ECOSYSTEMS

Soil CO_2 Emissions Associated with Termitaria in Tropical Savanna: Evidence for Hot-Spot Compensation

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ABSTRACT

Our understanding of carbon (C) dynamics within savannas is very limited, especially how source/sink dynamics are influenced by the resident biota. Previous measurements of epigeal termite mounds (termitaria), ubiquitous in many savannas, have shown that they are considerable point sources of soil carbon dioxide (CO_2), whereas CO_2 measurements collected outside the mounds were generally assumed to be independent of termite activity. However, no measurements were conducted along gradients away from the mounds to confirm this. We quantified daytime soil CO_2 emissions (soil respiration) along gradients from the center to 20 m from the mound edge in Serengeti National Park, and measured soil temperature/moisture, macro-invertebrate abundance, and vegetation height as variables potentially influencing these emissions. Further, we quantified how far into the savanna termitaria impact CO_2 emissions. As in other studies, we found the highest soil CO_2 fluxes at the termitaria-center and considerably lower fluxes in the surrounding savanna. Macro-invertebrate abundance was associated with the differences in emissions measured, whereas the other variables were not. The analysis of spatial autocorrelation revealed significantly lower fluxes between the termitaria edge and up to 9 m from the edge compared to the values measured at the termitaria-center and between 10 and 20 m from the termitaria edge. When extrapolating the emissions across the landscape our results suggest that the lower CO_2 emissions found between the edge and 9 m fully compensate for the high fluxes measured at the termitaria center. Consequently, our findings provide evidence that termitaria might influence the savanna C source-sink dynamics differently than previously thought.

Key words: termite mounds; Serengeti; soil micro-climate; Soil macro-invertebrates; vegetation height; spatial pattern.

INTRODUCTION

Savannas are most extensive in sub-Saharan Africa (tropical savannas), accounting for approximately 15 million km^2 of the total landmass (White and others 2000). Despite the importance of savannas, our understanding of carbon (C) dynamics within

these ecosystems is limited (Luo and Zhou 2006; Williams and others 2007; Merbold and others 2008; Ciais and others 2009). Mineral soil C turnover rates, and therefore the amount of carbon dioxide (CO_2) released from the soil to the atmosphere, are a function of soil organic matter quality and quantity, micro-climate (temperature, moisture), physical properties (texture, bulk density), chemical properties (pH, C/nutrient concentrations), and biological properties (microbial biomass, composition, diversity, activity; for example, Kirschbaum 1995; Lomander and others 1998; Epstein and others 2002). Thus, alteration of one or several of these parameters can influence rates of soil CO_2 emission.

Savannas are heterogeneous ecosystems in which fire, grazing by large herbivores and topographic gradients create spatial variability in soil texture and moisture, organic matter, above and belowground biomass and plant species richness (Du Toit and others 2003; Anderson and others 2008). Within savanna ecosystems termites are important components of soil invertebrate communities (Wood and Sands 1978) and are considered to be ''ecosystem engineers'', which alter the flow of energy and nutrients (Jones and others 1994; Dangerfield and others 1998; Sugimoto and others 2000). Consequently, termites are recognized as significant sources of heterogeneity within these ecosystems (for example, Glover and others 1965; Smith and Yeaton 1998; Palmer 2003; Jouquet and others 2005; Moe and others 2009; Sileshi and others 2010; Okullo and Moe 2012). Nest construction by termites ranges from inconspicuous belowground chambers to large aboveground mounds, called termitaria. The soil associated with termitaria typically has lower soil bulk density and elevated mineral C, nitrogen, phosphorus, magnesium, calcium, and clay content compared to the soils in the savanna surrounding the termitaria (see review by Sileshi and others 2010 and references therein). Similarly, higher microbial biomass (Holt 1998) and different compositions of the nematode community (Cadet and others 2004) were detected in termitaria soil compared to the surrounding soil. The modifications of soil properties associated with termitaria, in turn, affect tree establishment and plant species composition and richness (see review by Sileshi and others 2010 and references therein), which ultimately alter the distribution of other vertebrate and invertebrate animal species (for example, Holdo and McDowell 2004; De Visser and others 2008; Brody and others 2010; Pringle and others 2010).

Several field studies conducted in African savannas have shown that termite mounds are considerable point sources of soil CO_2 emissions (Seiler and others 1984; Kahlil and others 1990; Darlington and others 1997; Konaté and others 2003; Brümmer and others 2009). For example, Brümmer and others (2009) measured on average 322 mg CO_2–C per square meter termitaria per hour compared to only 100–157 mg CO_2–C per square meter non-termite influenced soil, while Konaté and others (2003) reported roughly 16 µmol CO_2 m^{-2} s^{-1} released from termitaria with fungus combs compared to 9 µmol CO_2 m^{-2} s^{-1} from non-termite-influenced grassy savanna. However, little is known about how termites affect CO_2 fluxes from soils in the surrounding savanna, for example, in soils in proximity of the termitaria. Given that termites not only influence the area covered by the termitaria (small scale), but also influence soil and plant properties along gradients into the surrounding savanna (Sileshi and others 2010; Okullo and Moe 2012), it is possible that termites impact soil CO_2 emissions at the termitaria and for several meters from the mound center into the savanna (intermediate scale). We are not aware of any studies, which have addressed the broader influence of termites on CO_2 fluxes by measuring emission gradients radiating from the center of the termitaria into the savanna. In addition, with the exception of two studies, one which quantified soil temperature (Kahlil and others 1990) and one that measured soil temperature/soil moisture (Brümmer and others 2009), no attempts have been made to link the biotic and abiotic factors controlling CO_2 emissions on termitaria. Kahlil and others (1990) reported increasing termitaria emissions with increasing termitaria temperature. In contrast, the opposite findings were made in a West African savanna where Brümmer and others (2009) measured lower termitaria fluxes when soil temperatures were over 32°C compared to fluxes at soil temperatures below 32°C. In addition, they reported termitaria fluxes to be correlated to soil moisture.

The main goal of our study was to quantify the pattern of soil CO_2 emissions associated with termite mounds in an African savanna ecosystem. We sought to address the hypothesis that termites, via potential ''off-mound'' influences within the savanna, may have greater effects on soil CO_2 emissions than previously thought. Therefore, we quantified the influence of termite mounds on soil CO_2 fluxes at the mound center (the termitaria itself) and along gradients from the mound center into the savanna. We measured underlying factors, which may control those fluxes—soil temperature, soil moisture, vegetation height, and macro-invertebrate abundance. Soil temperature and soil

moisture are known to influence soil CO$_2$ emissions in general (Luo and Zhou 2006). Vegetation height was measured as a proxy for general plant growing conditions and potential indicator for root biomass (therefore root respiration), whereas macro-invertebrate abundance was included as Ohashi and others (2007) hypothesized that respiration by soil inhabiting animals, in particular by macro-invertebrates, might be responsible for the variability in soil CO$_2$ emissions measured in tropical ecosystems. Furthermore, by quantifying the spatial pattern of soil respiration around the mounds we asked: how far into the savanna do the effects of termitaria on soil CO$_2$ emission extend?

MATERIALS AND METHODS

Study Area and Experimental Design

This study was conducted in Serengeti National Park, a semi-arid savanna that is characterized by large herds of migratory wildebeest (*Connochaetes taurinus*), Thomson's gazelle (*Eudorcas thomsonii*), and zebra (*Equus quagga boehmi*). The volcanic highlands to the southeast and Lake Victoria to the west create a strong ecological gradient that varies in elevation, rainfall, soil fertility, and woody species cover (Anderson and others 2008; Reed and others 2009). The Serengeti has two characteristic wet seasons: the short rains, typically lasting from November to December and the long rains, typically starting in March and lasting until May (Norton-Griffiths and others 1975). Our study sites were located within an approximately 370 km^2 area located south of Seronera, in the Serengeti plains.

Within our study area, 28 termitaria were randomly selected for CO$_2$ measurements. We made no attempt to assess which termite species inhabited the mounds as, according to Sileshi and others (2010), mounds can be inhabited and modified by several species through time. However, according to De Visser and others (2008), who investigated trophic interactions among invertebrates in 14 termitaria in the same area, 64.3% of their mounds were inhabited by *Odontotermes* sp., 28.5% by *Trinervitermes* sp., and 7.1% by *Macrotermes* sp. The average distance between two neighboring study mounds was 2.5 km (minimum = 2.0 km; maximum = 4.6 km). The elevations of the mound locations ranged from 1,532 to 1,654 m a.s.l. and average annual precipitation from 714 to 792 mm per year (Table 1). The mounds varied considerably in diameter (range 212–570 cm, average 405 cm) and height (36–127 cm, 84.5 cm; Table 1). Mound

densities across the 28 locations—determined with the point-centered quarter methods (Greig-Smith 1983)—ranged widely, from 0.02 to 52.9 mounds ha^{-1} (average 4.48 mounds ha^{-1}, average distance between mounds 92.5 m).

At each mound, we randomly selected an ordinal direction (between 0° and 360°) and established a 20-m-long transect with its origin being at 1 m from the edge of the mound (defined as 0 m). Sample subplots (20 × 20 cm) were arranged at 1-m-interval along each transect. One 20 × 20-cm sampling subplot each was also established on top of the mound (center), and one at the edge of the mound resulting in a total of 23 subplots per mound. Fieldwork was conducted in November 2010 at the end of the dry and beginning of the wet season. As we were interested in spatial and not temporal patterns in soil CO$_2$ fluxes, the temporal component (that is, measuring several times throughout the day or throughout the year) was omitted. However, rain started to fall during our measurement campaign; therefore, the measurements obtained from the 28 mounds covered conditions before (18 mounds) and after the first rains (10 mounds). We did not specify this in our analyses as we found no differences in soil CO$_2$ emission patterns when repeating our measurements on eight mounds (originally measured during dry conditions) after observing rain storms in the respective areas (Appendix Figure A1). The only difference we found was that the fluxes were higher after the rain events (Appendix Figure A1). Mainly resident ungulates were grazing our sites at the time of the study as the migratory animals were still in the northern part of Serengeti.

Soil CO$_2$ Emission, Soil Temperature, Soil Moisture, and Vegetation Height Measurements

On each of the 28 mounds, we measured in situ CO$_2$ emissions with a 15-cm high × 10-cm diameter (surface area 78.5 cm^2) PP-Systems SRC-1 soil respiration chamber (closed circuit) attached to a PP-System EGM-4 infrared gas analyzer (PP-Systems, Amesbury, Massachusetts, USA) at all the 23 subplot locations along the transects. The base of the chamber is equipped with a thin sharpened metal edge, which—when placed on the soil—results in a tight seal between soil surface and chamber. This eliminated the need for burying PVC collars for chamber placement prior to data collection. Measurements were conducted between 10.00 and 16.00 hrs. Plant material was removed with scissors where necessary at least 1 h prior to

Table 1. Locations (*x–y* Coordinates) and Elevation (Elev, m Above Sea Level) of Mounds, Total Annual Precipitation at Mound Location (Precip; mm), Average Mound Diameter (Diam; cm), Average Mound Height (cm), and Mound Density (mounds ha^{-1}) at Each Site

Mound	*x*	*y*	Elev (m)	Precip (mm)	Diam (cm)	Height (cm)	Density (ha^{-1})
1	705,645	9,727,198	1,557	779	347.0	66.25	1.73
2	710,698	9,723,516	1,594	744	447.5	88.75	0.02
3	703,192	9,726,112	1,543	781	451.5	82.25	0.39
4	702,960	9,723,868	1,543	775	380.0	100.75	0.40
5	703,901	9,721,616	1,559	768	570.0	110.25	2.85
6	701,749	9,721,518	1,560	770	263.5	55.50	4.00
7	700,219	9,724,404	1,547	776	304.5	89.25	16.66
8	696,890	9,731,012	1,534	792	212.0	36.25	52.89
9	696,849	9,727,904	1,532	791	365.0	126.75	10.93
10	698,083	9,723,442	1,572	779	385.0	73.50	0.70
11	705,446	9,719,090	1,587	753	445.0	88.25	1.52
12	701,016	9,718,154	1,586	763	397.5	71.00	5.81
13	699,248	9,716,308	1,599	762	395.0	112.00	0.23
14	700,040	9,714,526	1,601	750	440.0	92.00	0.87
15	702,545	9,715,062	1,599	750	495.0	78.50	0.11
16	707,013	9,716,638	1,610	744	530.0	86.50	1.23
17	709,202	9,715,898	1,623	738	495.0	87.25	0.31
18	711,782	9,716,368	1,630	731	305.0	57.50	4.67
19	711,295	9,718,758	1,598	733	395.0	118.00	1.32
20	713,477	9,719,392	1,610	723	485.0	82.00	1.48
21	710,160	9,728,118	1,590	765	455.0	80.25	1.13
22	712,697	9,727,960	1,584	749	370.0	76.75	1.49
23	717,338	9,724,940	1,623	721	340.0	68.25	1.80
24	715,454	9,722,076	1,644	716	390.0	72.50	2.58
25	716,917	9,719,978	1,638	714	475.0	114.50	0.74
26	713,897	9,714,950	1,640	717	382.5	91.00	2.64
27	714,191	9,712,954	1,654	717	410.0	76.75	1.92
28	711,163	9,714,122	1,652	726	425.0	85.75	5.05

the measurements. Immediately after the CO_2 emission measurements, we determined soil temperature with a waterproof digital pocket thermometer (Barnstead International, Dubuque Iowa, USA) and soil moisture with a field-scout TDR-100 time domain reflectometer; (Spectrum Technologies, Plainfield, Illinois, USA) for the 0–10 cm mineral soil depth. In addition, vegetation height (cm) was measured at each location (prior to the removal of green plant material) as a proxy for general plant growing conditions (nutrients, water, herbivory, and so on).

Abundance of Soil Macro-invertebrates

Macro-invertebrate abundance was assessed after the CO_2, temperature, moisture, and vegetation measurements by excavating a 20 × 20 × 20 cm (depth) soil monolith at all the subplots located at the mound edge and along the gradient (22 plots; center omitted to preserve the mounds) following the method of Anderson and Ingram (1989). From the excavated soils, macro-invertebrates were

hand-sorted (Dangerfield 1997; Lavelle and others 2003) on site for each sample separately. We defined macro-fauna as invertebrates with body length greater than 2-mm, counted the individuals and identified them to higher taxa (class, order/subclass, and family). After identification and quantification all soil and the invertebrates were discarded at the site.

Statistical Analyses

We calculated the average CO_2 emission, soil temperature, soil moisture, vegetation height, and macro-invertebrate abundance for our mounds for each distance the measurements were taken. To assess relationships between the abiotic and biotic factors and the CO_2 emissions measured, we used the Pearson's correlation index. For these analyses the center measurements were, however, omitted. Data were not transformed as the normality and homogeneity criteria were met.

Further, we assessed how far into the savanna the soil CO_2 emissions were affected by the

mounds. For this purpose, we calculated patterns of spatial autocorrelation of CO$_2$ emissions along the transects using Mantel's correlations. The Mantel test examines the relationship between distance matrices that can represent, but are not limited to, geographic distances (see for example, Sokal and Rohlf 1995). The center measurements were omitted, as these were considerably different from the rest of the measurements. Based on the Mantel analysis, we were able to delineate areas whose patterns in soil CO$_2$ emission around our mounds were spatially correlated with the termitaria and areas whose emission patterns were independent of the termitaria. Thus, we were able to calculate fluxes for different zones around the mound center. A one-way ANOVA was used to assess whether these values were significantly different from one another. All statistical analyses were performed with the IBM SPSS Statistics 19.0 statistical package (IBM SPSS, Chicago, Illinois, USA), with exception of the Mantel's correlation, which was performed with the "vegan" package (Oksanen and others 2011) in R (R Development Core Team 2011).

RESULTS

The average rate of soil CO$_2$ emissions at the center of the termite mounds was 1.91 $\pm$ 0.48 g CO$_2$ m^{-2} h^{-1}, whereas measurements collected along the remainder of the transect gradient varied from 0.28 $\pm$ 0.05 to 0.43 $\pm$ 0.09 g CO$_2$ m^{-2} h^{-1} (Figure 1A). Soil temperature, soil moisture, vegetation height, and macro-invertebrate abundance (Figure 1B–E) were also highly variable along this gradient. However, no statistically significant correlation was found between soil CO$_2$ emission and soil temperature, soil moisture, and vegetation height, respectively (Figure 2A–C). Instead, soil CO$_2$ emissions were positively correlated with the abundance of soil macro-invertebrates (Figure 2D). A rich array of macro-invertebrates was sampled, with the most commonly observed groups being termites, ants, beetles, and centipedes (Appendix Table A1). In general, fewer macro-invertebrates were observed near termitarias and this was associated with lower soil CO$_2$ emissions near the mounds compared to distances farther away (Figure 1E).

Spatial autocorrelation analyses (Mantel's test) revealed that the soil CO$_2$ fluxes were spatially correlated up to distances of 9 m from the termitaria edge (Figure 3), beyond which CO$_2$ fluxes were spatially independent of the termitaria itself. Indeed, the one-way ANOVA showed that average fluxes (center, edge to 9 m, 10–20 m) significantly differed from one another (df = 1, F = 8.67, p = 0.003,

Figure 3, inset) with fluxes at the center (1.91 $\pm$ 0.49 g CO$_2$ m^{-2} h^{-1}) being higher then the average fluxes from the other two zones, but also the termitaria edge to 9 m (0.34 $\pm$ 0.02 g CO$_2$ m^{-2} h^{-1}) being significantly lower than fluxes in the range of 10–20 m (0.38 $\pm$ 0.02 g CO$_2$ m^{-2} h^{-1}; Figure 3, inset).

When multiplying the center area (average mound diameter = 4.05 m; see Table 1) and all the 1-m-wide doughnut areas around the center with their respective CO$_2$ emissions measured, the savanna would release 3,795 g CO$_2$ ha^{-1} h^{-1} with the mounds present (using mound densities of 4.48 mounds ha^{-1}; see Table 1). The savanna without mounds would release an amount of 3,806 g CO$_2$ ha^{-1} h^{-1} when using an average soil CO$_2$ emission value obtained from the 10–20 m from the mounds (0.38 $\pm$ 0.02 g CO$_2$ m^{-2} h^{-1}); assuming that this value represents a rough estimate for savanna fluxes without mounds (for more detail see "Discussion").

DISCUSSION

Like previous studies (for example, Seiler and others 1984; Kahlil and others 1990; Darlington and others 1997; Konaté and others 2003; Brümmer and others 2009), we detected higher CO$_2$ emission values at the center of mounds compared to measurements taken away from the mounds. Although our average center values (1.91 g CO$_2$ m^{-2} h^{-1}) were similar in magnitude to other published reports, we caution against direct comparison as the studies used different techniques. Brümmer and others (2009) measured on average 1.64 g CO$_2$ m^{-2} h^{-1} per mound (n = 5) in West Africa and Seiler and others (1984) approximately 1.8 g CO$_2$ m^{-2} h^{-1} on a mound in South Africa when covering the entire mound with large chambers. Kahlil and others (1990) taking air samples from inside the mounds (n = 52) reported mean annual fluxes of 1.6 g CO$_2$ m^{-2} h^{-1} of Australian termite mounds, and Konaté and others (2003) conducting chamber-based measurements comparable to our approach measured between 1.4 and 3.0 g CO$_2$ m^{-2} h^{-1} from termite mounds (without and with fungi-combs) in grassy, shrubby, and woody savanna in West Africa (n = 18).

Patterns of Soil CO$_2$ Fluxes Around Termite Mounds

When assessing the variation in soil CO$_2$ emissions from the termitaria into the surrounding savanna, we found that not soil temperature or soil moisture, but the abundance of macro-invertebrates were
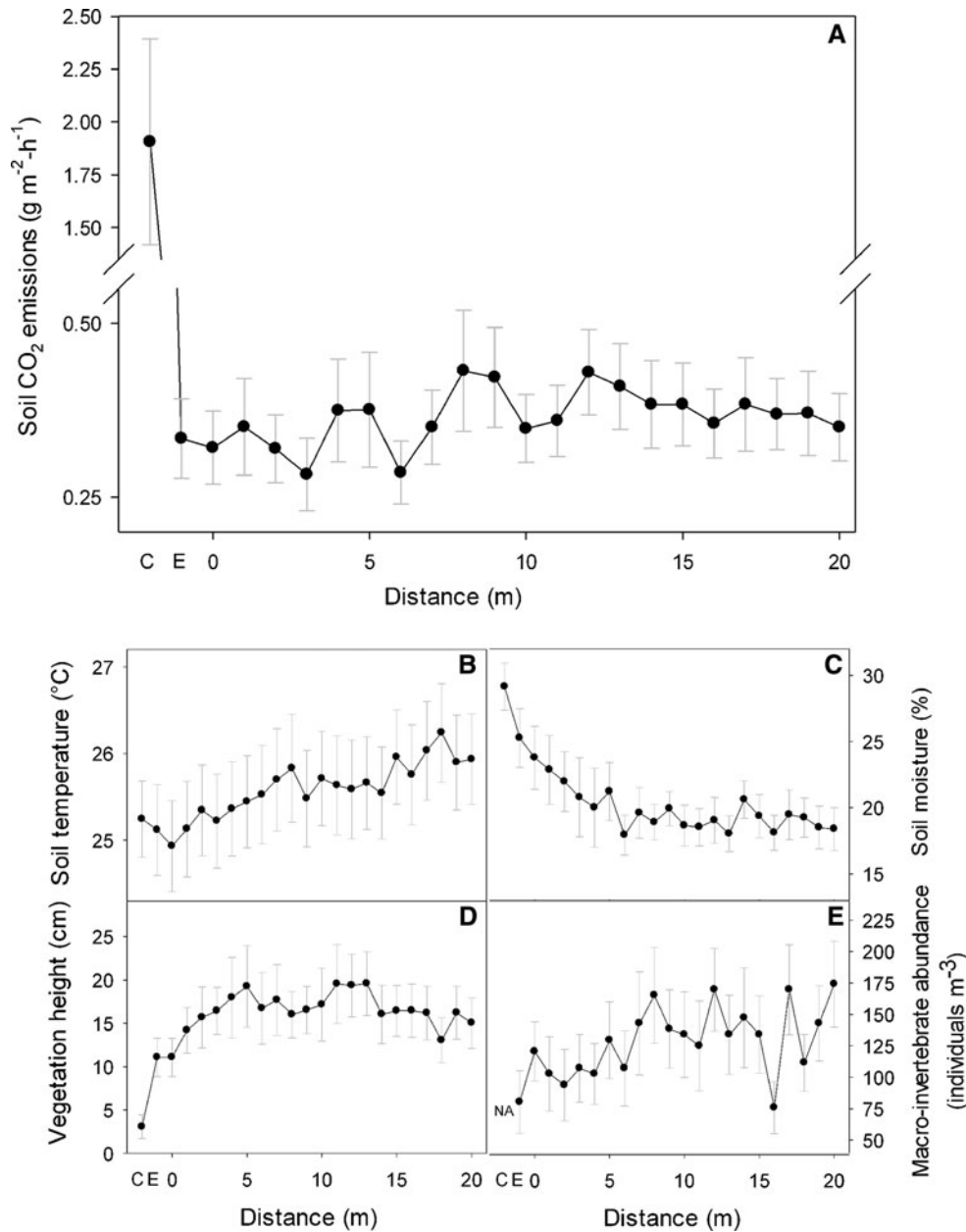
Figure 1. Soil CO_2 emission (**A**), soil temperature (**B**), soil moisture (**C**), vegetation height (**D**), and macro-invertebrate abundance (**E**) measurements collected from the center of the mound up to 20 m from the mound edge into the savanna. *C* mound center, *E* mound edge, *NA* not available.

correlated with the variability of soil CO_2 fluxes: high fluxes were detected at high abundances of macro-invertebrates, low fluxes where the abundance of macro-invertebrates was low. Thus, our results suggest that respiration by macro-invertebrates likely contributed more to the emissions measured then decomposition processes. These results correspond to findings of Lavelle and others (1993), who suggested that climatic factors likely would be less important for decomposition processes compared to the soil macro-fauna when reviewing the literature with regard to decomposition processes in tropical systems. Also Ohashi and others (2007) suggested that—in particular in

tropical systems—macro-invertebrates rather than differences in the soil micro-climate could explain the heterogeneity of soil CO_2 fluxes (among them the occurrence of hot-spots) measured in the field. However, it should be noted that neither of these studies was related to termite mounds. Yet, it is known that termites can impact the soil fauna. For example, Cadet and others (2004) showed that termitaria flattened by plowing in sugar cane fields (so called isiduli) held higher numbers and another community of nematodes then the surrounding soil. Thus, it is possible that termites, either directly or indirectly by modifying the soil environment around their mounds impact the abundance of
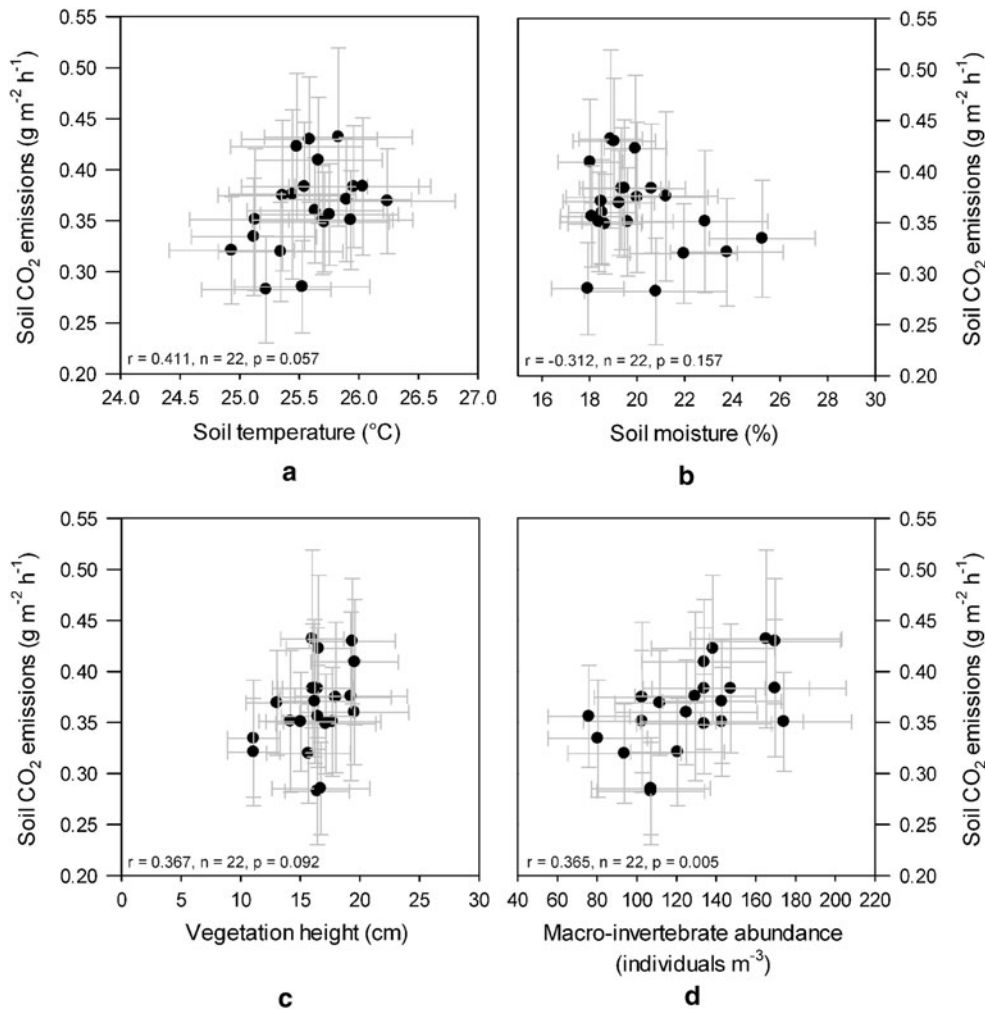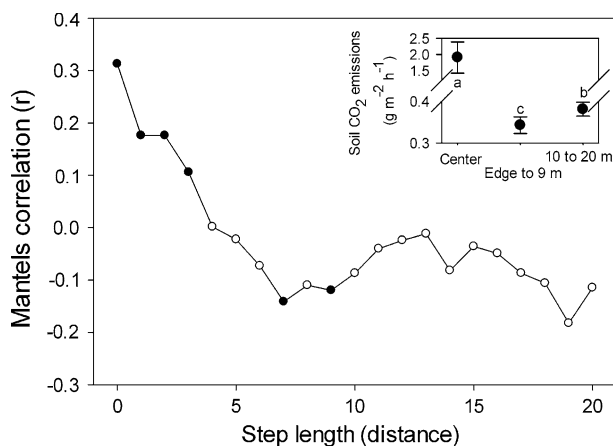
Figure 3. Spatial dependence of soil CO$_2$ emissions (Mantel's correlation) collected around the mounds. *Black dots* Significant spatial dependence at an alpha level of 0.05. *Inset* The average value for the mound center, mound edge to 9 m, and 10–20 m. *Different letters* Significant differences at alpha level of 0.05.

macro-invertebrates. These changes could, in turn, either directly or indirectly be responsible for the patterns in soil CO$_2$ emissions found in our study. More specifically, three explanations seem possible: (1) lower abundances of macro-invertebrates resulted in lower total macro-invertebrate respiration and therefore in lower soil fluxes. This was, for example, shown by Tripathi and others (2009) who reported that differences in soil respiration were related to differences in soil fauna population size in pastureland in the northwestern dry region of India. Also Jamali and others (2011) found a strong correlation between termite biomass and CO$_2$ emissions in an incubation experiment. (2) Lavelle and others (1993) suggested that decomposition—and therefore the release of soil CO$_2$ emission—is regulated by three components: the resource to be decomposed, the microorganisms responsible for the chemical transformation of the resource, and the macroorganisms which create suitable conditions for decomposition by microorganisms. Thus, it is possible that not only macro-

invertebrate respiration was lower on plots with lower macro-invertebrate abundance but also that these plots featured less suitable conditions for soil microorganisms resulting in lower decomposition and therefore the lower soil CO_2 fluxes. (3) Lower abundance of soil macro-invertebrates not only led to lower total respiration, but also to lower soil macro-pore density and therefore reduced diffusion of soil CO_2 from the soil matrix as the diffusion of CO_2 is strongly related to the porosity of the soil (see for example, Marshall 1957; Millington 1959).

Alternatively to these three (biological) explanations for the spatial variation in CO_2 fluxes observed discussed above, it is possible that directional air flows associated with the mound architecture (ventilation system) might have contributed to the observed patterns: under this hypothesis air and therefore CO_2 may be drawn in from the soil of the edge to 9-m zone and released through the mound center resulting in decreased emissions in a ring around the mound. Such air flows have been reported by several authors (for an overview see Korb 2003 or Worall 2011) and generally three different mechanisms have been proposed in the literature: (1) the air flow originates from temperature differences inside and outside of the mounds (thermal-convection) resulting in the mound acting as a ''thermosiphon'' with air flowing from the edges of the mound to and out of the center (see for example, Lüscher 1955). (2) The air flow is a phenomena of wind-induced ventilation where (i) higher wind speed and lower air pressure on top of the mounds compared to the channels located on the side of the termitaria results in ''sucking'' the air from the mound base through the mound openings (Bernoulli's law; see for example, Vogel and Bretz 1972; Kleineidam and others 2001) or (ii) the stagnant air is ''dragged'' from the tunnels by sheer stress (viscous dragging) and released through the central mound opening (for example, Darlington and others 1997; Kleineidam and others 2001). (3) More recently it has been proposed that the gas flow originates from interactions among the mound, wind, and differences in the buoyancy of the air due to the metabolic output of termites and their associated fungi (for example, Turner 2001).

However, all authors that reported about these air flows worked on the mound themselves comparing in- and outflows of gases between the top of the mound and mound walls or tunnels/channels in the walls. We are not aware of any study that would have investigated the air flow between the mound center and the surrounding of the mounds, thus, it is not clear whether such phenomena exist

on larger scales—such as in our case—between the edge to 9-m zone and the mound center. The fact that—according to Darlington (1982) who excavated underground termite passages around one termite mound inhabited by *Macrotermes michaelseni* in Kenya—the surroundings of the mound can be divided into (1) the inner zone characterized by underlying deep radial termite passages that extends up to 10 m from the termitaria, (2) the main foraging zone characterized by underground passages extending out to 40 m, and (3) the peripheral zone characterized by only small passages eventually ending blind extending out to 50 m indicates that many channels/tunnels exist in the zone where we found lower soil CO_2 fluxes. Consequently, airflows from the inner zone to the center of the mound associated with the underground passages might exist and provide an additional explanation for our patterns. Yet, this topic remains to be studied.

In summary, both biological (macro-invertebrate abundance) and physical (thermoregulation and ventilation) mechanisms could be responsible for the pattern in soil CO_2 emission found around our mounds during daytime when our measurements were conducted. Naturally, we do not know whether the same pattern would be found at night, as we did not collect any nighttime measurements. However, in other studies higher CO_2 emissions were measured on top of mounds during nighttime compared to daytime, which would suggest that the patterns we observed in our study might be identically directed but even more extreme at night (for example, Darlington and others 1997; Korb and Linsenmair 2000).

Extrapolation of Fluxes Across the Landscape

When extrapolating the fluxes across the landscape based on the spatial patterns detected we found—in contrast to our a priori hypothesis—that soil CO_2 emissions of termite mounds only represented hotspots at the center of the mound whereas when including the surroundings of the mounds into the calculations, high soil CO_2 emissions from the mound center would be compensated by lower emissions from the surroundings. Naturally, these values are only valid for the constrained study area and for the time of the day our measurements were conducted. We do not have measurements for CO_2 fluxes of non-termite influenced savanna as—based on Darlington's (1982) findings—none of the area covered in our study would feature non-termite-influenced savanna given that the average

distance between our mounds corresponded to 92.5 m. Collecting measurements in areas without termite mounds in the larger surrounding of Serengeti might have been possible, but we doubt that these measurements would represent accurate means of comparison as soil and vegetation properties might considerably differ from our study area with numerous termite mounds. Further, we do not know whether our findings would hold when measurements are conducted over several seasons as our sampling was only conducted during a constrained period. It is known that termitaria fluxes considerably differed between seasons, with higher fluxes during wet periods when termite biomass was higher compared to dry periods when fewer termites were found (Brümmer and others 2009; Jamali and others 2011). Such a pattern would also be expected in Serengeti as we found higher soil CO$_2$ respiration after rain events compared to measurements taken during dry conditions. Unfortunately neither Brümmer and others (2009) nor Jamali and others (2011) conducted measurements along gradients in the surroundings of the mounds. Thus, in a next step, the collection of diurnal and seasonal measurements along gradients from the termitaria into the savanna would be beneficial to assess whether our findings—that the high center fluxes originating from termitaria are compensated by lower fluxes released from the inner zone—would hold in general and over the entire span of a year.

We found only two other studies that extrapolated mound fluxes to the landscape level. Brümmer and others (2009) calculated total CO$_2$ emissions based on point sources (mound fluxes) for the West African savanna of Burkina Faso. They estimated that termite mounds covered less than 1% of the area and therefore contributed only marginally to the total soil CO$_2$ emissions of the system. However, they did not assess how far into the savanna the termites affected the fluxes. Also Konaté and others (2003) extrapolated point source fluxes from the mounds to the landscape level and estimated that mounds cover 3–5% of the Ivory Coast savanna they worked in. Given the much lower emissions measured in the surrounding savanna compared to the termite mounds, they concluded that the fluxes released from the mounds represented 4.9% of the total aboveground net primary production of the system.

In contrast to Konaté and others (2003) our results provide, however, some first evidence that when including the surroundings of the termitaria these features likely do not represent hot-spots of soil CO$_2$ fluxes at the landscape level as the high center fluxes were compensated by the lower fluxes measured in the immediate surroundings of the mounds. Thus, our findings suggest that termitaria might play a different role in soil CO$_2$ cycling in savanna systems than previously thought and that our current knowledge of sink-source dynamics within these systems might not yet be sufficient to accurately model C emissions within them. Whether the same holds true for the emissions of other greenhouse gases, such as methane (CH$_4$) that seemed to be correlated with CO$_2$ when measured in association with termite mounds (see for example, Kahlil and others 1990; Brümmer and others 2009), remains to be tested.

REFERENCES

Anderson JM, Ingram JSI. 1989. Tropical soil biology and fertility: a handbook of methods. Wallingford: CAB International.

Anderson TM, Dempewolf J, Metzger KL, Reed DN, Serneels S. 2008. Generation and maintenance of heterogeneity in the Serengeti ecosystem. In: Sinclair ARE, Packer C, Mduma SAR, Fryxell JM, Eds. Serengeti III: human impact on ecosystem dynamics. Chicago: The University of Chicago Press. p 3–71.

Brody AK, Palmer TM, Fox-Dobbs K, Doak DF. 2010. Termites, vertebrate herbivores, and the fruiting success of Acacia drepanolobium. Ecology 91:399–407.

Brümmer C, Papen H, Wassmann R, Brüggemann N. 2009. Fluxes of CH$_4$ and CO$_2$ from soil and termite mounds in south Sudanian savanna of Burkina Faso (West Africa). Glob Biogeochem Cycles 23:GB1001.

Cadet P, Guichaoua L, Spaull VW. 2004. Nematodes, bacterial activity, soil characteristics and plant growth associated with termitaria in a sugarcane field in South Africa. Appl Soil Ecol 25:193–203.

Ciais P, Piao SL, Codule P, Friedlingstein P, Chédin A. 2009. Variability and recent trends in the African terrestrial carbon balance. Biogeosciences 6:1935–48.

Dangerfield JM. 1997. Abundance and diversity of soil macrofauna in northern Botswana. J Trop Ecol 13:527–38.

Dangerfield JM, McCarthy TS, Ellery WN. 1998. The mound-building termite Macrotermes michaelseni as an ecosystem engineer. J Trop Ecol 14:507–20.

Darlington JPEC. 1982. The underground passages and storage pits used in foraging by a nest of the termite Macrotermes michaelseni in Kajiado, Kenya. J Zool 198:237–47.

Darlington JPEC, Zimmerman PR, Greenberg J, Westberg C, Bakwin P. 1997. Production of metabolic gases by nests of the termite *Macrotermes jeanneli* in Kenya. J Trop Ecol 13:491–510.

De Visser SN, Freymann BP, Schnyder H. 2008. Trophic interactions among invertebrates in termitaria in the African savanna: a stable isotope approach. Ecol Entomol 33:758–64.

Du Toit JT, Rogers KH, Biggs HC. 2003. The Kruger experience: ecology and management of savanna heterogeneity. Washington, DC: Island Press.

Epstein HE, Burke IC, Lauenroth WK. 2002. Regional patterns of decomposition and primary production rates in the US great plains. Ecology 83:320–7.

Glover PE, Trump EC, Waterridge LED. 1965. Termitaria and vegetation patterns on the Loita Plains of Kenya. J Ecol 52:367–77.

Greig-Smith P. 1983. Quantitative plant ecology. 3rd edn. Berkley: University of California Press.

Holdo RM, McDowell LR. 2004. Termite mounds as nutrient-rich food patches for elephants. Biotropica 36:231–9.

Holt JA. 1998. Microbial activity in the mounds of some Australian termites. Appl Soil Ecol 9:183–7.

Jamali H, Livesley SJ, Dawes TZ, Hutley LB, Arndt SK. 2011. Termite mound emissions of CH_4 and CO_2 are primarily determined by seasonal changes in termite biomass and behaviour. Oecologia 167:525–34.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Jouquet P, Tavernier V, Abbadie L, Lepage M. 2005. Nests of subterranean fungus-growing termites (Isoptera, Macrotermitinae) as nutrient patches for grasses in savannah ecosystems. Afr J Ecol 43:191–6.

Kahlil MAK, Rasmussen RA, Rench JRJ, Holt JA. 1990. The influence of termites on atmospheric trace gases: CH_4, CO_2, $CHCl_3$, N_2O, CO, H_2, and light hydrocarbons. J Geophys Res 95:3619–34.

Kirschbaum MUF. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol Biochem 27:753–60.

Kleineidam C, Ernst R, Roces F. 2001. Wind-induced ventilation of the giant nests of the leaf-cutting ant *Atta vollenweideri*. Naturwissenschaften 88:301–5.

Konaté S, Le Roux X, Verdier B, Lepage M. 2003. Effect of underground fungus-growing termites on carbon dioxide emissions at the point- and landscape-scales in an African savanna. Funct Ecol 17:305–14.

Korb J. 2003. Thermoregulation and ventilation of termite mounds. Naturwissenschaften 90:212–19.

Korb J, Linsenmair KE. 2000. Ventilation of termite mounds: new results require a new model. Behav Ecol 11:486–94.

Lavelle P, Blanchart E, Martin A, Martin S, Spain A. 1993. A hierarchical model for decomposition in terrestrial ecosystems: Application to soils of the humid tropics. Biotropica 25:130–150.

Lavelle P, Senapati B, Barros E. 2003. Soil macrofauna. In: Schroth G, Sinclair FL, Eds. CAB international, trees, crops and soil fertility. Wallingford: CABI Publishing. p 303–23.

Lomander A, Katterer TA, Andrean O. 1998. Carbon dioxide evolution from top- and subsoil as affected by moisture and constant and fluctuating temperature. Soil Biol Biochem 30:2017–22.

Luo Y, Zhou X. 2006. Soil respiration and the environment. Burlington: Academic Press.

Lüscher M. 1955. Der Sauerstoffverbrauch bei Termiten und die Ventilation des Nestes bei *Macrotermes natalensis* (Haviland). Acta Trop 12:289–307.

Marshall TJ. 1957. Permeability and size distribution of pores. Nature 180:664–5.

Merbold L, Ardö J, Arneth A, Scholes RJ, Nouvellon Y, deGrandcourt A, Archibald S, Bonnefond JM, Boulain N, Bruemmer C, Brueggemann N, Cappelaere B, Ceschia E, El-Khidir HAM, El-Tahir BA, Falk U, Lloyd J, Kregoat L, Le Dantec V, Mougin E, Muchinda M, Mukelabai MM, Ramier D, Roupsard O, Timouk F, Veenendaal EM, Kutsch WL. 2008. Precipitation as driver of carbon fluxes in 11 African ecosystems. Biogeosciences 5:4071–104.

Millington RJ. 1959. Gas diffusion in porous media. Science 130:100–2.

Moe SR, Mobaek R, Narmo AK. 2009. Mound building termites contribute to savanna vegetation heterogeneity. Plant Ecol 202:31–40.

Norton-Griffiths M, Herlocker D, Pennycuick L. 1975. The patterns of rainfall in the Serengeti ecosystem, Tanzania. Afr J Ecol 13:347–74.

Ohashi M, Kume T, Yamane S, Suzuki M. 2007. Hot spots of soil respiration in an Asian tropical rainforest. Geophys Res Lett 34:L08705.

Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner HH. 2011. Vegan: community ecology package. R Package Version 1.17-12. http://CRAN.R-project.org/package=vegan. Accessed 23 Nov 2011.

Okullo P, Moe SR. 2012. Termite activity, not grazing, is the main determinant of spatial variation in savanna herbaceous vegetation. J Ecol 100:232–41.

Palmer TM. 2003. Spatial habitat heterogeneity influences competition and coexistence in an African acacia ant guild. Ecology 84:2843–55.

Pringle RM, Doak DF, Brody AK, Joqué R, Palmer TM. 2010. Spatial pattern enhances ecosystem functioning in an African savanna. PLoS Biol 8:e1000377.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, url:http://www.R-project.org. Accessed 23 Nov 2011.

Reed DN, Anderson TM, Dempewolf J, Metzger KL, Serneels S. 2009. The spatial distribution of vegetation types in the Serengeti ecosystem: the influence of rainfall and topographic relief on vegetation patch characteristics. J Biogeogr 36:770–82.

Seiler W, Conrad R, Scharffe D. 1984. Field studies of methane emissions from termite nests into the atmosphere and measurement of methane uptake by tropical soils. J Atmos Chem 1:171–86.

Sileshi GW, Arshad MA, Konaté S, Nkunika POY. 2010. Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. J Veg Sci 21:923–37.

Smith FR, Yeaton RI. 1998. Disturbance by the mound-building termite, *Trinervitermes trinervoides*, and vegetation patch dynamics in a semi-arid, southern African grassland. Plant Ecol 137:41–53.

Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practices of statistics in biological research. 3rd edn. New York: WH Freeman. p 880.

Sugimoto A, Bignell DE, MacDonald JA. 2000. Global impact of termites on the carbon cycle and atmospheric trace gases. In: Abe TD, Bignell DE, Higashi M, Eds. Termites: evolution, sociality, symbioses, ecology. Dordrecht: Kluwer. p 409–35.

Tripathi G, Ram S, Sharma BM, Singh G. 2009. Fauna-associated changes in soil biochemical properties beneath isolated trees in a desert pastureland of India and their importance in soil restoration. Environmentalist 29:318–29.

Turner JS. 2001. On the mound of *Macrotermes michaelseni* as an organ of respiratory gas exchange. Physiol Biochem Zool 74:798–822.

Vogel S, Bretz WL. 1972. Interfacial organisms: passive ventilation in the velocity gradients near surfaces. Science 175:210–11.

White R, Murray S, Rohweder M. 2000. Pilot analysis of global ecosystems: grassland ecosystems technical report. World Resources Institute, Washington, DC. 69 pp.

Williams CA, Hanan NP, Neff JC, Scholes RJ, Berry JA, Denning AS, Baker DF. 2007. Africa and the global carbon cycle. Carbon Balance Manage 2:3. doi:10.1186/1750-0680-2-3.

Wood TG, Sands WA. 1978. The role of termites in ecosystems. In: Brian MV, Ed. Production ecology of ants and termites. Cambridge: Cambridge University Press. p 245–92.

Worall M. 2011. Homeostasis in nature: nest building termites and intelligent buildings. Intell Build Int 3:87–95.