at an altitude of 1420 m asl, latitude 0° 06' N and longitude 34° 24' E, and the slope is less than 2%. A mean annual rainfall of 1800 mm (sub-humid) is distributed over two rainy seasons: the long rainy season lasts from March until August and the short rainy season from September until January (Fig. 1). The soil was identified as a Ferralsol (FAO, 1998), with five distinctive soil horizons. The upper soil horizon (0–8 cm) had 58% clay, 24% sand, and 18% silt. Soil chemical characteristics of the same soil layer included pH (H₂O) 5.1, total N 0.16%, total C 2%, Bray P 8 ppm, Olsen P 8.1 mg kg⁻¹. The second soil horizon (9–40 cm) had 72% clay, 14% sand, 14% silt, and pH (H₂O) 5.6, total N 0.15%, total C 1.6%, Bray P 1 ppm, Olsen P 2.7 mg kg⁻¹ (Nic Jelinski, 2014, unpublished data).

2.2. Experimental design and trial management

The field experiment was established in March 2003, and has been managed by researchers and technicians of the International Center for Tropical Agriculture (CIAT). The trial was set up in a randomized block design ($n=4$) with tillage and crop residue retention as main factors. Each factor had two levels: conventional tillage (+T) or reduced tillage (-T) and residue retention (+R) or residue removal (-R). Individual plots measured 7 × 4.5 m. The crop rotation since trial establishment has consisted of soybean (*Glycine max* L.) during short rains and maize (*Zea mays* L.) during long rains. All plots were fertilized with 60 kg ha⁻¹ N (urea), 60 kg ha⁻¹ P (Triple Super Phosphate) and 60 kg ha⁻¹ K (Muriate of Potash) per

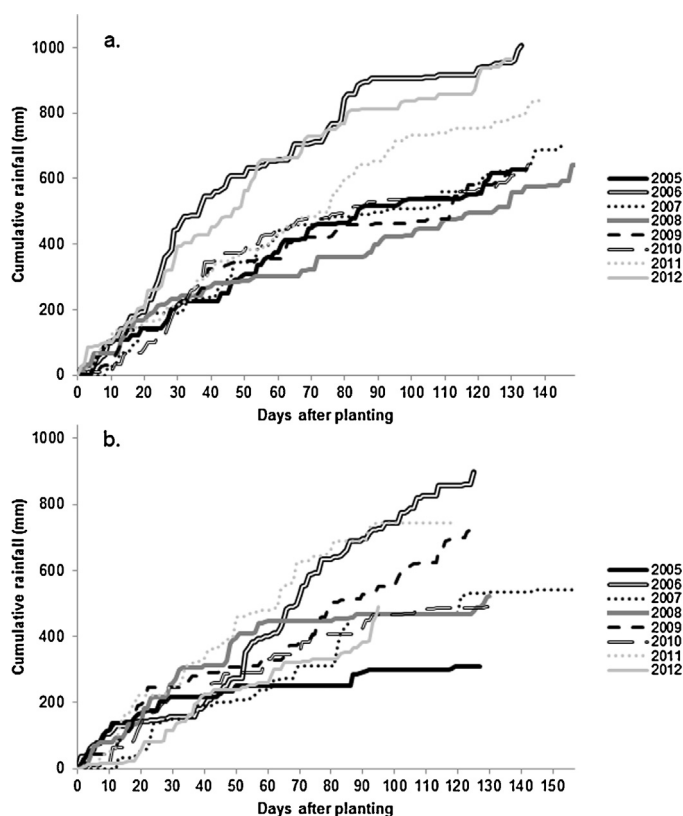


Fig. 1. Seasonal cumulative rainfall (mm) from 2006 to 2012 during the long rainy season (a) and short rainy season (b) in Nyabeda, Western Kenya. Maize was grown in the long rainy season (March/April–August) and soybean during the short rainy season (August/September–January/February). Cumulative rainfall is adjusted to planting and harvest dates per year.

growing season. To control stem borer, 5 kg ha⁻¹ of granulated Bulldock (beta-cyfluthrin) was applied in the funnel of the maize plants during the 5th week after planting in all treatments. Under conventional tillage (+T), the seedbed was prepared by hand hoeing to 15 cm soil depth. Weeding was performed three times per season, using the hand hoe. Under reduced tillage (-T), a 3 cm deep seedbed was prepared with the hand hoe. Weeding was performed three times per season by hand pulling until the long rainy season of 2009. Thereafter, herbicides (glyphosate and 2,4-dichlorophenoxyacetic acid) have been applied to all reduced tillage treatments before planting and subsequent weeding was done by hand pulling. Maize residues were collected after harvest, dried, chopped and stored during the dry season. At the time of soybean planting residues were reapplied at a rate of 2 t ha⁻¹ (+R). Since soybeans drop leaves prior to grain maturity, soybean residues (leaves and stems) always remained in the field after harvest, irrespective of treatment. These soybean residues were then either incorporated (+T) or remained at the soil surface (-T). Further details regarding maize and soybean planting and fertilizer application, are described in Paul et al. (2013).

A macrofauna exclusion experiment was superimposed on the tillage and residue management trial as a split-plot factor starting in the short rainy season of 2005. Subplots (2 × 4.5 m) with macrofauna exclusion (+Exc) were created through the application of insecticides, just before planting and every three weeks until harvest. Dursban was used at 0.8 l ha⁻¹, with 400 g ha⁻¹ of active ingredient (chlorpyrifos) to eliminate termite activity. Endocoton was applied at 0.9 l ha⁻¹, with 450 g ha⁻¹ of active ingredient (endosulfan) to exclude earthworm activity. These rates are based on effect levels determined by Ouédraogo et al. (2004). By lowering

the spraying tip to approximately 10 cm above the soil surface, contact with crops was minimized. The subplots with and without macrofauna exclusion were separated by 30 cm high metal sheets that were installed 15 cm into the soil to avoid contamination with insecticides in the -Exc treatment.

2.3. Soil macrofauna abundance and taxonomic diversity

Soil macrofauna was sampled in the short rainy season of 2005 (12 weeks after planting), long rainy season of 2006 (15 weeks after planting), and the short rainy season of 2009 (6 weeks after planting), corresponding to the 6th, 7th and 12th cropping season after the tillage trial establishment. We used monolith sampling as described by Bignell et al. (2008) and Anderson and Ingram (1993). One soil monolith measuring 25 cm × 25 cm × 30 cm depth was randomly taken in each replicate plot (n = 4). The extracted soil was divided into two depth increments (0–15 and 15–30 cm) and macrofauna was collected in the field by hand sorting on plastic trays. Macrofauna were killed in 70% ethanol, and then stored in sealed vials, whereas earthworms were first killed in 70% ethanol, then fixed in 4% formaldehyde before being transported to the laboratory for identification and enumeration. Macrofauna abundance was determined in all three years and classified according to the following main groups: earthworms (*Oligochaeta*), termites (*Isoptera*), ants (*Formicidae*) and other macrofauna. Complete identification to the genus level was done for the 2006 samples only. Specimens were identified in the Department of Invertebrate Zoology of the Nairobi National Museum, using keys and reference specimens in their collections.

2.4. Soil and crop analyses

During the long rainy seasons of 2006 (15 weeks after planting) and 2008 (14 weeks after planting) and in 2012 (4 weeks before maize planting), undisturbed soil samples were taken from all treatments (n = 4) at 0–15 cm and 15–30 cm soil depth for soil aggregate analysis. Soil samples in field moist conditions were pre-sieved over an 8 mm sieve and air dried before wet sieving into four aggregate size fractions as described by Elliot (1986): (a) large macroaggregates (LM; >2000 μm), (b) small macroaggregates (SM; 250–2000 μm), (c) microaggregates (Mi; 53–250 μm), (d) silt and clay sized particles (SC; ≤53 μm). 80 g of air-dried soil was evenly spread on a 2 mm sieve, which was placed in a recipient filled with deionized water and left to slake. After 5 min, the sieve was manually moved up and down 50 times in 2 min. The procedure was repeated passing the material on to a 250 μm and 53 μm sieve. Soil aggregates retrieved at each sieve were carefully backwashed into beakers, oven-dried at 60 °C for 48 h, weighed back and stored for C and N analysis. SC was calculated from the total volume of the suspension and the volume of the subsample. Mean weight diameter (MWD) was determined as the sum of the weighted mean diameters of all fraction classes (Van Bavel, 1950). In the same years total soil C and N was performed: composite samples consisting of 4 cores per subplot were taken at 0–15 cm and 15–30 cm soil depth. All samples were oven-dried at 60 °C for 48 h, ground and weighed, and then sent to UC Davis, California, USA. Total C and N were determined with a Dumas combustion method, using a PDZ Europa ANCA-GSL elemental analyzer (Sercon Ltd., Cheshire, UK). In 2012, a more detailed sampling took place. C and N sampling was done as previously but depths were 0–5 cm, 5–15 cm and 15–30 cm. Bulk density was measured for the same depths: two undisturbed samples (5 cm diameter metal rings; 100 cm³ volume) per subplot were taken at 0–5 cm, 7.5–12.5 cm and 20–25 cm. Samples were dried at 105 °C for 24 h prior to weighing. Soil C contents for 0–15 cm soil depth in 2012 were calculated from the 0–15 to 5–15 cm soil depth data taking into

account bulk density (weighted averages). Maize and soybean biomass and grain yields were determined as described in Paul et al. (2013) and reported on an oven-dry basis. Soybean yield data for the 2005 short rainy season were omitted from our data set because no distinction was made between the +/- insecticide treatments during harvest. Daily rainfall was measured with a rainfall gauge in the experimental field.

2.5. Statistical analyses

Analysis of variance (ANOVA) was carried out with R Studio Version 0.97.449 (R Core Team, 2013). A Linear Mixed Model was fitted by REML using the lmerTest package. ANOVA is calculated based on Satterthwaite's approximation (Kuznetsova et al., 2014). Tillage, residue management, and insecticide application and their interactions were included in the model as fixed factors, and effects were tested on macrofauna abundance, soil aggregate stability, soil C and crop yields. Block and year were defined as random factors, and the autocorrelations of plot (tillage and residue treatments) and subplot (insecticide treatment) were accounted for. Macrofauna and soil aggregate data were analysed independently for two soil depths (0–15 cm and 15–30 cm) and soil C for three depths (0–5 cm, 0–15 cm and 15–30 cm). Macrofauna abundance data were square-root transformed before analysis to fit ANOVA assumption

of normal data distribution. One monolith that contained a subterranean nest was removed from the dataset (year 2009; +T +R treatment; block 4; 0–15 cm depth 156 termites; 15–30 cm depth 2602 termites) and replaced by a missing value. Means are presented with standard errors. A P-value ≤ 0.05 was considered significant.

3. Results

3.1. Macrofauna abundance and species as affected by management

The most numerous macrofauna group present across all years and depths were termites, with an average abundance of 204 ind. m⁻² across all years, tillage and residue treatments. This constitutes 61% of all macrofauna. Ants were on average 68 ind. m⁻² or 20% of all macrofauna, earthworms were present in very low numbers (15 ind. m⁻²; 5%) and other macrofauna constituted 46 ind. m⁻² or 14% of total macrofauna (Table 1). Tillage and residue treatments did not affect macrofauna abundance except a significant residue-insecticide interaction effect for other macrofauna at 0–15 cm (P=0.049, Table 1). All genera of termites found (mostly *Pseudacanthotermes* and *Microtermes*) belong to the subfamily of Macrotermitinae, which are fungus growers and feed on wood, leaf litter and dead/dry grass (Table 2). Earthworms

Table 1
Soil macrofauna abundances (earthworms, termites, ants, others) in no m² across three sampling times (2005, 2006 and 2009) at 0–15 cm and 15–30 cm soil depths.

Soil macrofauna abundance (no m ⁻²)										
		Tillage	Residue	Exclusion	Termites	Earthworms	Ants	Other fauna		
0–15 cm soil depth										
	-	-	-	-	77.3 (22.2)	1.3 (1.3)	18.0 (8.4)	8.0 (3.1)		
	-	-	+	+	13.1 (7.1)	0 (0)	49.3 (45.1)	6.7 (4.1)		
	-	+	-	-	36.0 (11.1)	4.0 (4.0)	82.7 (54.5)	28.0 (10.8)		
	-	+	+	+	2.7 (2.7)	0 (0)	0 (0)	8.0 (6.7)		
	+	-	-	-	106.7 (45.9)	6.7 (3.7)	32.0 (29.1)	12.0 (4.9)		
	+	-	+	+	9.3 (4.1)	0 (0)	21.3 (18.5)	14.7 (6.9)		
	+	+	-	-	75.3 (26.0)	5.3 (4.1)	28.0 (23.8)	18.7 (4.3)		
	+	+	+	+	18.7 (14.8)	0 (0)	12.0 (12.0)	12.0 (7.4)		
S.V.										
					F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Tillage					0.63	0.431	1.18	0.293	0.48	0.491
Residue					1.43	0.235	0.01	0.919	0.12	0.724
Exclusion					31.05	<0.001***	6.99	0.017*	2.78	0.099
Til × Res					1.26	0.264	0.27	0.611	0.01	0.910
Til × Exc					0.04	0.850	1.19	0.291	0.79	0.376
Res × Exc					0.17	0.684	0.01	0.919	1.91	0.170
Til × Res × Exc					0.17	0.685	0.27	0.609	0.86	0.357
									6.58	0.012*
									0.18	0.672
									0.37	0.542
									3.98	0.049*
									0.01	0.916
15–30 cm soil depth										
	-	-	-	-	170.7 (56.8)	5.3 (5.3)	17.3 (8.2)	16.0 (8.8)		
	-	-	+	+	104.0 (55.4)	0 (0)	2.0 (1.4)	13.3 (6.5)		
	-	+	-	-	50.7 (18.7)	8.0 (6.7)	12.0 (8.1)	32.0 (18.0)		
	-	+	+	+	53.3 (37.4)	1.3 (1.3)	1.3 (1.3)	13.3 (8.1)		
	+	-	-	-	196.7 (58.9)	21.3 (9.1)	30.7 (16.6)	34.0 (19.5)		
	+	-	+	+	26.7 (10.5)	1.3 (1.3)	1.3 (1.3)	14.7 (6.9)		
	+	+	-	-	104.0 (55.4)	8.0 (4.2)	51.3 (33.4)	35.3 (15.1)		
	+	+	+	+	13.3 (6.2)	2.7 (1.8)	16 (14.6)	20.0 (12.4)		
S.V.										
					F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Tillage					2.23	0.161	2.68	0.127	1.78	0.195
Residue					2.58	0.134	0.03	0.855	0.08	0.775
Exclusion					4.91	0.046*	10.23	0.002**	8.63	0.007**
Til × Res					2.11	0.172	0.76	0.400	1.15	0.294
Til × Exc					0.49	0.497	1.99	0.163	0.57	0.457
Res × Exc					0.08	0.774	1.21	0.274	0.08	0.775
Til × Res × Exc					0.40	0.538	1.44	0.234	0.03	0.857

Treatments refer to combinations of reduced tillage (-) and conventional tillage (+); residue removal (-) and residue retention (+); without macrofauna exclusion (-) and with macrofauna exclusion (+). Mean values are indicated with standard errors in parenthesis. S.V. means source of variation. Levels of significance indicate single and interactive effects of tillage, residue and macrofauna exclusion over all three years. P values refer to the following levels of significance: * < 0.05, ** < 0.01, *** < 0.001.

included individuals of the epigeic Pareudrilinae (family Eudrilidae), and juveniles which could not be identified. Ants were represented by 10 different genera including several well-known predators such as *Dorylus* and *Hypoponera* that have been reported to attack termites. Other macrofauna included mainly Isopoda and Araneae, as well as Coleoptera and Lepidoptera larvae, Hemiptera, Chilopoda, Diplopoda and Dermaptera (Table 2).

3.2. Macrofauna exclusion efficacy

Insecticide application reduced termite numbers by 86% (0–15 cm soil depth; $P < 0.001$) and 62% (15–30 cm, $P = 0.046$, Table 1). Exclusion efficacy was higher for earthworms with 100% at 0–15 cm ($P = 0.017$) and 88% at 15–30 cm soil depth ($P = 0.002$). Insecticide was also effective for ants and other macrofauna, excluding 49% ($P = 0.099$) and 38% ($P = 0.012$) at 0–15 cm and 81% ($P = 0.007$) and 48% ($P = 0.055$) at 15–30 cm, respectively (Table 1).

3.3. Soil aggregate fractions, bulk density and soil carbon

Macrofauna exclusion did not have a significant effect on soil aggregate fractions and mean weight diameter (MWD) at 0–15 and 15–30 cm soil depth. The only marginal effect was seen in a smaller amount of SM fraction at 15–30 cm soil depth when macrofauna was excluded ($P = 0.058$, Table 3), but this was not reflected in any of the other size fractions. However, soil aggregate stability was strongly affected by soil tillage at 0–15 cm, decreasing LM by 49% ($P < 0.001$), and increasing Mi and SC by 29% ($P < 0.001$) and 45% ($P < 0.001$) respectively. This resulted in an overall 29% lower MWD under conventional tillage compared to reduced tillage ($P < 0.001$, Table 3). Likewise, soil macrofauna exclusion did not affect bulk density as measured in 2012. Bulk density ranged from 1.02/1.05 g cm³ (–ins/+ins) at 0–5 cm to 1.12/1.07 g cm³ at 5–15 cm to 1.07/1.06 g cm³ at 15–30 cm (data not presented). Macrofauna exclusion did not significantly affect soil C content at any soil depth. Highest soil C content was measured under reduced tillage with residue retention (–T+R 21.25 mg g^{–1}) and lowest soil C under

reduced tillage without residue retention (–T–R 18.33 mg g^{–1}) (Table 4).

3.4. Crop yields

Macrofauna exclusion resulted in 34% higher maize grain yields across all years ($P < 0.001$, Fig. 2, Table 5). A marginally significant interactive effect of tillage and residue on maize yields was found ($P = 0.067$; Table 5). No tillage without residue retention (–T–R) resulted in the lowest maize yields (4.61 t ha^{–1}) when compared with the other tillage and residue treatments which ranged between 5.12 and 5.54 t ha^{–1} (Fig. 2, Table 5).

Macrofauna exclusion increased soybean grain yields by 22% ($P < 0.001$, Fig. 3, Table 5). Tillage and residue showed a marginally significant interaction effect ($P = 0.051$) resulting in lowest soybean grain yields under no tillage without residue retention (–T–R; 922 kg ha^{–1}) when compared to the other treatments which ranged between 1053 kg ha^{–1} (+T+R) and 1111 kg ha^{–1} (+T–R, Fig. 3, Table 5).

4. Discussion

4.1. Termite dominance and diversity, and insecticide exclusion efficiency

Termites were the dominant group of soil macrofauna, followed by ants. Earthworms were present in very low numbers with an average density of 15 ind. m^{–2}, despite the sub-humid climate. These earthworm numbers are in line with Ayuke et al. (2011) who sampled different treatments of the same field experiment during the 2007 long rainy season and reported earthworm densities ranging from 0 to 11 ind. m^{–2} in arable plots compared to 117 ind. m^{–2} in an adjacent long-term fallow. Such results suggest that higher densities of earthworms can be found in sub-humid tropical climates, but that their densities are strongly affected by land use and soil management. The same study also showed that although adjacent long-term fallow had higher termite densities (475 m^{–2}; Ayuke et al., 2011) than the arable treatments in this study (204 m^{–2}), their overall abundance was still relatively high in the arable plots.

Insecticides proved to be effective in eliminating the main target organisms – termites and earthworms – and to a lesser extent reduced the abundances of ants and other macrofauna. Results underline that insecticide applications indeed resulted in the desired macrofauna exclusion, showing a considerable reduction in both termites (by 86 and 62%) and earthworms (by 100 and 88%) at 0–15 and 15–30 cm depth. Exclusion efficiencies were higher in the upper soil layer than at 15–30 cm depth since insecticides were applied at the soil surface and both Dursban and Endocoton readily adhere to soil particles. Soil macrofauna exclusion through insecticide application was proven to be effective in 2005, 2006 and 2009 and it was assumed to be effective until the end of the study period in 2012.

Termite diversity at the study site was low, only including genera of the subfamily of Macrotermitinae, namely *Microtermes* and *Pseudacanthotermes*. Although the identification was done only for samples collected in 2006, these finding corroborate with data from the same trial based on a combination of monolith and transect samplings (Ayuke et al., 2011), which showed the same genera with a strong dominance of *Pseudacanthotermes*. *Pseudacanthotermes* feed on litter, grass, and even live maize plants by covering them with their sheetings after which litter is carried to their nests. *Microtermes* feed both on litter and woody materials by hollowing out mostly dead, but sometimes live plant stems and twigs, and entering plant roots (Wood, 1996). *Microtermes* and *Pseudacanthotermes* are both fungus growing and have deep and

Table 2
Soil macrofauna identification for 2006 sampling (0–15 and 15–30 cm soil depths).

Macrofauna	Class or Order	Family	Subfamily	Genus
Termites	Isoptera	Termitidae	Macrotermitinae	<i>Microtermes</i> <i>Pseudacanthotermes</i> Others
Earthworms	Oligochaeta	Eudrilidae Juveniles (not identified)	Pareudrilinae	
Ants	Hymenoptera	Formicidae	Dolichoderinae Dorylinae Formicinae Myrmicinae Ponerinae	<i>Tecnomymex</i> <i>Dorylus</i> <i>Lepisiota</i> <i>Acanthomyrmex</i> <i>Carebara</i> <i>Rhoptromyrmex</i> <i>Cryptopone</i> <i>Euponera</i> <i>Harpegnathos</i> <i>Hypoponera</i>
Others	Araneae Chilopoda Coleoptera larvae Dermaptera Polyzonida (Diplopoda) Hemiptera Isopoda Lepidoptera larvae	Forficulidae		

Table 3Soil aggregate fractions (g 100 g⁻¹ soil) and mean weight diameter (mm) across 2006, 2008 and 2012 at 0–15 cm and 15–30 cm soil depths.

Q18

Aggregate fractions (g 100 g ⁻¹ soil) and mean weight diameter (mm)													
	Tillage	Residue	Exclusion	LM	SM	Mi	SC	MWD					
0–15 cm soil depth													
	–	–	–	15.2 (3.0)	49.9 (3.6)	24.9 (2.8)	8.0 (1.0)	1.32 (0.13)					
	–	–	+	15.0 (2.6)	49.8 (2.9)	25.4 (2.6)	6.7 (0.6)	1.33 (0.12)					
	–	+	–	11.8 (1.9)	52.7 (2.6)	26.0 (2.8)	7.4 (0.7)	1.21 (0.09)					
	–	+	+	11.5 (0.9)	51.9 (2.3)	26.4 (2.5)	7.7 (1.1)	1.17 (0.05)					
	+	–	–	5.9 (0.9)	51.1 (2.3)	32.5 (3.4)	10.3 (1.1)	0.89 (0.06)					
	+	–	+	6.6 (1.1)	46.0 (2.2)	34.3 (3.4)	10.9 (1.0)	0.87 (0.06)					
	+	+	–	6.5 (0.6)	48.9 (3.0)	32.9 (3.0)	11.7 (1.7)	0.89 (0.05)					
	+	+	+	8.1 (0.9)	47.7 (2.4)	33.1 (3.0)	10.4 (1.7)	0.95 (0.05)					
S.V.													
				<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value
Tillage				20.41	<0.001***	2.32	0.162	35.89	<0.001***	13.10	<0.001***	24.26	<0.001***
Residue				0.67	0.429	0.39	0.546	0.06	0.812	0.1	0.761	0.43	0.525
Exclusion				0.28	0.600	1.85	0.178	0.53	0.482	0.37	0.543	0.00	0.960
Til × Res				2.37	0.149	0.57	0.468	0.33	0.576	0.03	0.864	1.50	0.244
Til × Exc				0.59	0.444	1.02	0.316	0.06	0.809	0.02	0.897	0.12	0.724
Res × Exc				0.04	0.839	0.35	0.554	0.22	0.648	0.02	0.878	0.63	0.801
Til × Res × Exc				0.07	0.789	0.74	0.391	0.14	0.716	1.67	0.200	0.57	0.451
15–30 cm soil depth													
	–	–	–	23.2 (4.4)	56.0 (3.6)	14.8 (1.3)	4.6 (0.6)	1.79 (0.18)					
	–	–	+	26.3 (4.3)	49.5 (3.1)	16.3 (1.8)	5.9 (1.9)	1.87 (0.20)					
	–	+	–	24.0 (3.2)	52.9 (3.3)	16.7 (1.3)	6.4 (1.7)	1.81 (0.13)					
	–	+	+	20.9 (3.6)	55.2 (3.1)	17.6 (1.8)	5.1 (0.6)	1.67 (0.16)					
	+	–	–	24.0 (3.0)	54.1 (3.8)	16.5 (1.5)	5.1 (0.8)	1.82 (0.12)					
	+	–	+	21.9 (2.1)	50.3 (1.8)	19.6 (1.5)	5.4 (0.6)	1.67 (0.10)					
	+	+	–	16.9 (1.5)	56.9 (2.4)	18.6 (1.6)	7.3 (1.1)	1.49 (0.05)					
	+	+	+	18.9 (2.4)	53.7 (1.8)	19.3 (1.9)	6.0 (0.9)	1.56 (0.12)					
				<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value
Tillage				2.35	0.151	0.02	0.888	4.41	0.057	0.41	0.521	2.74	0.123
Residue				3.15	0.101	1.39	0.268	1.54	0.238	1.63	0.205	3.06	0.106
Exclusion				0.00	0.997	3.72	0.058	2.44	0.122	0.12	0.731	0.19	0.664
Til × Res				0.44	0.520	0.23	0.642	0.11	0.740	0.33	0.569	0.48	0.503
Til × Exc				0.00	0.972	0.23	0.631	0.12	0.724	0.09	0.769	0.00	0.957
Res × Exc				0.11	0.745	2.62	0.110	0.56	0.456	1.97	0.163	0.00	0.957
Til × Res × Exc				2.54	0.115	1.98	0.163	0.17	0.684	0.14	0.707	2.01	0.160

Aggregate fractions include large macroaggregates (LM; >2000 μm), small macroaggregates (SM; 250–2000 μm), micro aggregates (Mi; 53–250 μm) and silt and clay (SC; <53 μm). Mean weight diameter (MWD) is the sum of the weighted mean diameters of all fraction classes. Treatments refer to combinations of reduced tillage (–) and conventional tillage (+); residue removal (–) and residue retention (+); without macrofauna exclusion (–) and with macrofauna exclusion (+). S.V. means source of variation. Mean values are indicated with standard errors in parenthesis. Levels of significance indicate single and interactive effects of tillage, residue and macrofauna exclusion over all three years. *P* values refer to the following levels of significance: * < 0.05, ** < 0.01, *** < 0.001.

Table 4Soil C (mg g⁻¹) at 0–5 cm (2012 only), 0–15 cm and 15–30 cm (average for 2006, 2008 and 2012) soil depths.

Q19

Soil C (mg g ⁻¹)									
	Tillage	Residue	Exclusion	0–5 cm	0–15 cm	15–30 cm			
	–	–	–	18.47 (0.67)	19.91 (0.30)	16.33 (0.39)			
	–	–	+	18.18 (0.43)	19.57 (0.40)	16.76 (0.44)			
	–	+	–	21.20 (0.97)	21.02 (0.53)	18.25 (0.42)			
	–	+	+	22.30 (1.35)	20.74 (0.44)	18.69 (0.53)			
	+	–	–	19.47 (0.47)	20.12 (0.28)	18.31 (0.45)			
	+	–	+	19.48 (0.50)	20.36 (0.44)	18.71 (0.44)			
	+	+	–	19.54 (0.57)	20.51 (0.34)	18.78 (0.37)			
	+	+	+	19.70 (0.20)	20.44 (0.36)	18.40 (0.53)			
S.V.									
				<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value	<i>F</i> -ratio	<i>p</i> -value
Tillage				0.25	0.625	0.03	0.872	4.00	0.069
Residue				3.62	0.081	2.42	0.146	3.70	0.078
Exclusion				0.92	0.342	0.25	0.618	0.69	0.423
Til × Res				3.07	0.105	1.11	0.312	3.10	0.104
Til × Exc				9.44	0.509	1.04	0.310	0.63	0.443
Res × Exc				1.90	0.175	0.36	0.550	0.51	0.488
Til × Res × Exc				1.21	0.278	0.09	0.759	0.53	0.478

Treatments refer to combinations of reduced tillage (–) and conventional tillage (+); residue removal (–) and residue retention (+); without macrofauna exclusion (–) and with macrofauna exclusion (+). S.V. means source of variation. Mean values are indicated with standard errors in parenthesis. Levels of significance indicate single and interactive effects of tillage, residue and macrofauna exclusion over all three years. *P* values refer to the following levels of significance: * < 0.05, ** < 0.01, *** < 0.001.

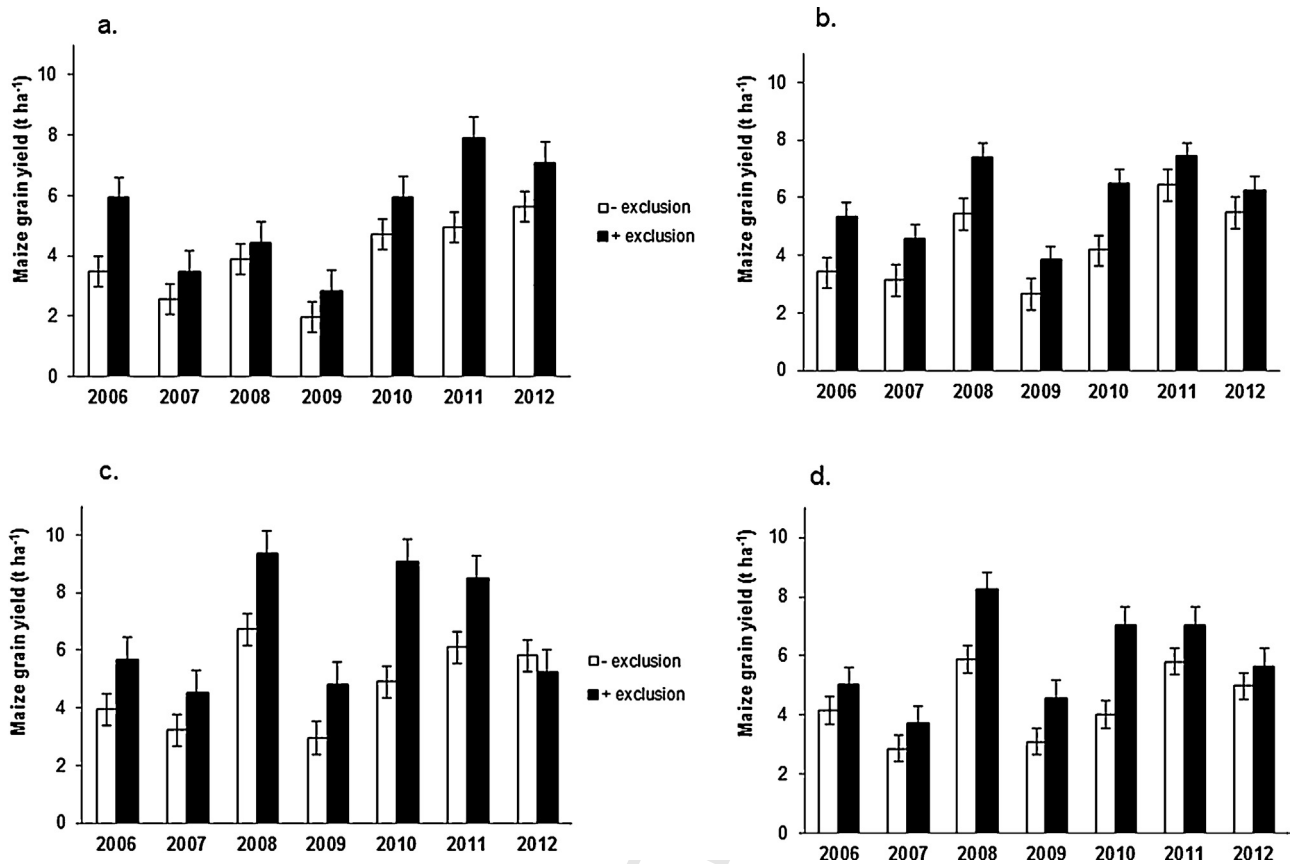


Fig. 2. Maize grain yields in t ha⁻¹ with and without macrofauna exclusion and for tillage and residue treatments -T-R (a), -T+R (b), +T-R (c), +T+R (d) from 2006 to 2012. Treatments refer to combinations of reduced tillage (-T) and conventional tillage (+T); residue removal (-R) and residue retention (+R); without macrofauna exclusion (-exc) and with macrofauna exclusion (+exc).

diffuse subterranean networks. *Microtermes* is strictly subterranean. A nest consists of a large number of chambers located between 10 cm and 2 m below the surface, although more than 80% occur between 10 and 50 cm depth (Kooyman and Onck, 1987). *Pseudacanthotermes* also constructs conical mounds outside of the cultivated field (Kooyman and Onck, 1987; Eggleton and Bignell, 1995).

4.2. Tillage and residue influence on soil macrofauna

Crop residues can provide an important food source for decomposer soil fauna and can moderate extremes in soil moisture and temperature, especially when maintained at the soil surface in the absence of soil tillage. Residue retention in the form of mulching has previously been shown to attract termites in humid and arid parts of West Africa (Tian et al., 1993; Ouedraogo et al., 2004). Similarly, past research has shown the impact of tillage on the abundance of soil ecosystem engineers. Holt et al. (1993) found that no-till soil maintained significantly more termite gallery structures than conventionally tilled soil, whereas Castellanos-Navarrete et al. (2012) showed the beneficial effects of reduced tillage and surface residue retention on earthworm numbers. In the present study, however, we did not detect any significant effects of tillage and/or residue management on soil macrofauna abundance. In case of earthworms, the overall low abundances and lack of residue effects may be attributed to the relatively low amounts and quality of organic matter inputs in the +R treatments (2 t ha⁻¹ yr⁻¹ of maize stover), whereas termites may also be limited by low amounts of available residues especially later on in the growing season (Kihara et al., 2015 in press). Macrofauna data,

especially in case of termites, were characterized by high variability between replicates in space and time. Taking into account the spatial and temporal variations in macrofauna abundance and nesting and/or foraging patterns, sampling methods are challenged to accurately measure macrofauna abundances in small experimental agronomic plots (Eggleton and Bignell, 1995). Nevertheless, our results were corroborated by Kihara et al. 2015 (in press) who did not find significant differences in termite activity in maize with or without residue application or tillage, based on counting of termite sheetings 14 and 16 weeks after residue application. The lack of tillage effect on termite abundance might be attributed to the termite species found. Only wood and litter feeding termites were present at the study site, whereas soil feeding termites are the most affected by tillage (Black and Okwakol, 1997). Moreover, we rarely encountered termite nests within our monolith samples, indicating that termites nested below ploughing depth or outside the plots where they are unaffected by tillage. *Pseudacanthotermes* spp. were observed to build mounds and extensive subterranean foraging tunnels outside of the agricultural plots, probably a strategy to escape from regular tillage disturbance within the plots (Kooyman and Onck, 1987).

4.3. Effect of termites on soil aggregate stability and carbon

Having shown that earthworm abundances are very low and that termites are the dominant soil macrofauna at our study site, we can relate effects of macrofauna exclusion primarily to termite activities. Termites have previously been found to contribute to higher nutrient contents (Mando and van Rheenen, 1988; Evans

Table 5
Maize grain yields in t ha⁻¹ (a) and soybean grain yields in kg ha⁻¹ (b) from 2006 to 2012.

Q20

Crop yields (maize t ha ⁻¹ ; soybean kg ha ⁻¹)				
Tillage	Residue	Exclusion	Maize	Soybean
-	-	-	3.87 (0.31)	729 (107)
-	-	+	5.35 (0.41)	1115 (144)
-	+	-	4.38 (0.30)	1019 (98)
-	+	+	5.87 (0.32)	1112 (126)
+	-	-	4.80 (0.29)	1047 (86)
+	-	+	6.27 (0.42)	1174 (119)
+	+	-	4.40 (0.25)	940 (76)
+	+	+	5.88 (0.35)	1165 (98)

S.V.	F-ratio	p-value	F-ratio	p-value
Tillage	4.38	0.058	2.10	0.149
Residue	0.06	0.803	0.39	0.531
Exclusion	72.78	<0.001***	14.05	<0.001***
Til × Res	4.06	0.067	3.83	0.051
Til × Exc	0.00	0.998	0.33	0.564
Res × Exc	0.00	0.972	0.77	0.380
Til × Res × Exc	0.00	0.998	3.12	0.079

Treatments refer to combinations of reduced tillage (-) and conventional tillage (+); residue removal (-) and residue retention (+); without insecticide (-) and with insecticide application (+). S.V. means source of variation. Mean values are indicated with standard errors in parenthesis. Levels of significance indicate single and interactive effects of tillage, residue and insecticide application over all three years. P values refer to the following levels of significance: * < 0.05, ** < 0.01, *** < 0.001.

et al., 2011) and improved physical soil quality (Mando and van Rheenen, 1988; Dawes, 2010). A small number of studies have characterized different termite-molded soil structures collected in the field and reported higher stability and/or C contents compared to bulk soil (Mora et al., 2003; Kooyman and Onck, 1987; Kihara et al., 2015 in press), but implications of termite activities for bulk

soil aggregate stability and soil C are not known (Kihara et al., 2015 in press). Contrary to our hypothesis, we did not find any significant effect of macrofauna exclusion on aggregate stability nor soil C content over a period of 7 years. The absence of a positive effect of macrofauna on soil C might be explained by residue translocation by termites to mounds outside of the arable plots or

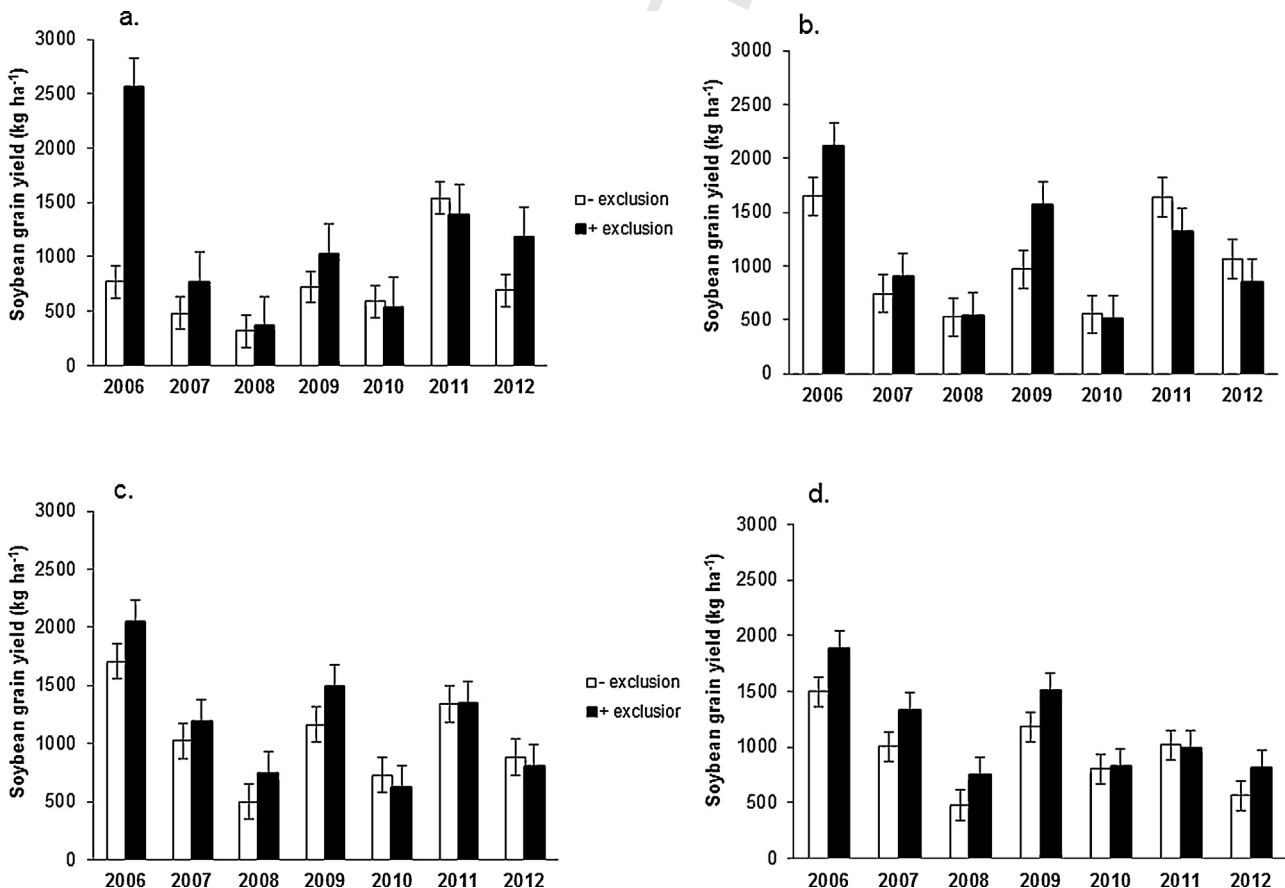


Fig. 3. Soybean grain yields in kg ha⁻¹ with and without macrofauna exclusion and for tillage and residue treatments -T-R (a), -T+R (b), +T-R (c), +T+R (d) from 2006 to 2012. Treatments refer to combinations of reduced tillage (-T) and conventional tillage (+T); residue removal (-R) and residue retention (+R); without macrofauna exclusion (-exc) and with macrofauna exclusion (+exc).

into deep subterranean networks. Kihara et al. 2015(in press) showed that in the same field trial, almost 40% of surface residue disappeared within the first 4 weeks after planting, and up to 85% had disappeared in 3.5 months, compared to 20% in the absence of macro- and mesofauna. Similarly, studies in Burkina Faso showed that soil fauna (including termites) strongly increase the rate of decomposition of organic residues in semi-arid areas (Mando and Brussaard, 1999; Ouedraogo et al., 2004).

Regarding the effects of termite activities on bulk soil aggregate stability it has been shown that the characteristics of different termite biogenic structures can be highly dependent on the feeding group present and the origin of the soil material. Fall et al. (2001) showed that mound structures from two species representing two different feeding groups (soil feeders versus litter feeders) in the semi-arid savanna of Senegal gave highly contrasting results. The fungus-growing litter feeder *Macrotermes bellicosus*, who build the nest from subsoil particles mixed with saliva (Wood and Cowie, 1988), had lower C content than the reference soil and no impact on soil C and soil aggregation was recorded (Fall et al., 2001). Macrotermitinae use feces exclusively for construction of fungus combs (Kooymann and Onck, 1987). By contrast, the soil feeding termites built their nests from feces and had a high impact on soil microaggregate structure, representing 60% of the total soil mass and 50% of the total carbon (Fall et al., 2001). For our research site, Kihara et al. 2015(in press) showed that termite sheetings collected from the soil surface of the arable plots were enriched in particulate organic matter and carbon compared to bulk soil, but did not show elevated aggregate stability. Results strongly suggest that the activities of litter feeding termites do not increase bulk soil aggregate stability in arable plots and that accumulation of particulate organic matter in termite molded soil is not reflected in bulk soil C contents. The low residue retention rate of 2 t ha⁻¹ in comparison to the large background soil C pool is likely to be insufficient to cause a significant impact on soil C, especially when large proportion of the material is exported by termites. This interpretation is supported by the observation that no significant effect on soil C at any soil depth was found due to residue treatment, irrespective of soil tillage. However, we cannot exclude with certainty that a potentially negative effect of macrofauna exclusion on soil aggregation was masked by increased biomass production (see Section 4.4) which would be expected to stabilize soil structure. Such an effect could have only been isolated through a no-plant control treatment. The negative effect of tillage on aggregate stability, as previously shown in Paul et al. (2013) for the period 2005–2008, was also confirmed by the additional data in this paper, showing a 29% decrease in MWD due to tillage at 0–15 cm soil depth.

4.4. Effect of termites on crop yields

We found a strong effect of macrofauna exclusion on crop yields, resulting in 34% higher maize yield and 22% higher soybean yield. The insecticides Dursban and Endocoton and other insecticides have been successfully used in previous studies to establish soil macrofauna exclusion plots for studying the effects of soil macrofauna on soil properties and crop production. However, contrary to our results, all these studies found higher crop yields or plant cover with soil macrofauna, and attributed this effect to soil rehabilitation and increased soil porosity and water infiltration through termite activity (Mando and Brussaard, 1999; Ouédraogo et al., 2004; Evans et al., 2011; Dawes, 2010).

Based on the composition of the insecticides used in terms of nutrient contents or pH we can exclude a direct effect on nutrient availability to plants. Therefore possible explanations might be a reduction in crop pest damage (including termites) in exclusion

plots, and/or an indirect effect in the form of enhanced residue retention in the absence of termites. The first mechanisms is supported by the fact that identified termite species all belong to the family of *Macrotermitinae*, which is responsible for 90% of damage in agriculture, forestry, urban settings (Mitchell, 2002). We cannot exclude that other pest species than termites may have played a role as both Endocoton and Dursban are known to impact on other pest organisms. However circumstantial evidence suggests that termite pests are at least partially responsible. Besides stemborer, which was controlled for in all treatments through the application of Bulldock (beta-cyfluthrin), termites are one major maize pests in Kenya (Mainaina et al., 2001). *Microtermes* and *Pseudacanthotermes* have been identified by local farmers as major pest species in the area (Ayuke et al., 2010), and have been recorded to attack maize in Ethiopia, Nigeria and Zambia (Rouland-Lefevre, 2011). In the southern Guinea savannah zone of Nigeria, virtually all maize crop damage was caused by *Microtermes* by entering roots commencing 10–12 weeks after planting and leading to plant lodging (Wood et al., 1980). Low species richness can lead to an increase in relative abundance of pest species, as the large majority of termite species are not pests under any circumstances and non-pest species of termites may compete with pest species for similar resources (Black and Okwakol, 1997). Damage in maize was higher than in soybean, indicating that non-indigenous crops like maize are more susceptible, presumably because they lack co-evolution. Indirect negative effects of termites on soil and moisture conservation through removing crop residue may also have played a role. Lowest maize and soybean yields were found in -T-R treatments, and rapid residue removal by termites can therefore quickly convert Conservation Agriculture (-T+R) into such unfavorable states.

5. Conclusions

Termites were the dominant soil macrofauna at our study site in sub-humid Western Kenya, while earthworm densities were extremely low. We did not find a significant effect of tillage nor crop residue management on the abundance of soil macrofauna. In addition, no effects of soil macrofauna on soil C content were observed upon macrofauna exclusion over a period of 7 years. Results are attributed to low residue retention rates and the specific feeding and nesting behavior of the termites found, which remove crop residues and transport them to deep subterranean networks or mounds outside of arable plots. Negative effects of tillage on aggregate stability as found previously for the same site were confirmed, but no relation with the presence of soil macrofauna was found. Further, increased crop yields in treatments that excluded soil macrofauna through insecticide application indicate significant crop loss due to pest problems, especially in maize. The low termite diversity, including termites which are well-known potential crop pests, supports this explanation. Indirect negative effects of termites on residue cover, soil and moisture conservation may have also played a role. Further research is needed to elucidate these mechanisms. Our study contradicts earlier work showing positive effects of termites on physical soil properties and crop production in (semi-) arid climates, suggesting a decisive influence of variations in agroecological conditions and production limiting factors such as climate, soil conditions and crop type, in combination with the behavior of the dominant termite species present.

Uncited references

Kihara et al. (2012), Maniania et al. (2001), Ouédraogo et al. (2006) and Ouédraogo et al. (2007).

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