



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

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ARTICLE INFO

Article history:

Received 6 August 2009

Received in revised form

24 November 2010

Accepted 25 November 2010

Available online 31 December 2010

Keywords:

Soil biodiversity

Earthworms

Termites

Agriculture

Crop management

Soil carbon

Climate

ABSTRACT

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. For each trial, a fallow representing a relatively undisturbed reference was also sampled. Earthworm taxonomic richness decreased in the direction fallow > high-C soil > low-C soil and earthworm abundance was higher in fallow than under continuous crop production. Termite abundance was not significantly different between fallow and high and low-C treatments and termite taxonomic richness was higher in fallow soil than in the two cropping systems. We concluded that fewer species of earthworms and termites were favored under agricultural management that led to lower soil C. Results indicated that the soil disturbance induced by continuous crop production was more detrimental to earthworms than to termites, when compared to the fallow.

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1. Introduction

Knowledge of the spatial distribution of different taxa of earthworms and termites in agricultural soils across climatic regions and soil types is necessary in determining how, and to what extent, the diversity and activities of these important soil ecosystem engineers are affected by climate versus agricultural land use and management. Site-specific studies by Kooyma 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 soil macrofauna species richness and abundance in general. Clearance and tillage of habitats result in the destruction of nests, nesting sites and burrow systems for termites and earthworms, respectively, thus exposing them to harsh environmental conditions and/or predators (House and Parmelee, 1985; Barros et al., 2002). Soil management practices such as use of organic inputs and crop diversification

through rotation favor macrofauna diversity due to improvements 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 (Smith et al., 1988; Zehnder and Linduska, 1987), such studies have mostly targeted aboveground fauna, and the effects on belowground invertebrate communities in cropped soils are little understood, especially in the case of termites. This study, therefore, aimed at assessing how agricultural management affects earthworm and termite diversity across humid to semi-arid tropical regions. 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, and (3) be higher under long-term agricultural management that has led to high-C soils than where it has led to low-C soils.

2. Materials and methods

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

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Western Africa (Tamale in Ghana, Ibadan in Nigeria, Sadore in Niger and Farakoba, Sarias I, II and III in Burkina Faso). The long-term trials were established in the past 1–4 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 1). The SOC content is known to increase due to improved long-term management practices, such as reduced tillage (Six et al., 1999; Pikul et al., 2009), organic matter and nutrient inputs (Ouédraogo et al., 2001; Palm et al., 2001; Vanlauwe et al., 2002) 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). A fallow located nearby the arable fields representing a reference with continuous plant cover and without soil disturbance was also included. 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.

2.1. Macrofauna sampling

Monolith sampling and transect sampling were used for termite assessments while earthworms were collected through monolith sampling only (Swift and Bignell, 2001; Bignell et al., 2008). Sampling was done 6–8 weeks after planting (July–September, 2006 in the Western Africa sites and February–June 2007 in Eastern Africa sites). One soil monolith of 25 cm × 25 cm × 30 cm depth was randomly taken in each replicate plot ($n=3$). The 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 m × 2 m transect (or 5 m × 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 min, 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).

2.2. Macrofauna preservation and identification

Termites were preserved in 75% alcohol and earthworms were killed in 75% alcohol before fixation in 4% formaldehyde. Termites and earthworms were stored in sealed vials before being transported to the laboratory for identification and enumeration. Earthworms and 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. Adult earthworms and termites were identified to species or where this proved difficult, to numbered morphospecies. Unidentified earthworm specimens were sent to the Hungarian Natural History Museum (HNHM), Budapest, Hungary, for further analysis. Voucher specimens are being held at the NMK, Nairobi and HNHM, Budapest.

Taxonomic richness (S) was calculated as the number of taxa per monolith and transect sample (pooled together from each experimental plot for termites).

2.3. 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). 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). With CANOCO, a preliminary detrended correspondence analysis (DCA) was conducted to determine the length of the gradient, test the homogeneity of the data for the abundance of earthworms and termites, identified to the lowest taxonomic level possible, 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 the lowest taxonomic level possible. 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 abundance of earthworms and termites. 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 the management treatments were nested within the trial sites, we restricted permutations to a split-plot design, such that trial sites were treated as whole plot factors, while management treatments within trial sites were treated as split plot factors (Ter Braak and Smilauer, 1998).

3. Results

3.1. Earthworm and termite taxonomic richness and abundance

Mean earthworm taxonomic richness across all sites was significantly higher in the fallow (1.72) than in the high-C treatments (1.02), where, in turn, the richness was significantly higher than in the low-C (0.64) treatments. However, site–treatment interactions were also significant and there were significant differences in taxonomic richness between sites (Table 2). Differences in mean earthworm abundance showed the same pattern as differences in mean taxonomic richness, but the difference between high-C and low-C treatments was not significant at any of the sites (Table 2).

Mean termite taxonomic richness across all the sites showed a pattern similar to that of earthworms, also following the order fallow > high-C > low-C treatments. Whereas the difference between fallow and low-C treatments was significant, this was not the case for the difference between fallow and high-C treatments, and between high-C and low-C (Table 2). Also, not at all sites the taxonomic richness followed the order high-C > low-C treatment (Table 2). Hence, site–treatment interactions were not significant. Termite abundance was highly variable across replicates and no significant differences were found between treatments (fallow, high-C

Table 1
Treatment description of selected sites and their soil organic C content (g kg^{-1} soil) at 0–15 and 15–30 cm depths.

Trial	Embu	Kabete	Impala	Nyabeda	Chitala	†Ibadan	Tamale	Sadore	Farakoba	Saria I	Saria II	Saria III
Year established	1993	1976	2000	2003	1995	1996	1996	1986	1993	1960	1980	1990
Treatments	Fallow											
Fallow type	Woodland since 1993	Bushland since 1976	Shrubland since 2000	Shrubland since 2003	Grass fallow since 1995	Bushland since 1986	Grass fallow since 1996	Shrubland since 1986	Grass fallow since 1993	Grass fallow since 1959 (common for Sarias)	Grass fallow since 1959	Grass fallow since 1959
Soil C (g kg^{-1} soil)	40.0 ^a , 28.4 ^b	23.7 ^a , 20.8 ^b	24.5 ^a , 16.9 ^b	28.2 ^a , 16.6 ^b	13.6 ^a , 9.4 ^b	12.4 ^a , 7.5 ^b	9.0 ^a , 4.8 ^b	1.5 ^a , 1.2 ^b	3.6 ^a , 2.9 ^b	3.3 ^a , 3.1 ^b	See Saria I	See Saria I
High-C	Rotation											
Rotation	Cont. maize	Maize–bean	Maize– <i>Tephrosia candida</i> relay	Maize–soybean	Maize–pigeonpea	Maize–cowpea	Cont. maize	Cont. millet	Cont. sorghum	Sorghum–cowpea	Cont. sorghum	Cont. sorghum
Tillage	Hand hoeing	Hand hoeing	Hand hoeing	No till	Tractor till	Light surface hoeing	No till	Hand hoeing	Tractor till	Tractor till	Tractor till	Tractor till
Organic	<i>Leucaena leucocephala</i> (5 t ha ⁻¹)	10 t ha ⁻¹ manure	<i>T. candida</i> residues (5 t ha ⁻¹)	Maize stover (2 t ha ⁻¹)	Crop residues: stem + leaves (5 t ha ⁻¹)	<i>Senna siamea</i> (5 t ha ⁻¹)	None	Crop residues	Compost (5 t ha ⁻¹)	Manure (5 t ha ⁻¹ every 2 years)	Manure (10 t ha ⁻¹)	Manure (10 t ha ⁻¹)
Inorganic	None	CAN (120 kg N ha ⁻¹) and TSP (52.8 kg P ha ⁻¹)	None	NPK fertilizer (60:60:60)	(NH ₄) ₂ SO ₄ fertilizer (96 kg N ha ⁻¹ year ⁻¹)	NPK fertilizer (60:30:30 ha ⁻¹ year ⁻¹)	None	13 kg P ha ⁻¹ ; no N	PK fertilizer (25:14)	NPK (100 kg ha ⁻¹) and urea (50 kg ha ⁻¹) every 2 years	23 kg N ha ⁻¹	NPK (100 kg ha ⁻¹ year ⁻¹) and urea (50 kg ha ⁻¹ year ⁻¹)
Soil C (g kg^{-1} soil)	27.5 ^a , 24.9 ^b	21.9 ^a , 17.2 ^b	27.9 ^a , 21.8 ^b	22.8 ^a , 17.8 ^b	8.8 ^a , 9.9 ^b	10.6 ^a , 6.7 ^b	5.7 ^a , 3.7 ^b	1.4 ^a , 1.2 ^b	3.6 ^a , 2.4 ^b	2.6 ^a , 3.7 ^b	3.5 ^a , 3.3 ^b	2.4 ^a , 3.3 ^b
Low-C	Rotation											
Rotation	Cont. maize	Maize–bean	Cont.	Maize–soybean	Cont. maize	Maize–cowpea	Cont. maize	Millet–cowpea	Cont. sorghum	Cont. sorghum	Cont. sorghum	Cont. sorghum
Tillage	Hand hoeing	Hand hoeing	No till	Hand hoeing	Tractor till	Light surface hoeing	Bullock plough	Animal traction	Tractor till	Tractor till	Tractor till	Hand hoeing
Organic	None	None	None	None	None	None	None	Crop residues	None	Manure (5 t ha ⁻¹ every 2 years)	None	No organic inputs, 4=
Inorganic	None	None	None	NPK fertilizer (60:60:60)	None	None	None	30 kg N ha ⁻¹ ; 13 kg P ha ⁻¹	None	NPK (100 kg ha ⁻¹) and urea (50 kg ha ⁻¹ year ⁻¹)	None	NPK (100 kg ha ⁻¹) and urea (50 kg ha ⁻¹ year ⁻¹)
Soil C (g kg^{-1} soil)	24.6 ^a , 23.9 ^b	17.7 ^a , 16.2 ^b	22.0 ^a , 21.2 ^b	19.9 ^a , 18.4 ^b	8.2 ^a , 7.1 ^b	5.7 ^a , 3.9 ^b	3.1 ^a , 2.6 ^b	1.0 ^a , 0.9 ^b	2.7 ^a , 2.3 ^b	3.3 ^a , 3.2 ^b	1.8 ^a , 2.5 ^b	2.2 ^a , 3.0 ^b

Notes: Soil C data source: Eastern Africa (from monolith soils), Western Africa (Zida et al., unpublished), †Ibadan (Vanlauwe et al., 2002). Lower case superscripts (a, b) denotes 0–15 and 15–30 cm depths, respectively.

Table 2

Macrofauna (earthworm and termite) mean taxonomic richness and abundance across fallow and arable systems of Eastern and Western Africa.

Site	Earthworm						Termite					
	Taxonomic richness (S)			Abundance (no m ⁻²)			Taxonomic richness (S)			Abundance (no m ⁻²)		
	Fallow ^a	High-C ^a	Low-C ^a	Fallow ^a	High-C ^a	Low-C ^a	Fallow ^a	High-C ^a	Low-C ^a	Fallow ^a	High-C ^a	Low-C ^a
Embu	2.67 ^a	0.33 ^b	0.67 ^b	1264 ^a	32 ^b	27 ^b	1.33 ^a	1.33 ^a	1.00 ^a	139 ^a	528 ^a	32 ^a
Kabete	3.00 ^a	2.00 ^{ab}	1.00 ^b	363 ^a	395 ^a	272 ^a	1.00 ^a	0.33 ^a	0.67 ^a	203 ^b	1029 ^a	384 ^{ab}
Impala	3.33 ^a	0.67 ^b	0.67 ^b	165 ^a	32 ^b	16 ^b	2.00 ^a	1.68 ^a	1.33 ^a	987 ^a	43 ^b	1104 ^a
Nyabeda	0.67 ^a	0.33 ^a	0.33 ^a	117 ^a	11 ^{ab}	0 ^b	3.00 ^a	2.68 ^a	2.67 ^a	475 ^a	208 ^{ab}	0 ^b
Chitala	1.00 ^a	1.00 ^a	1.00 ^a	53 ^a	5 ^a	5 ^a	2.33 ^a	2.00 ^a	2.00 ^a	752 ^{ab}	117 ^b	1744 ^a
Ibadan	1.67 ^b	4.67 ^a	1.67 ^b	96 ^b	933 ^a	117 ^b	2.00 ^a	1.33 ^a	0.00 ^b	320 ^b	1483 ^a	0 ^b
Tamale	2.00 ^a	1.00 ^{ab}	0.00 ^b	37 ^a	32 ^a	16 ^a	2.00 ^a	1.68 ^a	1.00 ^a	149 ^b	1179 ^a	32 ^b
Sadore	0.00 ^a	0.00 ^a	0.00 ^a	0 ^a	0 ^a	0 ^a	2.00 ^a	1.00 ^a	2.00 ^a	256 ^a	181 ^a	0 ^a
Farakoba	2.33 ^a	0.67 ^b	0.33 ^b	453 ^a	59 ^b	11 ^b	0.68 ^b	3.00 ^a	1.00 ^b	59 ^b	693 ^a	160 ^{ab}
Saria I	1.33 ^a	0.67 ^a	0.00 ^a	69 ^a	27 ^a	21 ^a	1.68 ^a	1.00 ^a	1.00 ^b	112 ^a	0 ^a	0 ^a
Saria II	1.33 ^a	0.33 ^{ab}	0.00 ^b	69 ^a	11 ^a	0 ^a	1.68 ^a	1.33 ^a	0.68 ^a	112 ^a	256 ^a	0 ^a
Saria III	1.33 ^{ab}	0.67 ^b	2.00 ^a	69 ^a	80 ^a	59 ^a	1.68 ^a	1.00 ^a	1.33 ^a	112 ^a	11 ^a	112 ^a
Mean	1.72 ^a	1.02 ^b	0.64 ^c	230 ^a	135 ^b	45 ^b	1.78 ^a	1.53 ^{ab}	1.22 ^b	306 ^{ab}	477 ^a	297 ^b

SV	Earthworm						Termite					
	Taxonomic richness (S)			Abundance (no m ⁻²)			Taxonomic richness (S)			Abundance (no m ⁻²)		
	df	F-ratio	p-Value	df	F-ratio	p-Value	df	F-ratio	p-Value	df	F-ratio	p-Value
Site	11	7.40	<0.001	11	10.07	<0.001	11	4.83	<0.001	11	2.74	0.005
Treatment	2	16.02	<0.001	2	20.37	<0.001	2	3.69	0.030	2	2.54	0.086
Site × treatment	22	3.44	<0.001	22	4.73	<0.001	22	1.41	0.142	22	2.35	0.004
Residual	70			70			70			70		

Means of S or abundance followed by same lower case letters within rows across treatments are not statistically significant at $p < 0.05$.^a Treatments.

and low-C) (Table 2). Termite abundance, like taxonomic richness, differed significantly between sites.

3.2. Correlations between 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 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 (Fig. 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 was mainly a temperature/altitudinal gradient ($r = -0.83$ and 0.86 , respectively), while the second axis was a precipitation/latitudinal gradient ($r = 0.12$ and -0.16 , respectively) (Fig. 1A). Axis 1 separated 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 (Fig. 1A and B).

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 (Fig. 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 was a precipitation/latitudinal gradient ($r = 0.81$ and -0.63 , respectively), while the second axis was a temperature/texture/longitudinal gradient ($r = -0.84$, -0.77 and 0.85 ,

respectively). A higher than average number of taxa occurred in the sites with warmer and drier climatic conditions (Fig. 2A). Axis 2 mainly separated 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 (Fig. 2B).

4. Discussion

At most sites, soil C in the fallow treatments was relatively higher than in the arable (high-C and low-C) treatments. Differences between high-C and low-C in some cases, especially in Sarias I and III, however, were relatively small (Table 1). Variability in soil C across sites was large. Sites in Eastern Africa had higher soil C than sites in Western Africa (Table 1). In view of the large variability in the data, results can be considered robust, wherever differences in macrofauna diversity between treatments were significant.

4.1. Influence of environmental factors

The number of taxa of both earthworms and termites was low in most of the sites. Mean taxonomic richness ranged between 0 and 5 for earthworms and 0 and 3 for termites. 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 3–5 taxa recorded by Okwakol (2000) across arable sites in Uganda.

Highly significant correlations were observed between macrofauna richness, and environmental variables, reflecting the influence of climate and soil type. The two RDA biplots for earthworms (Fig. 1) and termites (Fig. 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 numbers of earthworm and termite taxa were found under relatively warmer, drier conditions. This is not in line with the observation that earthworm and termite diversity increases

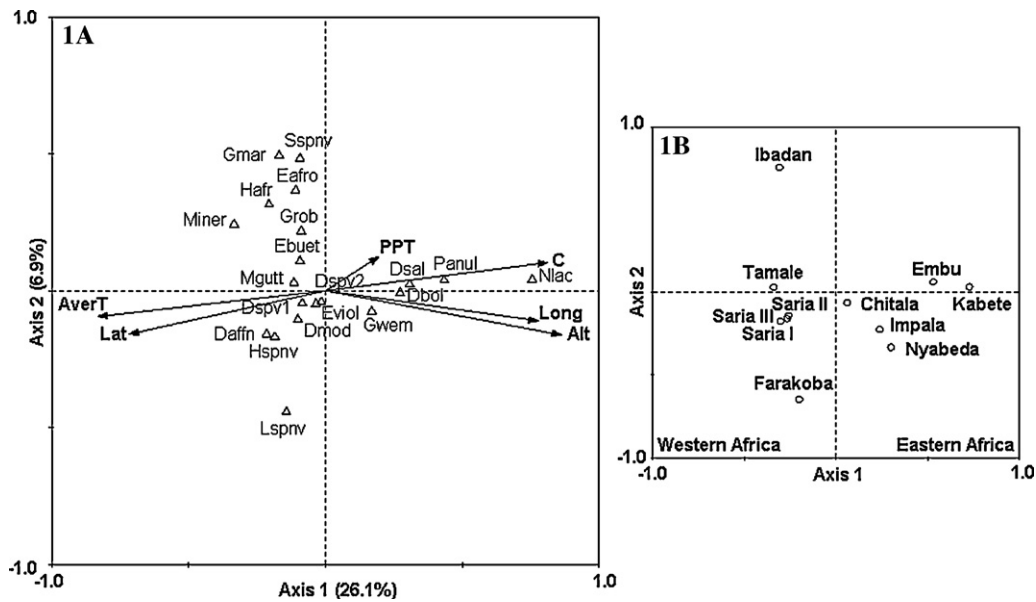


Fig. 1. RDA biplot showing correlation between earthworm species abundance and selected environmental variables. Earthworm taxa are represented by triangles, while environmental parameters are represented by pointed arrows. Sites are represented by open symbols. Earthworm species abbreviations: *Nematogena lacuum* (Nlac), *Gordiodrilus robusta* (Grob), *Gordiodrilus wemanus* (Gwem), *Gordiodrilus marcusii* (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. (Lsprnv), *Millsonia inermis* (Miner), *Millsonia guttata* (Mgutt), *Dichogaster* (Dt.) *saliens* (Dsal), *Dichogaster* (Dt.) *affinis* (Daffn), *Dichogaster* (Dt.) *bolau* (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).

with increase in rainfall or soil moisture, as generally found at least in temperate climates (Bohlen et al., 1995; Curry, 2004). However, seasonality of rainfall in the tropical regions means rainfall amount per season may be more important than annual total. We attributed lower taxonomic richness among the sites in Eastern Africa to less favorable conditions arising from high rainfall and low temperatures at higher altitudes. These observations were consistent with those of Collins (1980) and Gathorne-Hardy et al. (2001),

who noted that high altitudes harbour less termite taxa, especially of the subfamily Macrotermitinae. It however, contradicted findings by Buxton (1981), who observed an increase in the number of termite species with increasing rainfall. The widespread presence of *Microtermes* spp. across all sites illustrated 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

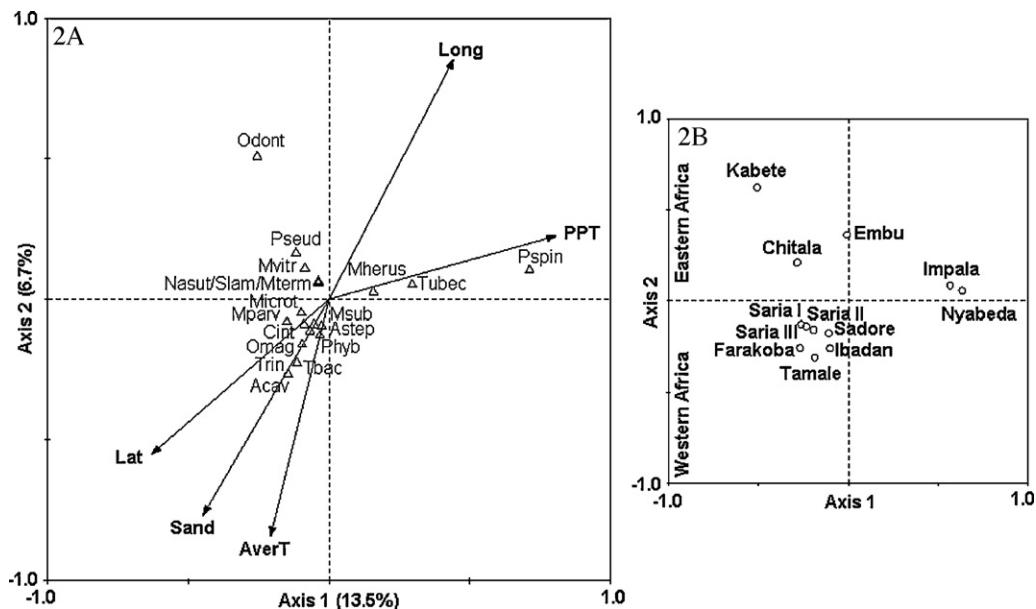


Fig. 2. RDA biplot showing correlation between termite species abundance and selected environmental variables. Termite taxa are represented by triangles, while environmental parameters are represented by pointed arrows. Sites are represented by open symbols. Species abbreviations: *Amitermes stephensoni* (Astep), *Ancistrotermes cavithorax* (Acav), *Captotermes intermedius* (Cint), *Macrotermes* nr. *vitriolatus* (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), *Psammitermes hybostoma* (Phyb), *Pseudacanthotermes spiniger* (Pspn), *Pseudacanthotermes* sp. (Pseud), *Schedorhinotermes lamanianus* (Slam), *Termes baculi* (Tbac), *Tubeculitermes* sp. (Tubec). Environmental abbreviations: average temperature (AverT), latitude (Lat), longitude (Long), precipitation (PPT).

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 (Figs. 1A and 2A).

4.2. Effect of contrasting agricultural management

In agreement with our hypothesis, higher earthworm taxonomic richness and abundance was recorded in the fallow than in the agricultural systems. Similarly, under continuous crop production, higher earthworm taxonomic richness 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.

Contrary to our hypothesis, no difference in termite taxonomic richness and abundance was observed between fallow and high-C arable systems. We attributed this to the wide feeding and foraging habits 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 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 our hypothesis, higher termite abundance 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 favored by the addition of organic resources characteristic of many of our high C treatments.

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 Centre 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.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2010.11.021.

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