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Carbon dioxide and methane fluxes from mounds of African fungus-growing termites

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Abstract. Termites play an essential role in decomposing dead plant material in tropical ecosystems and are thus major sources of gaseous C emissions in many environments. In African savannas, fungus-growing termites are among the ecologically most influential termite species. We studied the gas exchange from mounds of two closely related fungus-growing species (*Macrotermes subhyalinus* and *M. michaelseni*, respectively) in two habitats representing different vegetation types (grassland, bushland) together with soil fluxes around the mounds. The fluxes from active termite mounds varied from 120 to 2100 mg CO₂-C m⁻² h⁻¹ for carbon dioxide (CO₂) and from 0.06 to 3.7 mg CH₄-C m⁻² h⁻¹ for methane (CH₄) fluxes. Mound CO₂ fluxes varied seasonally with a 64 % decrease and 41 % increase in the fluxes from the dry to wet season at the grassland and bushland sites, respectively. During the wet season, the CO₂ fluxes were significantly correlated with termite mound volume. The diurnal measurements from two *M. michaelseni* mounds suggest that the gas fluxes peak during the daytime, possibly reflecting changes in mound internal air circulation. Soil fluxes of both CO₂ and CH₄ were enhanced at up to 2 m distance from the mounds compared to the local soil respiration, indicating that, in addition to mound ventilation structures, a

small proportion of the metabolic gases produced also leave the nest via surrounding soils.

1 Introduction

Termites are major degraders of dead organic plant matter in many tropical and subtropical ecosystems (Bignell and Eggleton, 2000; Jouquet et al., 2011), also making them a significant source of atmospheric carbon dioxide (CO₂) and methane (CH₄) (Zimmerman et al., 1982; Khalil et al., 1990). Especially in African dry savannas, the fungus-growing species comprise the most common and ecologically important termite group that may recycle a quarter of total dead plant matter and even 90 % of the woody litter in some arid ecosystems (Collins, 1981; Buxton, 1981). Fungus-growing termites cultivate symbiotic termite fungi (*Termitomyces* spp., Basidiomycota) in fungus combs, which are specialized structures within underground nest chambers. The combs are built from feces of termite workers and consist of largely undigested plant matter, initially ingested by foraging termites, that the *Termitomyces* further degrades (Rouland-Lefèvre, 2000; Vesala et al., 2022a). Eventually, termite hosts get their energy and nutrition from the de-

graded plant matter and/or the fungal mycelium (Sieber and Leuthold, 1981; Hyodo et al., 2003; Vesala et al., 2019a).

Fungus cultivation by termites is always associated with a complex caste system including numerous workers, soldiers and reproductive individuals, and the total number of termites within a colony typically ranges from hundreds of thousands to up to a few million individuals (Darlington, 1986, 1990). Such large insect populations are notable sources of CO₂ already in themselves, but, within nests of fungus-growing termites, a major proportion of the nest CO₂ emission is produced by the extensive fungus gardens whose total biomass in mature termite colonies may exceed 20 kg (Darlington, 1986; Darlington et al., 1997; Noirot and Darlington, 2000). Due to their methanogenic gut symbionts, termites are also among the major sources of atmospheric CH₄ although estimates about their contribution to the global CH₄ budget vary highly (currently considered to represent 1%–4% of the natural sources) due to uncertainties in methane-related processes and global termite biomass (Sanderson, 1996; Kirschke et al., 2013; Saunio et al., 2020). Methane can also be oxidized by soil methanotrophic microbes occurring within and around termite nests (Chiri et al., 2020). It has been evaluated that methane-oxidizing bacteria can mitigate even half of the methane produced in nests of some mound-building termite species (Sugimoto et al., 1998; Nauer et al., 2018).

Maintenance of large termite populations and the extensive fungal gardens necessitates effective gas exchange and stable conditions within the nest interior. Termites of the genera *Macrotermes* and *Odontotermes* build aboveground soil mounds to stabilize temperature, maintain humidity and enhance gas exchange (Noirot and Darlington, 2000; Korb, 2003, 2011). Mound structure can vary a lot depending on termite species and environmental conditions (Korb and Linsenmair, 1998; Korb, 2003, 2011). Even closely related species may rely on fundamentally different mechanisms of nest ventilation, as in cases of Kenyan *Macrotermes michaelseni* and *Macrotermes subhyalinus*, which build closed and open mounds, respectively (Darlington 1984, 1985). The open *M. subhyalinus* mounds have multiple large ventilation shafts at different elevations on the mound surface that promote the wind-induced Venturi effect, resulting in airflow through the shafts that ventilate the underground nest (Weir, 1973; Korb, 2011). The closed mounds of *M. michaelseni* lack these openings, and, instead, the air is circulated internally within the mound until the gas exchange between the nest interior and ambient air takes place through the porous mound surface (Noirot and Darlington, 2000; Ocko et al., 2017). Direct measurements of air velocities and temperatures within closed mounds have shown that air moves in convective cells following a diurnally oscillating thermal schedule (King et al., 2015; Ocko et al., 2017).

Despite the well-recognized importance of termite mounds as significant sources of greenhouse gases, field studies quantifying gas fluxes from termite mounds are

rare and often limited to species that build relatively small mounds. Previous CO₂ flux measurements from termite mounds have ranged from 40 to 2200 mg CO₂–C m^{–2} h^{–1} (van Asperen et al., 2021; Jamali et al., 2013; Brümmer et al., 2009). For wood-feeding termites in Australia, the seasonal variability in CO₂ and CH₄ was high with larger fluxes occurring during the wet season (Jamali et al., 2013). For soil- and wood-feeding termites, the relationship between mound CO₂ and CH₄ fluxes has been species-specific (Jamali et al., 2013). With the assistance of *Termitomyces* symbionts, fungus-growing termites can utilize widely different types of plant matter including grasses, leaf litter and dead wood (Collins, 1981; Lepage, 1981a), and the proportion of utilized food sources may vary both geographically and seasonally (Boutton et al., 1983; Lepage et al., 1993; Vesala et al., 2022b). Alternative food sources may also differ in their nutritional value with potential consequences for the gas fluxes (Zhou et al., 2023). For example, a lower nitrogen content associated with grass-based compared to woody plant-based fungus combs found in Vesala et al. (2022b) could necessitate relatively high CO₂ and CH₄ emissions, as more carbon needs to be eliminated to gain sufficient protein from the N-deficient diet (Higashi et al., 1992; Eggleton and Tayasu, 2001). Whether such factors could affect the mound gas fluxes is currently not known.

In this study, we used the static chamber method to investigate CO₂ and CH₄ fluxes originating from mounds of two common species of fungus-growing termites, *M. michaelseni* and *M. subhyalinus*, in southern Kenya during periods in the dry and the wet season. As, in the area, both species inhabit a wide range of different environments, termite mounds were measured in two contrasting habitats (open grassland and dense bushland). Distribution of the two species is not completely overlapping, and, thus, in our sampling *M. michaelseni* was dominant at the grassland and *M. subhyalinus* at the bushland site. In Kenyan grasslands, *M. michaelseni* mounds are surrounded by dense networks of foraging tunnels with several openings to soil surface per square meter (Lepage, 1981a; Darlington, 1982) that could also increase soil CO₂ and CH₄ fluxes in mound proximity. Thus, in addition to direct gas fluxes from the mounds, we also measured soil CO₂ and CH₄ fluxes around the mounds. The study objectives were (1) to quantify the gas fluxes from the fungus-growing termite mounds with variable mound volumes and from the soil around the mounds, (2) to study the interactions between the fluxes and different environmental variables, and (3) to observe the diurnal and seasonal variation in mound fluxes.

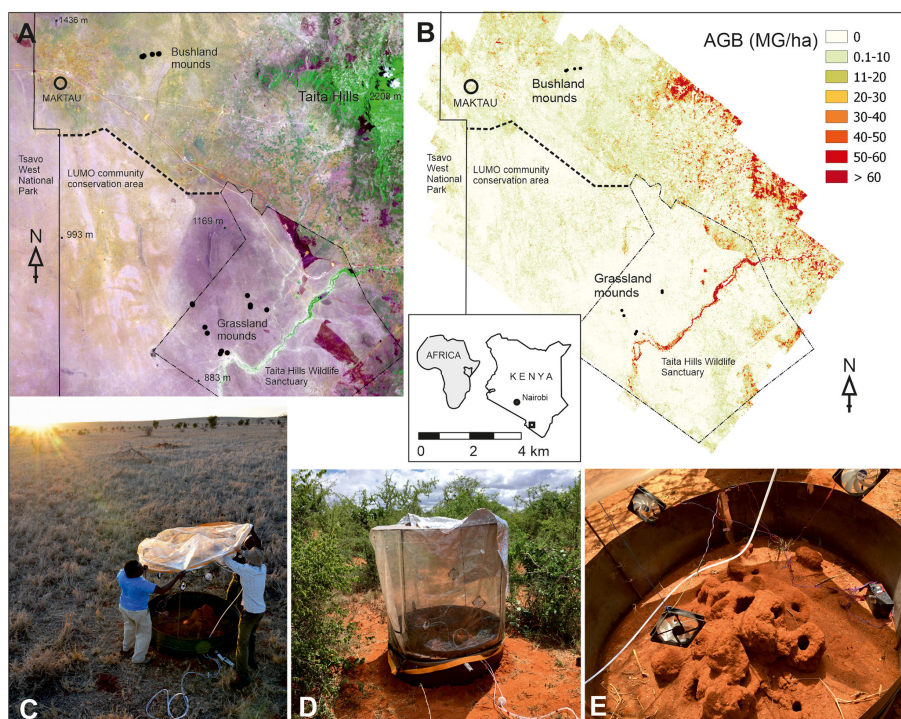


Figure 1. Locations of the measured termite mounds (dots) at two study sites and the Maktau weather station shown in (a) Sentinel-2A satellite imagery (acquired 20 December 2020; magenta color indicate grasslands, while brownish colors indicate bushlands) and (b) an aboveground biomass map (Amara et al., 2020; Pellikka et al., 2018). Chamber measurement at the grassland (c) and the bushland site (d). Metal collar and wire frame of the measurement chamber around an open *M. subhyalinus* mound (e). Copernicus Open Access Hub (ESA, 2015). Photo credits: Petri Pellikka (c) and Markus Jylhä (d, e).

Table 1. Characteristics of the measured *Macrotermes* termite mounds. R is the average mound radius, H is height and V_m is calculated aboveground mound volume (see Sect. 2.2). The status (active or dead) of the colonies was determined after the second measurement campaign by excavation.

Mound ID	Termite species (mound type)	Site location	R (m)	H (m)	V_m (m ³)	Status in April 2017
MR1	<i>M. michaelseni</i> (closed)	Bushland	0.75	0.50	0.256	active
MR2	<i>M. subhyalinus</i> (open)	Bushland	0.65	0.15	0.058	active
MR3	<i>M. subhyalinus</i> (open)	Bushland	0.28	0.33	0.023	dead
MR4	<i>M. subhyalinus</i> (open)	Bushland	0.75	0.45	0.231	active
MR5	<i>M. subhyalinus</i> (open)	Bushland	0.30	0.25	0.020	active
MR6	<i>M. subhyalinus</i> (open)	Bushland	0.40	0.30	0.044	active
S1	<i>M. michaelseni</i> (closed)	Grassland	0.75	0.70	0.259 ^a	active
S2	<i>M. michaelseni</i> (closed)	Grassland	0.65	0.35	0.106 ^a	active
S3	<i>M. michaelseni</i> (closed)	Grassland	0.55	0.30	0.217 ^a	dead
S4	<i>M. michaelseni</i> (closed)	Grassland	0.35	0.40	0.074 ^a	dead
S5 ^b	<i>M. subhyalinus</i> (open)	Grassland	0.75	0.40	0.193 ^a	active
S6	<i>M. subhyalinus</i> (open)	Grassland	0.72	0.15	0.072	dead

^a These values were estimated using a photogrammetric technique. ^b The gas fluxes of this mound were not estimated due to nonlinear concentration time series (Fig. S2).

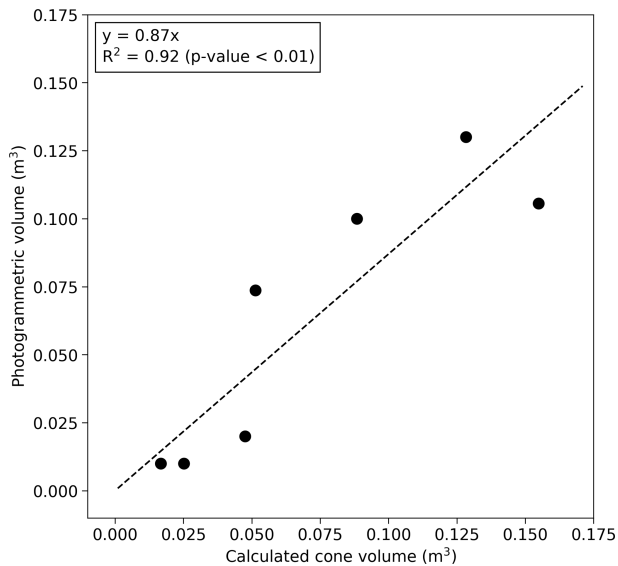


Figure 2. The relationship between the photogrammetrically measured mound volume and calculated cone volume according to Eq. (1). The data points include grassland mounds (S2 and S4) of this study and five additional mounds measured in Vesala et al. (2019b) (Table S1).

2 Materials and methods

2.1 Site description

The chamber measurements were conducted in the lowland areas surrounding the Taita Hills, Kenya (Fig. 1). The mean annual rainfall is 433 mm based on measurements at the Maktau weather station (Räsänen et al., 2020). Termite mounds were measured at bushland and grassland locations that are 15 km apart. The bushland is characterized by over 50 % of thorny shrubs and small *Acacia* spp. and *Commiphora* spp. trees (Wachiye et al., 2020). All termite mounds measured in bushland were located in shaded locations. The grassland site is located at a private game sanctuary for wildlife conservation. The vegetation is characterized by common savanna grasses such as *Chloris roxburghiana* and *Cenchrus ciliaris* and scattered trees (e.g., *Acacia tortilis*, *Albizia anthelmintica*, *Balanites aegyptiaca*). The majority of bushland mounds were open mounds built by *M. subhyalinus*, whereas most of the grassland mounds were closed type and built by *M. michaelseni* (Table 1, Fig. S1 in the Supplement). The grassland ecosystem is assumed to be a result of decades-long wildlife conservation, which has caused a high population of mega-herbivores, namely elephants, which forage for leaves of the trees and bushes, thus destroying the tree cover. The tree cover and aboveground biomass are much higher in the bushland areas, which are not inhabited by elephants, as shown in Fig. 1b (Amara et al., 2020; Pellikka et al., 2018).

2.2 Estimation of mound volume

Volumes of the grassland mounds S1–S5 (Table 1) were measured photogrammetrically by taking a large number of digital images from different positions around the mound (method described in Vesala et al., 2019b). To increase the number of observations, these data were supplemented with five additional comparably sized mounds measured earlier in a close-by area (Vesala et al., 2019b). Linear regression with zero intercept was fitted between the equivalent cone volume and photogrammetric mound volume (Fig. 2). This relationship was used to estimate the volume at the bushland site where the photogrammetric method was not feasible due to the surrounding dense vegetation. The equivalent cone volume was calculated as

$$V_{\text{cone}} = \frac{1}{3}\pi R^2 \times H, \quad (1)$$

where R is the average of north–south and west–east measured radii and H is height. The aboveground termite mound volume (V_{m}) was $0.87 \cdot V_{\text{cone}}$ for mounds that were not sampled using the photogrammetric method. The aboveground termite mound volumes ranged from 0.3 % to 10 % of the total chamber volume.

2.3 Gas flux measurements from termite mounds and soil

CO₂ and CH₄ fluxes were measured using a static chamber method in November 2016 (end of the long dry season) and April 2017 (wet season) (Table S2). The chamber collar was installed before each measurement, and surrounding sand was applied to insulate the collar. The chamber closure time was 15 min, and each mound was measured three times with 5 min breaks in between the repetitions. The mean and standard deviation of the flux were calculated from the three repeated measurements. Daytime flux measurements were made between 10:00 and 16:00 (all times in this paper are given in local time, GMT+3). To study diurnal variation in gas fluxes, the mounds S1 and S2 were measured during at least three different time periods from the evening until the next day with three repeated measurements each time. Mound S1 was measured on 15 November 2016, and mound S2 was measured on 7 November 2016.

The size of the measurement chamber was a compromise between practicality and the typical size of termite mounds in the area. The radius of the chamber was 0.75 m and height was 1.5 m, still excluding the vast majority of *Macrotermes* mounds occurring in the area, which are larger on average. The metal collar height was 40 cm. Four upright-positioned steel rods and an attaching circular steel frame were used to support the cylindrical shape of the custom-made polyvinylchloride sheet. A rubber band was used to seal the polyvinylchloride sheet against the collar. Three people were needed to open and close the chamber. The gas analyzer (LGR Ultra-portable Greenhouse Gas Analyzer Model 915-0011) was

connected to the collar using Swagelok fittings. Chamber air was sampled continuously into the gas analyzer and circulated back to the chamber. The air was sampled inside the chamber using a 2.5 m long Teflon tube which had small holes along its length. The sampling line was attached in a spiral shape by supporting it from the middle points of the supporting steel rods, and it was connected to the inlet of the gas analyzer at the inside wall of the collar. The air inside the chamber was mixed using three 12 cm fans that were hanging in the middle point of the chamber. The gas analyzer recorded concentration every second. Temperature and relative humidity inside the chamber were measured using a Campbell CS215 *T*–RH sensor attached to the collar. A cell-phone timing application (Time Meter) was used to record the precise start and end times of each measurement because the gas analyzer produces one continuous measurement file per day. Also, the manual soil moisture and temperature measurements were noted in the timing application. The notes were exported to a CSV file, which was parsed into numerical form. This procedure enabled us to automate flux calculation from raw data and minimize note-taking errors.

After termite mound measurement, the inlet lines were connected to a small opaque soil chamber (radius 7 cm, height 22 cm) to measure soil CO₂ and CH₄ fluxes around the termite mound. The soil gas flux measurements were made once for two opposing directions at 2, 4 and 6 m distance from the perimeter of the mound. The soil chamber was placed on patches of bare soil to minimize the effect of vegetation. The sampling time was 2 min. One CH₄ flux measurement around S1 mound at 6 m distance during the wet season was discarded because the flux was over 1000 times higher than the mean of other measurements around the mound (most likely due to an underground termite nest).

Methane and carbon dioxide fluxes were calculated as

$$F = \frac{PV}{RTA} \frac{dC}{dt}, \quad (2)$$

where $V = V_c - V_m$ for termite mound measurements and $V = 0.0034 \text{ m}^3$ for the soil measurements, $V_c = 2.65 \text{ m}^3$ is the termite chamber volume, P is pressure (Pa), A is the area of the chamber (m^2), R is the gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$) and T is the air temperature in kelvins. The slope of concentration increase $\frac{dC}{dt}$ ($\mu\text{mol mol}^{-1} \text{ s}^{-1}$) was determined from a linear regression of the 1 Hz concentration measurements.

2.4 Environmental measurements

The soil moisture and temperature were measured manually near the mound during each chamber measurement. A handheld soil moisture probe, the Campbell Scientific HydroSense II, was used to measure surface soil moisture. Soil temperature was measured using a stainless-steel temperature probe. Termite nest temperature measurements were used from an earlier study (Vesala et al., 2019b), where small

temperature sensors (iButton Thermochron DS1922L) were placed next to the first fungus combs that were encountered by digging a small hole to the mound. Nest temperature measurements made at the grassland location in 2015 from large open and closed mounds (IDs TS56 and TS19 in Vesala et al., 2019b) were used. These nest temperatures were compared to continuous soil temperature measurements at the Maktou weather station. The weather station soil temperature (Campbell Scientific CS650) probe measured at 30 cm depth inside a fenced area.

The CO₂ and CH₄ fluxes measured for each mound were combined with aboveground biomass (AGB) data, assessed using airborne laser scanning and field measurements (Amara et al., 2020; Pellikka et al., 2018). This combination aimed to investigate the working hypothesis that fluxes might be related to the C : N ratios of termite diets that correlate negatively with vegetation density in the area (Vesala et al., 2022b).

2.5 Statistical analysis

Simple linear regression was used to test the statistical relationship between the measured fluxes and explanatory variables. The relationship between fluxes and mound volume was tested separately during the dry season ($n = 11$) and wet season ($n = 7$). The relationship of the environmental variables to the fluxes and to the ratio of CH₄ to CO₂ flux was tested using all the measurements ($n = 18$). The mound flux–AGB relationship was tested with simple linear regression during the dry season ($n = 11$). Statistical analyses were done using the SciPy Python package (Virtanen et al., 2020).

3 Results

3.1 Environmental conditions

Total precipitation before the first measurement campaign was 10 mm from September to early November (Fig. 3), meaning that the short rainy season had not yet started. The precipitation between the campaigns was 153 mm, corresponding to a typical dry-year amount. The annual mean precipitation during this period between the campaigns was 287 mm, with 154 mm standard deviation calculated from 6 years of precipitation measurements at the weather station. The surface soil moisture was twice as high during the second campaign compared to the first campaign (Fig. 3a). The wind speed had a consistent trend during the measurement campaign days, showing a minimum around 06:00 and a maximum during the early afternoon. Revisiting the data collected in Vesala et al. (2019b) shows that termite mounds in the area have a consistent diurnal temperature rhythm, with the maximum nest temperature being always around 20:00, whereas the soil temperature at 30 cm depth has a maximum around midnight.

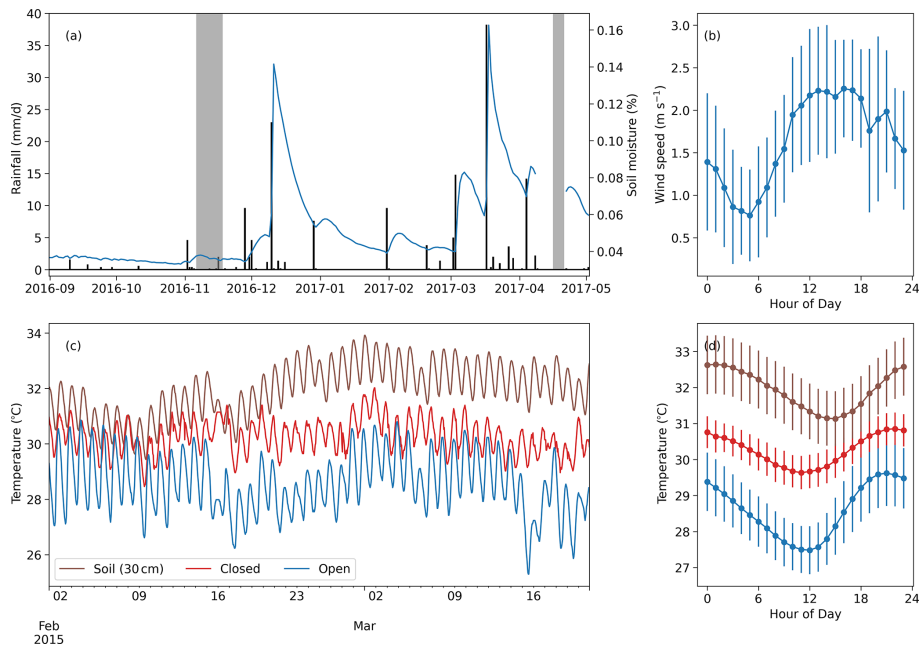


Figure 3. Meteorological data from the study area. **(a)** Time series of daily rainfall (black bars) and daily mean soil moisture at 10 cm depth (blue line). The gray blocks indicate the days of the two measurement campaigns. **(b)** Diurnal mean and standard deviation of the wind speed during the first measurement campaign. **(c)** Soil temperature at 30 cm depth compared with nest temperatures within an open (TS56) and a closed (TS19) termite mound at the grassland site (measured in 2015 during a period of no rainfall; Vesala et al., 2019b). **(d)** Diurnal mean of the soil and nest temperatures during the time period presented in **(c)**. The error bars indicate 1 standard deviation.

3.2 Mound CO₂ and CH₄ fluxes

The mean CO₂ fluxes ranged from 35 to 2100 mg CO₂-C m⁻² h⁻¹ for closed *M. michaelseni* mounds and from 120 to 800 mg CO₂-C m⁻² h⁻¹ for open *M. subhyalinus* mounds (Fig. 4). The mean CO₂ flux was 1000 mg CO₂-C m⁻² h⁻¹ for the grassland site and 380 mg CO₂-C m⁻² h⁻¹ for the bushland site from the active mounds listed in Table 1. The largest CO₂ fluxes were measured during the dry season at the grassland site. The site level mean CO₂ flux decreased 64 % at the grassland and increased 41 % at the bushland from the dry to wet season. The lowest CO₂ fluxes were registered from the grassland mounds S3 and S4, which turned out to be dead when excavated after the second measurement campaign (Table 1).

The mean CH₄ fluxes ranged from 0.02 to 3.7 mg CH₄-C m⁻² h⁻¹ for closed *M. michaelseni* mounds and 0.06 to 1.2 mg CH₄-C m⁻² h⁻¹ for open *M. subhyalinus* mounds. The ratio of mound CH₄ flux to mound CO₂ flux ranged from 0.4×10^{-3} to 2.8×10^{-3} , with no clear difference between termite species or mound volume. The mean ratio was 1.6×10^{-3} for grassland and 1.2×10^{-3} for bushland sites. The ratio of CH₄ flux to CO₂ flux reduced by 36 % at the grassland and 49 % at the bushland site from dry to wet season. The dry-season mound CO₂ and CH₄ fluxes were not significantly correlated with the AGB (Fig. S3).

Based on diurnal measurements in two closed mounds, the largest CO₂ flux was measured around noon at the mound S1 (Fig. 5). However, the CO₂ flux also increased at midnight for both S1 and S2 mounds. For both mounds, the difference between the maximum nighttime CO₂ flux compared with the daytime maximum was less than 2 standard errors. For the S1 mound, the maximum flux value was 1.4 times the daily average for CO₂ and 1.5 times that for CH₄. The nighttime peak in the CO₂ flux coincides with the maximum soil temperature at 30 cm depth at midnight (Fig. 3d). The diurnal cycle of the ratio of CH₄ to CO₂ flux showed one peak around noon for the S1 mound and at 18:00 for S2, which was not sampled at noon. These peaks are due to the increase in CH₄ flux in proportion to CO₂ flux during the daytime.

3.3 Drivers of mound CO₂ and CH₄ fluxes

The mean mound CO₂ flux was significantly correlated with the termite mound volume during the wet season ($R^2 = 0.96$, p value < 0.01; Fig. 6b), while the relation was not statistically significant during the dry season ($R^2 = 0.12$, p value = 0.30; Fig. 6a). The CO₂ flux and CH₄ flux were not explained by surface soil moisture or soil temperature during the dry or wet season (Fig. S4). The soil moisture values were low for most mounds due to low precipitation amounts during the wet season. The mean CO₂ and CH₄ fluxes were linearly related (Fig. 6c). The ratio of CH₄ and CO₂ fluxes had no significant correlation with environmental variables

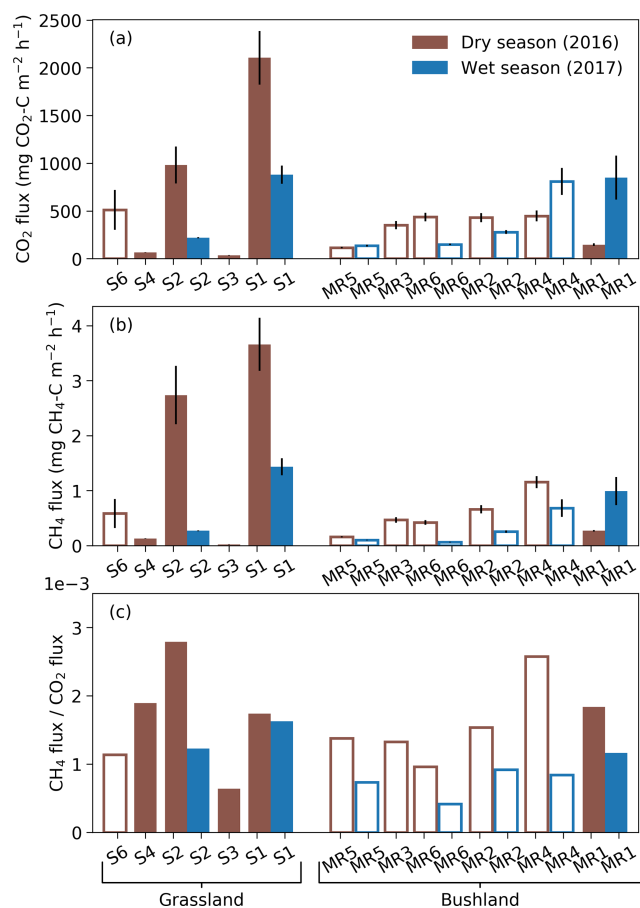


Figure 4. Mean termite mound CO₂ (a) and CH₄ (b) fluxes and their relationship, i.e., CH₄-to-CO₂ flux ratios (c), measured from grassland and bushland sites during dry and wet seasons. Each mound was sampled once during each season by three repeated measurements. All measurements shown in this figure took place between 10:00 and 16:00. Error bars in (a) and (b) indicate standard errors. Hollow bars represent open and solid bars closed mounds. Termite colonies that were found to be dead in April 2017 (S3, S4, S6 and MR3) were left out from the wet-season measurements. The mounds are presented in order of increasing volume for each site.

and only a weak correlation with the magnitude of the CH₄ flux ($R^2 = 0.34$, p value = 0.01). The CH₄ flux was significantly correlated with the mound volume during the wet season ($R^2 = 0.85$, p value < 0.01; Fig. 6e). The standard deviation of the CO₂ flux increased linearly with the mean flux magnitude (Fig. 6f).

3.4 Soil CO₂ and CH₄ fluxes around termite mounds

The soil CO₂ and CH₄ fluxes around the mounds were sampled to determine the effect of termites on soil fluxes around the mound. The site mean soil CO₂ and CH₄ were always higher at a 2 m distance compared to 4 and 6 m distances from the perimeter of the mound (Fig. 7 and Table 2). The mean soil CO₂ flux at the bushland was only 29% of the

mean soil flux at the grassland. The dry-season means of all soil CO₂ flux measurements were 62 and 27 mg CO₂-C m⁻² h⁻¹ at 2 and 4 to 6 m distance (Table 2). The difference between soil CO₂ flux at 2 and 4 to 6 m distance from the mound was less pronounced during the wet season. The mean mound CO₂ fluxes were a factor of 25 and 6 higher in the dry and wet seasons, respectively, in comparison to the 4 to 6 m distance soil CO₂ fluxes (Table 2). The dry-season means of all soil CH₄ flux measurements were 0.07 and 0.02 mg CH₄-C m⁻² h⁻¹ at 2 and 4 to 6 m distance (Table 2). The dry-season mean soil CH₄ flux was positive at the grassland and bushland sites, whereas the mean wet-season flux was nearly zero with most fluxes being negative (Figs. 7, S5 and S6). The soil CH₄ fluxes at a 2 m distance from the mound are much higher in proportion to fluxes at a 4 m distance at the grassland site compared to the bushland site (Fig. 7).

4 Discussion

4.1 Mound CO₂ and CH₄ fluxes

The measured CO₂ fluxes (from 35 to 2100 mg CO₂-C m⁻² h⁻¹) were in a similar range to that reported in two earlier comparable studies, where chamber measurements were used to study greenhouse gas emissions from termite mounds in Australia (up to 1600 mg CO₂-C m⁻² h⁻¹; Jamali et al., 2013) and Amazonia (190–2200 mg CO₂-C m⁻² h⁻¹; van Asperen et al., 2021). Methane fluxes ranged from 0.02 to 3.7 mg CH₄-C m⁻² h⁻¹ and were 2–20 times lower than those reported in earlier studies (0.4–6 mg CH₄-C m⁻² h⁻¹; van Asperen et al., 2021; Jamali et al., 2013). In most fungus-growing species studied so far, workers have exhibited relatively high CH₄ production rates (Rouland et al., 1993; Zhou et al., 2023). Thus, the lower CH₄ emissions, in relation to CO₂, observed in this study compared to mounds of previously studied termite species (which have all been termite types other than fungus-growing) could be attributed to the fact that a large proportion of the total CO₂ in our measurements originated from the aerobic fungus gardens which do not produce CH₄ (Darlington et al., 1997). Our biased sampling design, with one termite species dominating the bushland and the other the grassland site, does not allow us to reliably compare the two termite species. However, the relatively similar gas fluxes of the two species or mound types (Figs. 4 and 6) imply that they do not exhibit major differences in terms of CO₂ or CH₄ emissions. This result is also highly expected as the two termite species are closely related (Bagine et al., 1994; Vesala et al., 2017), have very similar population sizes and compositions (Darlington, 1984), and also share their dietary niches (Vesala et al., 2022b). The highest fluxes of both gases were registered from two closed mounds of *M. michaelsoni* in the grassland. It is important to note that we did not obtain any information about the pop-

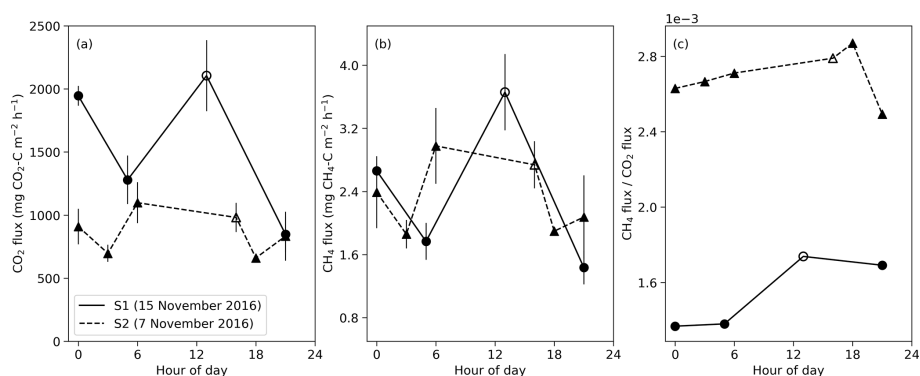


Figure 5. Diurnal variation in CO₂ and CH₄ fluxes during the 2016 dry season for closed mounds S1 (measured 15 November) and S2 (measured 7 November). Error bars indicate the standard error calculated from three repeated measurements. The hollow symbols indicate daytime measurements that were done 9 d before nighttime measurements for S1 and 1 d before for S2.

Table 2. Mean CO₂ and CH₄ fluxes of termite mounds and surrounding soils during the dry and wet season. Data include all active mounds measured at the grassland and the bushland sites. The range of measured values for each group is given in parentheses.

	CO ₂ flux (mg CO ₂ -C m ⁻² h ⁻¹)	CH ₄ flux (mg CH ₄ -C m ⁻² h ⁻¹)
Dry season		
Termite mound	666 (116 to 2105)	1.294 (0.159 to 3.659)
Soil at 2 m distance	62 (10 to 122)	0.065 (0.001 to 0.186)
Soil at 4–6 m distance	27 (6 to 123)	0.020 (–0.003 to 0.108)
Wet season		
Termite mound	475 (136 to 881)	0.542 (0.062 to 1.433)
Soil at 2 m	90 (29 to 243)	0.006 (–0.034 to 0.104)
Soil at 4–6 m	83 (15 to 251)	–0.004 (–0.032 to 0.065)

ulation sizes, and, thus, these two *M. michaelsoni* mounds may simply have housed larger termite populations with correspondingly larger fungus gardens than the studied *M. subhyalinus* mounds.

As found by previous studies, the mound outer dimensions of both *Macrotermes* species correlate positively with the size of the termite population and the total biomass of fungus combs (Darlington and Dransfield, 1987; Darlington, 1990). Thus, the fluxes of metabolic gases should logically also show correlation with the mound volume. However, considering the high variation associated with the fluxes, it seems obvious that if the sizes of the studied mounds are too close to each other, the relationships between the mound volume and gas fluxes are difficult to detect. In this study, the mound volumes ranged from 0.023 to 0.259 m³ (Table 1), including notably more size variance than the earlier comparable studies (0.02 to 0.077 m³) (Jamali et al., 2013; van Asperen et al., 2021). We found that the measured CO₂ fluxes were linearly correlated with the termite mound volume during the wet season (Fig. 6b) but that the relationship was more indistinct during the dry season (Fig. 6a). Determining the relationship between the mound volume and gas fluxes more reliably would require measurements from still much larger

mounds, which however is problematic due to technical limitations. In East Africa, average volumes of *Macrotermes* mounds range from 2 to 3 m³ depending on the geographical area, and the maximum volumes can exceed 12 m³ (Pomeroy, 1977). Also in our study area, *M. subhyalinus* mounds with volumes of up to 6 m³ have been recorded (Vesala et al., 2019b), which is more than 20 times the volume of the largest mound measured here. Thus, the reported average flux values in this study are representative of the smallest *Macrotermes* mounds, but when scaling the results to the level of larger *Macrotermes* mounds (or calculating area-based estimates), the effect of mound volumes should be considered to avoid serious underestimations.

The mounds at the grassland and bushland sites had contrasting seasonality of CO₂ fluxes with a 64 % decrease at the grassland and 41 % increase at the bushland site from the dry to wet season (Fig. 4). This seasonal change is smaller than what has been measured for grass- and wood-feeding termites in Australia, which had a 90 % decrease in CO₂ flux from the wet to dry season (Jamali et al., 2013). For fungus-growing termites, intra-annual variation can be caused by the annually produced brood of alates that, in Kenyan *M. michaelsoni*, reaches its maximum biomass just

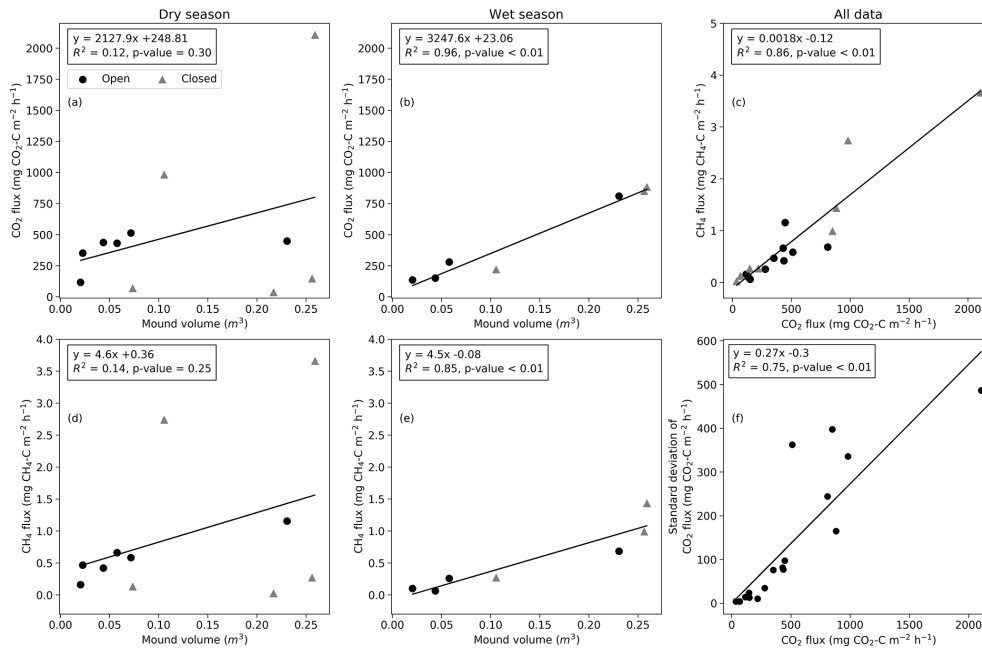


Figure 6. The relationship between the mound volume and mean CO₂ and CH₄ fluxes during dry and wet seasons (a–b, d–e). (c) The relationship between CH₄ and CO₂ fluxes. Circles indicate open mounds, and triangles indicate closed mounds. (f) The relationship between the standard deviation and mean of the CO₂ flux calculated from three repeated measurements.

before swarming in October–November (Darlington, 1986). Correspondingly, storage of fungus combs is typically at its largest soon after the long rains in May–June, after which it starts to decline (Lepage, 1981b). Such seasonal changes in biomasses of different nest components could cause intra-annual variation in gas fluxes. Additionally, differences in food quality could potentially affect nest CO₂ emissions. Within our study area, fungus combs of grassland mounds had significantly lower nitrogen contents than those situated in more wooded habitats, suggesting that, on average, grass-based diets have lower nutritional value than wood-based diets (Vesala et al., 2022b). Such differences in food nutritional quality may reflect nest CO₂ fluxes as more carbohydrates need to be eliminated to accumulate sufficient proteins from low-nitrogen food sources compared to those with a higher nitrogen content (Higashi et al., 1992). Most likely, food nutritional quality also changes during the year, with the changes possibly being more dramatic in grasslands, which have fewer and more contested food sources available for termites than bushlands with their more abundant and diverse food sources. Such local differences in food availability and quality could potentially lead to different seasonality in nest living biomass, which might explain the contrasting seasonal changes observed in CO₂ fluxes between the two habitats and the higher intra-annual variance in gas fluxes observed in grassland compared to those in bushland mounds. We note that our seasonal sampling was limited to one measurement period during the dry and wet season, which does not capture the seasonal variability throughout the whole year.

There was a clear decrease in CH₄-to-CO₂ flux ratios from dry-season to wet-season measurements at both study sites. This difference might be partially explained by the smaller biomass of fungus gardens (which produce only CO₂) in relation to that of termites (which produce both CO₂ and CH₄) during the dry season than during wet season (Darlington, 1986). Another explanation could be linked to the activity of methanotrophic bacteria within mound structures and/or surrounding soils that have been reported to consume a notable proportion of CH₄ produced in the nests of several mound-building termite species (Sugimoto et al., 1998; Nauer et al., 2018). Although the humidity within termite nests remains at a constantly high level throughout the year (Lüscher, 1961; Agarwal, 1980), water content in surrounding soils and mound soil structures can decrease notably during periods with low precipitation (Jamali et al., 2011; Chen et al., 2019) (Fig. 3a). Dry soil conditions during periods with low precipitation most likely limit microbial activity (including the methane-oxidizing bacteria) within termite mound walls and surrounding soils, whereas increases in soil water content after rains could oppositely lead to increased microbial activity and enhanced methanotrophy. This result is also in congruence with our measurements of nest internal gas concentrations within *M. michaelseni* mounds, which tended to have higher CH₄-to-CO₂ concentration ratios during the driest period compared to seasons with higher soil moisture (Vesala et al., 2023).

Four mounds that were measured during the first campaign were determined to be dead at the end of the second cam-

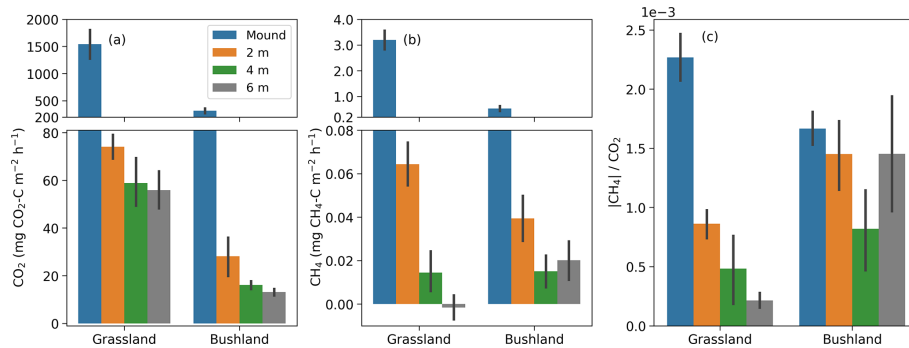


Figure 7. (a–b) Mean CO₂ and CH₄ fluxes from termite mounds and surrounding soils during the dry season. Soil fluxes were always measured on two opposite sides of the mounds at distances of 2, 4 and 6 m from the mound perimeter (three repeated measurements at each specific location). Mean values and standard errors are calculated from all (dry-season) measurements at the site. (c) The ratio of the absolute value of CH₄ and CO₂ flux.

paign (Table 1). The exceptionally low CO₂ fluxes measured from the mounds S3 and S4, however, strongly suggest that these two mounds were already dead, or at least seriously weakened, during the first measurement campaign. An average lifespan of a *Macrotermes bellicosus* colony is thought to be around 4 years, whereas the mounds that they build persist typically for much longer (Pomeroy, 1976). However, a recent long-term monitoring study in Namibia found that 57 % of initially active *M. michaelseni* mounds were still active after 12 years (Wildermuth et al., 2022), demonstrating that some colonies can live much longer. These authors also found that small mounds were more likely to be dead than large mounds after 12 years, showing that large well-established colonies are less vulnerable to disruptions. Hence, dead *Macrotermes* mounds are a common feature in many landscapes, and for example, in many places within our study area, their number exceeds that of the active mounds (Vesala et al., 2017). Thus, determination of the proportion of active mounds in a landscape is a necessary precondition for ecosystem-level termite flux estimations for all such termite species that build persistent soil mounds.

4.2 Diurnal variation

Diurnal variations in CO₂ and CH₄ fluxes were measured in two closed *M. michaelseni* mounds over a period of 1 d. The afternoon peaks were on average 46 % and 57 % higher compared to the daily averages for CO₂ and CH₄ fluxes, respectively (Fig. 5). Our observations are in congruence with the nest internal CO₂ concentration measurements by Ocko et al. (2017), who found that CO₂ levels within *M. michaelseni* nests in Namibia peaked in the early afternoon, whereas concentrations at nighttime and especially soon after sunrise were somewhat lower. A corresponding trend has also been documented from outflow chimneys of Kenyan *Macrotermes jeanneli*, which had the highest CO₂ concentrations at 15:00 and the lowest around 03:00–06:00 (Darlington et al., 1997). The daily maximum CO₂ flux in the early afternoon

found in this study (Fig. 5) agrees well with these earlier data, suggesting that the internal CO₂ concentrations within *M. michaelseni* mounds show similar diurnal patterns to the mound CO₂ fluxes. A positive relationship between the nest internal gases and mound fluxes has been demonstrated for a few mound-building termites (Khalil et al., 1990; Jamali et al., 2013). In agreement with our CH₄ measurements, a similar peak in CH₄ fluxes soon after midday was documented by Jamali et al. (2011) from mounds of three Australian termite species.

The lower CO₂ and CH₄ fluxes during the nighttime compared to daytime fluxes are probably mostly associated with the diurnal movements of termites: after sunset a proportion of termite workers and soldiers leave the nest due to foraging activities, thus decreasing the CO₂ and CH₄ production within the nest. During the night, termites also open the numerous foraging passages that directly connect the nest interior space to the soil surface near the mound (Lepage, 1981a; Darlington, 1982). This might lead to enhanced nest ventilation and could additionally affect gas fluxes originating from the mound. In addition to the afternoon flux peaks, we registered another peak in both CO₂ and CH₄ fluxes at midnight, which was not documented in earlier studies (Fig. 5). However, more measurements would be needed to understand the drivers of diurnal variation because we measured only two mounds in one location during the dry season. It would be especially useful to continuously measure the mound internal gas concentrations together with the mound fluxes.

In addition to the daily cycles of CO₂ and CH₄ fluxes, the relationship between CO₂ and CH₄ showed a clear diurnal pattern. The mound CH₄-to-CO₂ flux ratio was higher during the daytime than during the nighttime measurements (Fig. 5c). This result also supports the hypothesis that the termite population within the mound is smaller during the nighttime than during the daytime due to foraging activity. The metabolism of termites (together with gut microbiota) produces both CH₄ and CO₂, but a major proportion of CO₂

originates from the fungal gardens, which are sessile and do not produce CH₄ (Darlington et al., 1997). Thus any changes in termite biomass within the nest should inevitably reflect the mound CH₄-to-CO₂ flux ratios.

After all, the diurnal changes in gas fluxes measured in this study were relatively small. This underlines the fact that plant biomass degradation within mounds of fungus-growing termites is a continuously ongoing process and shows only minor diurnal changes. Therefore, a large proportion of termites also stay constantly in the nest, taking care of the fungal gardens, and thus the diurnal biomass changes within the nest are relatively small. The stable diurnal flux variability is in line with the stable humidity and temperature conditions within mounds of fungus-growing termites. Constant temperature and high humidity are of key importance for the fungal *Termitomyces* symbionts, which have a relatively narrow range of optimal microclimatic conditions (Lüscher, 1961; Thomas, 1981; Wood and Thomas, 1989).

4.3 Soil CO₂ and CH₄ fluxes around the mounds

The soil CO₂ and CH₄ fluxes were always higher close to the mound (at 2 m distance from the mound perimeter) compared to further distances (4 to 6 m from the mound perimeter) (Fig. 7). The mean soil CO₂ flux from 4 to 6 m distance was 27 mg CO₂-C m⁻² h⁻¹ during the dry season, which is comparable to the measured soil CO₂ flux seasonal minimum of 20 mg CO₂-C m⁻² h⁻¹ at the grassland site (Wachiye et al., 2020). Correspondingly, the mean soil CH₄ fluxes at 4 to 6 m distances from the mounds were 0.020 and -0.004 mg CH₄-C m⁻² h⁻¹ in the dry and wet seasons, respectively (Table 2), which is similar to an earlier field study where the soil CH₄ fluxes were slightly negative with no seasonality at the grassland site (Wachiye et al., 2020). Our results thus demonstrate that, although the majority of the gas exchange between termite nests and ambient air takes place through the mound structures, a small proportion of gases also leave the nest via adjacent soils at up to 2 m distance. These results differ from the earlier measurements in soil-feeding termites in the Amazon, which showed enhanced soil fluxes around the mound only up to 0.5 m from the perimeter of the mound (van Asperen et al., 2021). The difference can be largely explained by the much larger size of the measured mounds in our study, but it most likely also reflects some fundamental differences between the mounds of soil-feeding and fungus-growing termites. While within soil-feeding species the mound itself acts as a nest for the colony, mounds built by especially *Macrotermes michaelseni* are more or less empty of insects and the actual nests are largely located underground below the mounds (Noirot and Darlington, 2000; Korb, 2011). Thus, the actual nests of fungus-growing termites may be much larger and extend to a somewhat wider area than their aboveground mounds. *Macrotermes* termites also have an extensive network of foraging tunnels surrounding their nest, with the largest radial tunnels having widths of 4–7 cm (Darling-

ton, 1982). Such structures increase soil porosity around the mounds, enhancing water infiltration (Jouquet et al., 2011) and, obviously, also enabling some gas exchange to occur through the soil.

Soil CH₄ fluxes around the mounds were systematically lower during the wet than during the dry season at all three distances (Table 2, Figs. S5 and S6). As the CH₄ fluxes from the soils unaffected by termite mounds are shown to be slightly negative in grasslands of the same ecosystem (Wachiye et al., 2020), we are confident that termites were the main source of the soil CH₄ fluxes detected in the current study. Seasonal changes in soil fluxes could thus be caused by changes in either the number of termites or their CH₄ production rates or methane oxidation. During the rainy seasons, termite foraging activity is at its lowest (Lepage, 1981a), which could potentially decrease CH₄ fluxes in mound surroundings as the foragers move from foraging tunnels towards the nests. This should, however, concurrently increase the CH₄ fluxes from the mounds, which was not observed. Instead, we also found the mound CH₄ fluxes to be lower during the rainy season than during the dry season. Thus, we suspect that, similarly to that discussed above in the case of mound fluxes, the soil CH₄ fluxes near the mounds are largely regulated by CH₄ oxidation within the soils surrounding the mounds, which could be enhanced by the increased soil water content after rains (Fig. 3a).

5 Conclusions

The CO₂ and CH₄ fluxes from fungus-growing termite mounds show diurnal and seasonal variation, albeit lower in magnitude than their wood-, grass- and soil-feeding counterparts. The likely reason for this stability is the temperature and humidity control needed for the fungal symbiont. The CO₂ and CH₄ fluxes scale with mound volume over a large volume range during the wet season. The soil flux measurements around the mound also show that the soil CO₂ and CH₄ fluxes are significantly affected by the termites at a 2 m distance from the perimeter of the mound. The fungus-growing termite mounds have lower CH₄ fluxes per unit of CO₂ than soil- and grass-feeding termites, which is due to the plant matter decomposition by *Termitomyces* fungi that do not emit CH₄. For upscaling the greenhouse gas fluxes originating from mounds of fungus-growing termites, the work highlights the need to include the mound volume in the models, as well as to consider the potentially high proportion of inactive termite mounds in the landscape.

Data availability. The data used in this study are available online: <https://doi.org/10.6084/m9.figshare.21739484.v1> (Räsänen et al., 2022).

Supplement. The supplement related to this article is available online at: <https://doi.org/10.5194/bg-20-4029-2023-supplement>.

Author contributions. MR, PM, MJ, PP and JR conducted the measurements; MR, RV, PR, LA, PP and JR designed the analysis; all authors contributed to the final version of the manuscript.

Competing interests. The contact author has declared that none of the authors has any competing interests.

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