



The relationships between termite mound CH₄/CO₂ emissions and internal concentration ratios are species specific

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Abstract. We investigated the relative importance of CH₄ and CO₂ fluxes from soil and termite mounds at four different sites in the tropical savannas of northern Australia near Darwin and assessed different methods to indirectly predict CH₄ fluxes based on CO₂ fluxes and internal gas concentrations.

The annual flux from termite mounds and surrounding soil was dominated by CO₂ with large variations among sites. On a carbon dioxide equivalent (CO₂-e) basis, annual CH₄ flux estimates from termite mounds were 5- to 46-fold smaller than the concurrent annual CO₂ flux estimates. Differences between annual soil CO₂ and soil CH₄ (CO₂-e) fluxes were even greater, soil CO₂ fluxes being almost three orders of magnitude greater than soil CH₄ (CO₂-e) fluxes at site. The contribution of CH₄ and CO₂ emissions from termite mounds to the total CH₄ and CO₂ emissions from termite mounds and soil in CO₂-e was less than 1 %.

There were significant relationships between mound CH₄ flux and mound CO₂ flux, enabling the prediction of CH₄ flux from measured CO₂ flux; however, these relationships were clearly termite species specific.

We also observed significant relationships between mound flux and gas concentration inside mound, for both CH₄ and CO₂, and for all termite species, thereby enabling the prediction of flux from measured mound internal gas concentration. However, these relationships were also termite species specific. Using the relationship between mound internal gas concentration and flux from one species to predict mound fluxes from other termite species (as has been done in the

past) would result in errors of more than 5-fold for mound CH₄ flux and 3-fold for mound CO₂ flux.

This study highlights that CO₂ fluxes from termite mounds are generally more than one order of magnitude greater than CH₄ fluxes. There are species-specific relationships between CH₄ and CO₂ fluxes from a mound, and between the inside mound concentration of a gas and the mound flux emission of the same gas, but these relationships vary greatly among termite species. Thus, there is no generic relationship that will allow for the accurate prediction of CH₄ fluxes from termite mounds of all species, but given the data limitations, the above methods may still be used with caution.

1 Introduction

Savannas cover 20 % of the global land surface and are recognized for producing almost 30 % of global net primary production (Grace et al., 2006; Hutley and Setterfield, 2008), thus playing an important role in the global carbon cycle. An important component of the carbon and greenhouse gas (GHG) balance of savanna ecosystems is the exchange of methane (CH₄). Methane exchange in tropical savannas is dominated by fire emissions (Russell-Smith et al., 2009), with soil-derived fluxes being of smaller magnitude. Soil-derived CH₄ fluxes are the net product of soil CH₄ oxidation (Livesley et al., 2011) by methanotrophic bacteria under aerobic soil conditions and soil CH₄ production by methanogenic bacteria under anaerobic soil conditions and from termite gut bacteria (Jamali et al., 2011a).

Within the savanna landscape, seasonally inundated soils or ephemeral wetlands are likely to be a significant source of CH₄ emission into the atmosphere, although the magnitude of this emission is unknown for north Australian savannas. Many of these processes are poorly quantified, both spatially and temporally, which leads to large uncertainties regarding the regional- to global-scale methane budget of savannas (Brümmer et al., 2009).

Termites play a critical role in nutrient cycling in savannas, particularly Australian savannas, which often lack dominant grazing and browsing mega-fauna, but these termites can also be a significant source of greenhouse gas emissions. Emissions of CH₄ from termites are usually highlighted more than emissions of CO₂ (Bignell et al., 1997; Fraser et al., 1986; Jamali et al., 2011a, b, c; MacDonald et al., 1998; Sanderson, 1996) because of their significant contribution to the CH₄ balance of savanna ecosystems as compared to their negligible contribution to savanna CO₂ balance. For example, in an African savanna, mound CH₄ emissions measured from one termite species contributed 8.8 % to the total (soil + mounds) CH₄ emissions of that landscape, whereas termite CO₂ emissions contributed 0.4 % to the total (soil + mounds) CO₂ emissions (Brümmer et al., 2009). In this study, termite mound emissions of CH₄ were an order of magnitude smaller than termite mound emissions of CO₂ (Brümmer et al., 2009). As such, it is important to investigate whether the relative contribution of CH₄ and CO₂ emissions is consistent among termite species across savanna landscapes.

There is a general consensus that termite mounds are a large point source of CH₄ and CO₂ when compared to adjacent soils (Brümmer et al., 2009; Jamali et al., 2011b; Khalil et al., 1990; MacDonald et al., 1998; Seiler et al., 1984), but their contribution at plot to site and regional scales is highly uncertain because of variable mound density and species differences. There are limited studies that have investigated CH₄ fluxes from termites in the field, particularly in the tropics, due to the challenges associated with making such measurements, which rely on specialised chamber installations often in remote locations. An indirect method for estimating CH₄ fluxes from intact termite mounds could be based on the relationship between mound CO₂ flux and mound CH₄ flux. Fluxes of CO₂ can be measured more cheaply and relatively easily using an infrared gas analyser (IRGA), whereas CH₄ fluxes are most often measured through conventional syringe gas sampling and concentration analysis through gas chromatography back in a laboratory.

In a laboratory experiment, Jamali et al. (2011c) demonstrated that CH₄ and CO₂ emissions from termites (not mounds) of *Microcerotermes nervosus* species were a strong function of termite biomass, which also suggests a correlation between CH₄ and CO₂ emissions from termites and termite mounds. If true, such a relationship will make it possible to use “easier-to-measure” CO₂ fluxes for predicting mound CH₄ fluxes.

Another indirect method for estimating mound CH₄ flux could be based on the relationship between mound CH₄ flux and CH₄ concentration inside that mound, first used by Khalil et al. (1990), as below:

$$F = \lambda (C_m - C_0), \quad (1)$$

where F is mound CH₄ flux, C_m and C_0 are CH₄ concentrations inside mound and in ambient air outside the mound, respectively, and λ is a constant derived from this equation. The constant λ calculated using Eq. 1 is then used to estimate mound CH₄ flux from termite mounds for which only C_m and C_0 are measured in field. Khalil et al. (1990) calculated a λ value using field measurements of one termite species and used it to estimate mound CH₄ fluxes from different termite species, thus assuming that the relationship between mound CH₄ flux and CH₄ concentration inside a mound is consistent among different species. This assumption may not be true as the mound structure can be variable for different termite species. The same approach (Eq. 1) may also be used to predict mound CO₂ fluxes but with the same uncertainty for the mounds of different termite species. Additionally, given the possible correlation between mound CH₄ flux and mound CO₂ flux, we also hypothesize a correlation between mound CH₄ flux and CO₂ concentration inside mounds which should enable the prediction of mound CH₄ flux by only measuring CO₂ concentration inside a mound. It is important to investigate the relationships of gas concentration and mound flux, and the validity of these relationships across the mounds of different termite species.

The objectives of our study were (1) to study the relative importance of CH₄ and CO₂ emissions from termite mounds at four savanna sites with variable mound density and termite species distribution; (2) to study the relative importance of CH₄ and CO₂ fluxes from soils at four savanna sites; (3) to investigate the relationship between mound CO₂ flux and mound CH₄ flux; (4) to investigate the relationship between inside-mound concentrations of CH₄ and CO₂ and their respective mound fluxes; (5) to investigate the relationship between inside-mound CO₂ concentration and mound CH₄ fluxes.

2 Materials and methods

2.1 Site characteristics

This study was conducted at 50 m × 50 m plots, one each in four savanna locations near Darwin in the Northern Territory, Australia. Site 1 was located at CSIRO's Tropical Ecosystems Research Centre (TERC) on the outskirts of Darwin city and is dominated by *Eucalyptus miniata* A. Cunn. ex Schauer, and *Eucalyptus tetradonta* F. Muell. trees over an understorey of annual/perennial C4 grasses with a thick litter layer. TERC, with a tree basal area of 16.8 m² ha⁻¹ (Table 1), has been protected from fires for > 20 yr (R. Eager,

Table 1. Site characteristics including location, tree basal area, litter mass, and soil bulk density; standard errors of the mean in parentheses.

Site	Location	Tree basal area (m ² ha ⁻¹)	Litter mass (kg m ⁻²)	Soil bulk density (g cm ⁻³)
TERC	12°24′ S, 130°55′ E	16.8	0.84 (0.06)	1.27 (0.02)
CDNP	12°27′ S, 130°50′ E	10.9	0.92 (0.04)	1.57 (0.03)
HS-savanna	12°29′ S, 131°00′ E	4.2	0.12 (0.05)	1.79 (0.02)
HS-wetland	12°31′ S, 131°07′ E	1.5	0.00 (0.00)	1.55 (0.02)

Table 2. List of mound-building termite species collected from the 50 m × 50 m plots at four sites.

Site	Family	Species	Feeding group
TERC	Termitidae	<i>Amitermes darwini</i>	Grass
	Termitidae	<i>Ephelotermes melachoma</i>	Litter/soil
	Termitidae	<i>Ephelotermes taylori</i>	Wood
	Termitidae	<i>Macrognathotermes errator</i>	Soil
	Termitidae	<i>Macrognathotermes sunteri</i>	Wood/soil
	Termitidae	<i>Microcerotermes nervosus</i>	Wood
	Termitidae	<i>Nasutitermes eucalypti</i>	Litter/soil
	Termitidae	<i>Nasutitermes longipennis</i>	Wood
	Rhinotermitidae	<i>Coptotermes acinaciformis</i>	Wood
	Rhinotermitidae	<i>Schedorhinotermes actuosus</i>	Wood
CDNP	Termitidae	<i>Amitermes germanus</i>	Grass
	Termitidae	<i>Drepanotermes septentrionalis</i>	unknown
	Termitidae	<i>Ephelotermes melachoma</i>	Litter/soil
	Termitidae	<i>Macrognathotermes sunteri</i>	Wood/soil
	Termitidae	<i>Microcerotermes nervosus</i>	Wood
	Termitidae	<i>Microcerotermes serratus</i>	Wood
	Termitidae	<i>Nasutitermes eucalypti</i>	Litter/soil
	Termitidae	<i>Nasutitermes longipennis</i>	Wood
	Termitidae	<i>Tumulitermes pastinator</i>	Grass
	Rhinotermitidae	<i>Schedorhinotermes actuosus</i>	Wood
HS-savanna	Termitidae	<i>Microcerotermes nervosus</i>	Wood
	Termitidae	<i>Tumulitermes hastilis</i>	Grass
	–	Unidentified species	Unknown
HS-wetland	Termitidae	<i>Amitermes meridionalis</i>	Grass

personal communication, 2008). Total termite mound basal area at this site was 18.4 m² ha⁻¹, with 21 % of this basal area contributed from *M. nervosus* mounds and the remainder from nine other termite species (Table 2). Five mounds of *M. nervosus* were selected for repeat measurement of CO₂ and CH₄ fluxes and associated environmental drivers over a complete wet–dry seasonal cycle. Mound walls of *M. nervosus* are soft, with an internal honeycomb-like structure and with an average mound size of 0.01 m³.

Site 2 was established at Charles Darwin National Park (CDNP), located ~ 5.5 km east of Darwin city with the same dominant vegetation as TERC and has not been burnt for over 10 years (P. Brooks, personal communication, 2008). Tree basal area was 10.9 m² ha⁻¹ at CDNP site (Table 1), typical for this savanna type (O’Grady et al., 2000). At this site

mounds of *Tumulitermes pastinator* contributed 11 % and mounds of *M. nervosus* contributed 10 % to the total mound basal area of 8.5 m² ha⁻¹. The remaining mound basal area was made up from eight other termite species (Table 2). Five mounds of *T. pastinator* were selected for repeated measurements. Mounds of *T. pastinator* have a very hard outer wall with internal honeycomb-like structure surrounding a large central gallery. The average mound size of *T. pastinator* was 0.02 m³.

Site 3 was located 21 km south-east of Darwin at Howard Springs (HS-savanna) and was also an open-forest savanna similar to Sites 1 and 2, but with a smaller tree basal area of 4.2 m² ha⁻¹ and negligible litter (Table 1). This site was burnt almost every year in early dry season (May). Total termite mound basal area at this site was 18.1 m² ha⁻¹ more

than 50 % of which was covered by the mounds of *Tumulitermes hastilis* (Table 2). The remaining mounds were of *M. nervosus* and other species, which could not be identified (Table 2). Fluxes were repeatedly measured from five mounds of *T. hastilis* at this site. The mound wall of *T. hastilis* was softest of all with honey comb-like mound structure. Average mound size for *T. hastilis* at this site was 0.01 m³.

Site 4 was an ephemeral wetland (HS-wetland) with a low tree basal area of 1.5 m² ha⁻¹ comprising of mainly *Eucalyptus polysiada* (Table 1). This site was located 30 km south-east of Darwin in the Howard River catchment. This site was inundated during the wet season between December and April. The C4 grass understorey is burnt approximately twice in every 3 yr. All termite mounds at this site were of *Amitermes meridionalis* covering a total mound basal area of 6.2 m² ha⁻¹ (Table 2). Always occurring in seasonally flooded depressions, mounds of *A. meridionalis* are uniquely constructed with a sail like mound aligned on a north–south magnetic axis for temperature regulation inside mound and are often more than two meters in height (Anderson et al., 2005). Fluxes were measured from seven mounds of *A. meridionalis* at this site. Mound wall was softer for the smaller mounds and harder for the larger, older mounds, with an average mound volume for this species of 0.12 m³ at this site.

2.2 CH₄ and CO₂ flux measurements from mounds and soil

Methane and CO₂ fluxes were measured from termite mounds and soil using manual chambers in situ, every four to six weeks between February and November 2009, which covers the wet and dry seasons and the transition months between these seasons. Fluxes from termite mounds were always measured between 10 and 12 h as this time best represents the daily average flux (Jamali et al., 2011b). Chamber bases were permanently fixed around selected mounds throughout the measurement campaign and were connected to chamber tops of the same circumference. Chambers were constructed from polyvinyl chloride with their sizes ranging from 0.02 and 0.20 m³ for termite mounds and 0.009 m³ for soil. Flux of CH₄ and CO₂ was measured in a closed dynamic set up (non-steady state and non-vented) by connecting each chamber in turn to the Fast Greenhouse Gas Analyser (Los Gatos Research, Mountain View, CA, USA) – hereafter referred to as FGGA – using an inlet and outlet gas line with Swagelok™ push fittings (Jamali et al., 2011c). Chamber closure time was five minutes for measuring mound fluxes and ten minutes for soil fluxes, during which the FGGA collected and analysed gas samples at 1 Hz frequency. The measuring cell of the FGGA is 0.0004 m³ and the internal pump rate is 0.0033 m³ min⁻¹; this translates into a complete flush of the measuring cell every 7.4 s.

2.3 Internal mound CH₄ and CO₂ concentrations

The internal mound CH₄ and CO₂ concentrations were measured once each in the wet and the dry seasons from the same mounds of four termite species that were also repeat-measured for fluxes of CH₄ and CO₂. Nylon tubes were permanently installed 5 cm into the mound wall at a mid-level height of the mound with the outer end of the tube connected to a two-way stopcock, which was opened only at the time of gas sample collection. Gas samples of 20 mL were collected from inside the mounds by connecting a syringe to the stopcock immediately after measuring mound fluxes, and injected into the FGGA in field. The concentrations of CH₄ and CO₂ in the gas samples were determined by using a calibration equation developed in the laboratory by injecting 20 mL of known concentrations of CH₄ and CO₂ in the same way as in the field.

2.4 Environmental variables

Mound temperature was measured immediately after flux measurements by inserting a hand held Cole-Palmer stainless steel temperature probe 6 cm into the mound at a mid-level height of the mound. Soil temperature was measured at a 3 cm soil depth. Soil water content was measured gravimetrically by collecting soil cores from the top 6 cm and oven dried at 105 °C. Mound water content was not measured as it would have required destructive sampling which was not possible as it was important to keep the mounds intact for repeat-measurements. As our previous data (not shown) showed a strong relationship between soil water content and mound water content ($R^2 > 0.8$), we decided to use soil water content instead of mound water content in our statistical analysis. Monthly rainfall and air temperature data for the year 2009 was obtained from the Darwin Airport meteorological station of the Bureau of Meteorology, Australia. Water table data for the HS-wetland site was obtained from the Northern Territory Government.

2.5 Data analysis

Data were checked for normal distribution of residuals via visual inspection of residual histograms, fitted-value plots and half normal plots. Single factor and multiple linear regression procedures were used to examine relationships of CH₄ and CO₂ flux from termite mounds with mound temperature and soil water content. This was repeated for fluxes of CH₄ and CO₂ from soil with soil temperature and soil water content. Simple linear regressions were used to analyse the relationship of mound CH₄ flux with mound CO₂ flux separately for each of the four termite species. Additionally, the Mann–Whitney *U* test was used to analyse the significance of differences in slopes of the regression lines between mound CH₄ flux and mound CO₂ flux for individual mounds between different termite species. Simple linear regressions

were used to analyse the relationship between the gas (CH₄ and CO₂) concentration inside mound and mound flux of the respective gases measured for the same mound. The relationship between mound CH₄ flux and CO₂ concentration inside mound was also analysed by using simple linear regression.

2.6 Annual CH₄ and CO₂ flux calculation

Annual flux was calculated for each termite species based on field measurements of CH₄ and CO₂ from mounds, thus accounting for seasonal variations in flux. For months with a direct flux measurement, the mean daily flux (m⁻² d⁻¹) was estimated from measured flux (m⁻² h⁻¹) scaled up to a 24 h day. For months without direct flux measurement, the mean daily flux for that month was estimated as being the average of the nearest preceding “measured” month and nearest successive “measured” month.

Annual flux of CH₄ and CO₂ (kg CO₂-e ha⁻¹ yr⁻¹) from termite mounds was scaled up to a site (landscape) level using total mound basal areas (m² ha⁻¹) from circumference measurements of each mound at ground level within each 50 m × 50 m site. Termite soldiers were then collected from each mound and the termite species identified at CSIRO laboratories in Darwin. For mounds built by termite species for which flux had not been measured, the average flux from the four measured species was used.

Annual soil flux of CH₄ and CO₂ was calculated in kg CO₂-e ha⁻¹ yr⁻¹ from the field measurements of soil flux as described for mounds. Total tree stem basal area (A_{tree} ; m² ha⁻¹) was calculated from circumference measurements of all tree stems at 1.3 m height above the soil surface in each 50 m × 50 m site. The soil area (A_{soil} ; m² ha⁻¹) was calculated as

$$A_{\text{soil}} = A_{\text{site}} - (A_{\text{mound}} + A_{\text{tree}}), \quad (2)$$

where A_{site} is 50 m × 50 m and A_{mound} is the total basal area of termite mounds.

3 Results

3.1 Mound CH₄ flux

Mound CH₄ fluxes were greater in the wet season when compared to the dry season for all species except *T. hastilis*, which did not show an obvious seasonal pattern in flux (Fig. 1). Mean CH₄ flux was lowest from the mounds of *M. nervosus* ranging between 379 ± 111 (dry season) and 1857 ± 718 μg CH₄-C m⁻² h⁻¹ (wet season), while fluxes from the mounds of the other three species were almost three fold greater than *M. nervosus* (Fig. 1). There was a significant positive linear relationship between soil water content and the mound CH₄ fluxes of *M. nervosus* ($p \leq 0.05$, $R_{\text{adj}}^2 = 0.60$) and *A. meridionalis* ($p \leq 0.001$, $R_{\text{adj}}^2 = 0.64$) (Table 3). Methane flux of *T. pastinator* was also positively

correlated with soil water content ($p \leq 0.01$, $R_{\text{adj}}^2 = 0.83$), but a greater proportion of flux variability could be explained when both soil water content and mound temperature were included in the model ($p \leq 0.001$; $R_{\text{adj}}^2 = 0.98$) (Table 3). Methane fluxes from *T. hastilis* did not show any significant relationships with soil water content or mound temperature (Table 3).

3.2 Mound CO₂ flux

Mound CO₂ fluxes of all species showed a distinct seasonal pattern with greater fluxes in the wet season as compared to the dry season (Fig. 1). Mean mound CO₂ fluxes were similar for *M. nervosus* and *T. pastinator*, ranging between 76 ± 2 (dry season) and 731 ± 237 mg CO₂-C m⁻² h⁻¹ (wet season), and were more than 2-fold greater than that measured for *T. hastilis* and *A. meridionalis* (Fig. 1). Mound CO₂ flux of *M. nervosus* was significantly positively correlated to soil water content ($p \leq 0.05$; $R_{\text{adj}}^2 = 0.61$) (Table 3). Mound CO₂ fluxes from *T. pastinator* showed a positive linear relationship with soil water content ($p \leq 0.05$; $R_{\text{adj}}^2 = 0.66$), but a greater proportion of flux variability could be explained when both soil water content and mound temperature were included in the model ($p \leq 0.001$; $R_{\text{adj}}^2 = 0.98$) (Table 3). Mound CO₂ fluxes of *T. hastilis* and *A. meridionalis* did not show any significant relationships with mound temperature or soil moisture (Table 3).

3.3 Soil CH₄ flux

No distinct seasonal patterns were observed in soil CH₄ flux at TERC, CDNP and HS-savanna sites. At TERC and HS-savanna sites, some individual chambers showed CH₄ emissions, but the mean soil CH₄ flux ($n = 5$) was negative (i.e. soil CH₄ uptake) on all six measurement occasions (Fig. 2). The CH₄ flux at CDNP switched between emission and uptake in different seasons, ranging between +8.3 ± 18.2 and -11.7 ± 8.8 μg CH₄-C m⁻² h⁻¹ (Fig. 2). The relationship between soil CH₄ flux and soil water content and soil temperature was not significant at TERC, CDNP and HS-savanna sites (Table 4). At the HS-wetland site (ephemeral wetland), we observed a seasonal pattern with mean CH₄ fluxes ($n = 5$) being positive (i.e. soil CH₄ emissions) during the middle of the wet season, and negative (i.e. soil CH₄ uptake) in the drier months (Fig. 2d). Mean CH₄ fluxes ($n = 5$) at this site ranged between -18.4 ± 4.4 and +82.1 ± 130.3 μg CH₄-C m⁻² h⁻¹ in different months of measurement, with emissions occurring when the water table was within 5 meters of the soil surface in the wet season (Fig. 2d). Standing water of up to 3 cm above ground was observed in two of the chambers in the wet season (February and April) at HS-wetland site. Soil CH₄ flux at HS-wetland site showed a positive linear relationship with soil water content ($p \leq 0.001$; $R_{\text{adj}}^2 = 0.40$), and the coefficient of determination was slightly greater when both soil

Table 3. Significant linear regression models of mound CH₄ and CO₂ fluxes with mound temperature (T_{mound} in °C) and gravimetric soil water content (W_{soil} in %) as determined by single factor and multiple linear regression procedure for individual termite species.

	T_{mound}	W_{soil}	Constant	R_{adj}^2	p value
Mound CH ₄ flux ($\mu\text{g CH}_4\text{-C m}^2 \text{h}^{-1}$)					
<i>M. nervosus</i> (TERC)	–	101	–108	0.60	≤ 0.05
<i>T. pastinator</i> (CDNP)	–	697	–1245	0.83	≤ 0.01
	460	616	–15 399	0.98	≤ 0.001
<i>T. hastilis</i> (HS-savanna)	–	–	–	–	n.s.
<i>A. meridionalis</i> (HS-wetland)	–	113	1771	0.64	≤ 0.001
Mound CO ₂ flux ($\text{mg CO}_2\text{-C m}^2 \text{h}^{-1}$)					
<i>M. nervosus</i> (TERC)	–	42	–43	0.61	≤ 0.05
<i>T. pastinator</i> (CDNP)	–	62	–49	0.70	≤ 0.05
	63	42	–1847	0.98	≤ 0.001
<i>T. hastilis</i> (HS-savanna)	–	–	–	–	n.s.
<i>A. meridionalis</i> (HS-wetland)	–	–	–	–	n.s.

Table 4. Significant linear regression models of soil CH₄ and CO₂ fluxes with soil temperature (T_{soil} in °C) and soil water content (W_{soil} in %) as determined by single factor and multiple linear regression procedure for individual study sites.

	T_{soil}	W_{soil}	Constant	R_{adj}^2	p value
Soil CH ₄ flux ($\mu\text{g CH}_4\text{-C m}^2 \text{h}^{-1}$)					
<i>TERC</i>	–	–	–	–	n.s.
<i>CDNP</i>	–	–	–	–	n.s.
<i>HS-savanna</i>	–	–	–	–	n.s.
<i>HS-wetland</i>	–	1.07	–21.37	0.40	≤ 0.001
	–2.26	1.14	43.8	0.44	≤ 0.001
Soil CO ₂ flux ($\text{mg CO}_2\text{-C m}^2 \text{h}^{-1}$)					
<i>TERC</i>	–	22.29	–58.6	0.53	≤ 0.001
	0.65	23.63	–87	0.55	≤ 0.001
<i>CDNP</i>	–	15.28	47.8	0.34	≤ 0.001
	–8.8	14.45	313	0.24	≤ 0.05
<i>HS-savanna</i>	–	7.69	7.1	0.38	≤ 0.001
	3.74	6.99	–107	0.34	≤ 0.01
<i>HS-wetland</i>	–	–	–	–	n.s.

water content and mound temperature were included in the regression model ($p \leq 0.001$; $R_{\text{adj}}^2 = 0.44$; Table 4).

3.4 Soil CO₂ flux

Soil CO₂ flux showed a distinct seasonal pattern at TERC, CDNP and HS-savanna sites with greater fluxes measured in the wet season and smaller in the dry season (Fig. 2), and a significant ($p \leq 0.01$) relationship with soil water content at all three sites (Table 4). Soil CO₂ flux at TERC was greatest and similar to that at CDNP, ranging between 45 ± 6

and $268 \pm 20 \text{ mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$, and smallest at the HS-wetland site ranging between 15 ± 5 and $98 \pm 8 \text{ mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$ (Fig. 2). Soil CO₂ flux showed a positive linear relationship with soil water content in models including only soil water content, and in models including soil water content and soil temperature at TERC, CDNP and HS-savanna sites (Table 4). Seasonal flux pattern at HS-wetland differed from other sites as the greatest flux occurred during the early dry season and the lowest in the wet season when the heavy clayey soils were saturated and the water table was within 5 m of the surface (Fig. 2d). Soil CO₂ flux at the HS-wetland

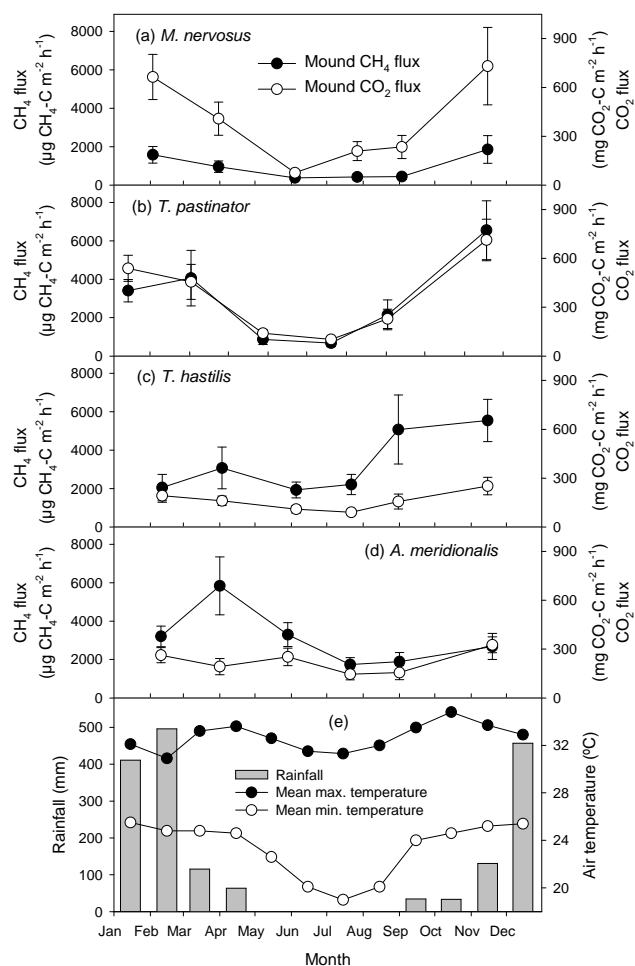


Fig. 1. Mean fluxes of CH₄ and CO₂ repeat-measured from mounds ($n = 5-7$) of four termite species at four different savanna sites; error bars are standard error of the mean; panel (e) shows 2009 monthly climate data for Darwin Airport (Bureau of Meteorology, Australia).

site did not show any significant relationships with soil temperature and soil water content (Table 3).

3.5 Mound CH₄ and CO₂ flux relationship

In general, mound fluxes of CH₄ showed similarly positive linear relationships with measured fluxes of CO₂ for all termite species (Fig. 3). The correlation between fluxes of CH₄ and CO₂ from termite mounds was stronger for *M. nervosus* ($R^2 = 0.93$; $p \leq 0.001$) and *T. pastinator* ($R^2 = 0.82$; $p \leq 0.001$) as compared to *T. hastilis* ($R^2 = 0.15$; $p \leq 0.05$) and *A. meridionalis* ($R^2 = 0.24$; $p \leq 0.001$) (Fig. 3). It is evident that the regression functions are similar for *T. pastinator*, *T. hastilis* and *A. meridionalis*, in that for every 1 mg of CO₂-C emitted, approximately 9 to 11 μg of CH₄-C is emitted. For *M. nervosus* mounds, $< 3 \mu\text{g}$ of CH₄-C is emitted for every 1 mg of CO₂-C. Mann–Whitney *U* tests confirmed that

Table 5. Annual CO₂-e fluxes of CH₄ and CO₂ from termite mounds of the four common species sampled.

Species	Site	Annual flux from termite mounds ($\text{kg CO}_2\text{-e m}^{-2} \text{yr}^{-1}$)	
		CH ₄	CO ₂
<i>M. nervosus</i>	TERC	0.3	13.9
<i>T. pastinator</i>	CDNP	1.1	13.0
<i>T. hastilis</i>	HS-savanna	1.0	5.5
<i>A. meridionalis</i>	HS-wetland	0.9	7.4

the regression function slope of *M. nervosus* mounds were significantly different ($p \leq 0.01$) from that for the other three species (Fig. 3).

3.6 Internal mound gas concentrations and fluxes

There was a significant positive correlation between mound CH₄ flux and CH₄ concentration inside a mound for all four species (Fig. 4). Greater internal CH₄ concentrations resulted in greater CH₄ fluxes. This correlation was stronger for *M. nervosus*, *T. pastinator* and *A. meridionalis* species ($R^2 > 0.8$) as compared to *T. hastilis* ($R^2 = 0.58$) (Fig. 4). We also observed significant correlations between mound CO₂ flux and CO₂ concentration inside a mound for all species, again with stronger R^2 of > 0.70 for *M. nervosus*, *T. pastinator* and *A. meridionalis* and a weaker R^2 of 0.54 for *T. hastilis* (Fig. 4). There was a significant correlation between mound CH₄ flux and CO₂ concentration inside a mound for each separate measured species, with R^2 ranging between 0.58 (*A. meridionalis*) and 0.78 (*M. nervosus*) (Fig. 5).

3.7 Annual fluxes from termite mounds and soil

Termite species with the greatest mound CH₄ emissions were not the same as those termite species with the greatest mound CO₂ emissions (Table 5). Annual CH₄ flux estimates on a per m² basis from the mounds of *M. nervosus* were 3-fold to 4-fold smaller than those from the other three termite species (Table 5). By contrast, the annual CO₂ flux estimates on a per m² basis from *M. nervosus* and *T. pastinator* were approximately 2-fold greater than those from *T. hastilis* and *A. meridionalis* (Table 5). Annual CH₄ flux estimates were between 5-fold (*T. hastilis*) and 46-fold (*M. nervosus*) smaller than the concurrent annual CO₂ flux estimates on a CO₂-e basis.

Total mound basal area was 2-fold to 3-fold greater at TERC and HS-savanna sites as compared to CDNP and HS-wetland sites (Table 6). After accounting for mound basal area at each site, annual CH₄ fluxes from the termite mounds were similar at TERC and HS-savanna sites, and almost 2-fold greater compared to the CDNP and HS-wetland sites (Table 6). Annual CO₂ fluxes from termite mounds were an order of magnitude greater than CH₄ flux at the same sites

Table 6. Annual mean fluxes of CH₄ and CO₂ in kg CO₂-e ha⁻¹ yr⁻¹ from termite mounds and soil at each of the four sites.

Site	Mound basal area (m ² ha ⁻¹)	Termite mounds			Soil		
		CH ₄	CO ₂	Total	CH ₄	CO ₂	Total
TERC	18.4	+13.4	+155.6	169	-73.0	+51,117	51 044
CDNP	8.5	+7.0	+166.6	174	+2.9	+49 523	49 526
HS-savanna	18.1	+16.6	+140.4	157	-41.7	+18 654	18 612
HS-wetland	6.2	+5.6	+45.5	51	+18.8	+13 463	13 482

(Table 6). CDNP had the greatest annual flux of CO₂ from termite mounds (+166.6 kg CO₂-e ha⁻¹ yr⁻¹) even though it had very low annual CH₄ flux from mounds. The HS-wetland site had the lowest annual fluxes of CO₂ from termite mounds and the lowest flux for CH₄ (Table 6).

Soil was a net CH₄ sink at TERC and HS-savanna and a net CH₄ source at CDNP and HS-wetland, with TERC being the greatest CH₄ sink at -73.0 kg CO₂-e ha⁻¹ yr⁻¹ and HS-wetland the greatest CH₄ source at +18.8 kg CO₂-e ha⁻¹ yr⁻¹ (Table 6). When expressed on a CO₂-e basis, annual soil CO₂ fluxes were almost three orders of magnitude greater when compared to soil CH₄ fluxes at the same respective sites. Annual soil CO₂ fluxes at TERC and CDNP sites were 2- to 4-fold greater than those at HS-savanna and HS-wetland sites (Table 6).

The contribution of CH₄ and CO₂ emissions from termite mounds to the total CH₄ and CO₂ emissions from termite mounds and soil was between 0.3 and 0.8% in CO₂-e (Table 6).

4 Discussion

4.1 CH₄ and CO₂ fluxes from termite mounds

At a hectare scale, annual fluxes (CO₂-e) from termite mounds were dominated by CO₂ emissions and mound CH₄ emissions contributed only 4 to 11% to total mound GHG emissions. The annual termite mound emissions (CH₄+CO₂) in CO₂-e, after accounting for mound basal area on each site, were greater at TERC, CDNP and HS-savanna sites than the HS-wetland site, which corresponds to the mound basal area (Table 6) and thus termite biomass at these sites. Termite biomass may be related to vegetation biomass. A linear regression analysis showed a significant positive relationship between tree basal area and number of *M. nervosus* mounds at 12 plots (Fig. 6; $R^2 = 0.69$; $p \leq 0.001$) surveyed during this study and an earlier study (Jamali et al., 2011a). We did not test this relationship for non-wood-feeding species. At a hectare scale, the annual CO₂-e emissions (CO₂ and CH₄) from termite mounds at these four sites (51–174 kg CO₂-e ha⁻¹ yr⁻¹) are comparable to the 80 kg CO₂-e ha⁻¹ yr⁻¹ from the mounds of *Cubitermes fungifaber*

in the savannas of Burkina Faso, Africa (Brümmer et al., 2009).

The seasonal pattern in fluxes of CH₄ and CO₂ for all species, except *T. hastilis*, concur with previous findings (Brümmer et al., 2009; Holt, 1987; Jamali et al., 2011b), and is derived primarily from the seasonal population dynamics of termites that inhabit mounds (Jamali et al., 2011c). It is not clear why the seasonal pattern of CH₄ fluxes from the mounds of *T. hastilis* was different from that of the mounds of other species (Fig. 1).

4.2 CH₄ and CO₂ fluxes from soil

Annual soil fluxes were dominated by CO₂ at all sites, with soil CH₄ fluxes contributing $\leq 0.2\%$ to the combined soil flux of CH₄ and CO₂. Soil CH₄ fluxes at TERC and HS-savanna resulted in a net annual CH₄ uptake, while soil fluxes at CDNP and HS-wetland sites produced net annual CH₄ emissions. Soil CH₄ emissions from the HS-wetland site were not unexpected as this is an ephemeral wetland where anaerobic methanogenic activity in saturated soils often leads to wet season emissions (Brümmer et al., 2009). At CDNP, the annual soil CH₄ flux was a net emission of +2.9 kg CO₂-e ha⁻¹ yr⁻¹ mainly because CH₄ emissions from a small number of soil chambers, resulting from subterranean termite activity, offset the CH₄ uptake by the rest of the chambers, as shown elsewhere (MacDonald et al., 1999). Such high spatial variability in soil CH₄ flux among sites suggests that scaling up to regional level will be problematic in tropical savanna landscapes of northern Australia and other ecosystems with patchy distributions of subterranean termite activity.

4.3 Relationship between mound CH₄ and CO₂ fluxes

The linear regression analysis (Fig. 3) suggests that mound CO₂ fluxes can be used to predict mound CH₄ fluxes but with variable accuracy across species. For example, this relationship was stronger ($R^2 > 0.8$) for *M. nervosus* and *T. pastinator* but weaker ($R^2 < 0.3$) for *T. hastilis* and *A. meridionalis*, which suggests this method will predict fluxes more accurately for some species as compared to others. However, as yet there is insufficient data to enable species-specific “mound CH₄–mound CO₂ relationships” for the wide range

of common termite species in northern Australia or in savannas globally. Therefore, this method, if used with caution, may provide a less expensive way of estimating mound CH₄ fluxes where direct CH₄ flux measurements are difficult. The inconsistent accuracy of this method across species may also be derived from the highly variable regression slopes for different species (Fig. 3). For example, the slope of *M. nervosus* is approximately 3 times smaller than that of the other three species, and therefore will result in a 3-fold error if the regression equation of *M. nervosus* is used to predict fluxes of the other three species and vice versa. The slopes of mound CH₄ flux vs. mound CO₂ flux vary among termite species because of the variable CH₄ per unit CO₂ production rates for different species. For example, mounds of *M. nervosus* had the smallest CH₄ fluxes but greatest CO₂ fluxes compared to other species (Table 5). A similar observation was made by Khalil et al. (1990), who reported that CH₄ emissions from the mounds of *Amitermes laurenensis* were 10-fold greater than *Coptotermes lacteus*, but CO₂ emissions were 30-fold smaller. There are a number of possible explanations for this observation. First, a considerable portion of CH₄ produced inside a mound can be oxidized by methanotrophic bacteria in and on mound wall material, or even the soil beneath the mound, before CH₄ passes through the mound wall and is emitted to the atmosphere. Using CH₄ isotopes, Sugimoto et al. (1998) found that, for the mounds of different species from family Termitidae, 53% to 83% of total CH₄ produced inside mounds was oxidized before being emitted to the atmosphere. For the thick-walled and therefore less porous mounds of *Macrotermes annandalei*, almost all the CH₄ produced by termites inside the mounds was oxidized because the longer CH₄ residence time enabled methanotrophs to consume most of the internal mound CH₄ (Sugimoto et al., 1998). In our study, mounds of *T. pastinator* had the hardest mound walls. Mean CH₄ concentration inside the mounds of *T. pastinator* was almost 3 to 5 fold greater when compared to *T. hastilis* and *A. meridionalis*, despite similar mound CH₄ fluxes. These results suggest that CH₄ oxidation may be greater for the mounds of *T. pastinator* as compared to other species because of the longer residence time for CH₄ produced inside mounds. This variation in CH₄ oxidation determined by wall properties may contribute to the observed variation in Fig. 3.

Second, termite respiration is not the only source of CO₂ emissions from termite mounds, as microbial respiration also occurs in the mound wall. Holt (1998) reported highly variable microbial populations among the mounds of five Australian termite species (including *T. pastinator*) and concluded that the mound microenvironment in some termite species can be more conducive for microorganisms as compared to others, due to differences in properties such as mound bulk density and wall thickness. Thus, the proportional contribution of microbial respiration to the total CO₂ emissions (termite respiration + microbial respiration from mound) will vary among mound-building termite species. A

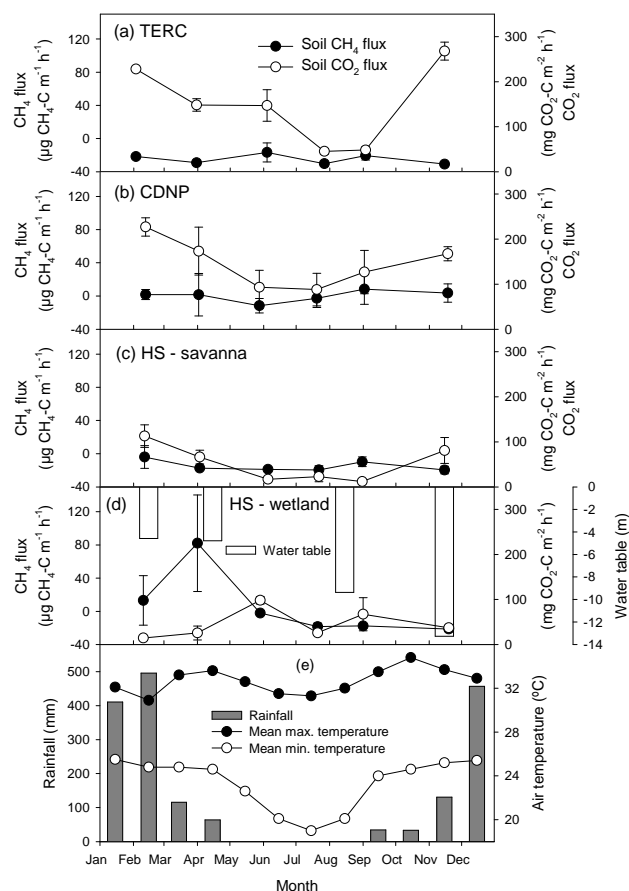


Fig. 2. Mean soil fluxes ($n = 5$) of CH₄ and CO₂ measured at four different sites; error bars are standard error of the mean; panel (e) shows the climate data of 2009 from the Darwin Airport meteorological station of the Bureau of Meteorology, Australia.

simple laboratory experiment (data not shown) indicated that microbial respiration in the mound material represented approximately 5% of total CO₂ emissions from a *M. nervosus* termite mound. However, we did not conduct such experiments for any of the other three species. Given the strong correlation between mound CH₄ and CO₂ flux of *M. nervosus* (Fig. 3), it can be hypothesized that species with a smaller proportion of microbial respiration in total CO₂ fluxes from mounds would tend to show stronger correlation between CH₄ and CO₂ fluxes and vice versa.

4.4 Internal mound gas concentrations and fluxes

The correlation between mound flux and gas concentration inside mound was stronger and more consistent across species for CO₂ as compared to CH₄. This variability among species may be attributed to the variation in mound structure as explained in Sect. 4.3. The linear regression analysis between mound flux and internal mound gas concentration (CH₄ and CO₂) suggests that this method may be used to predict mound fluxes for a given species. However, using

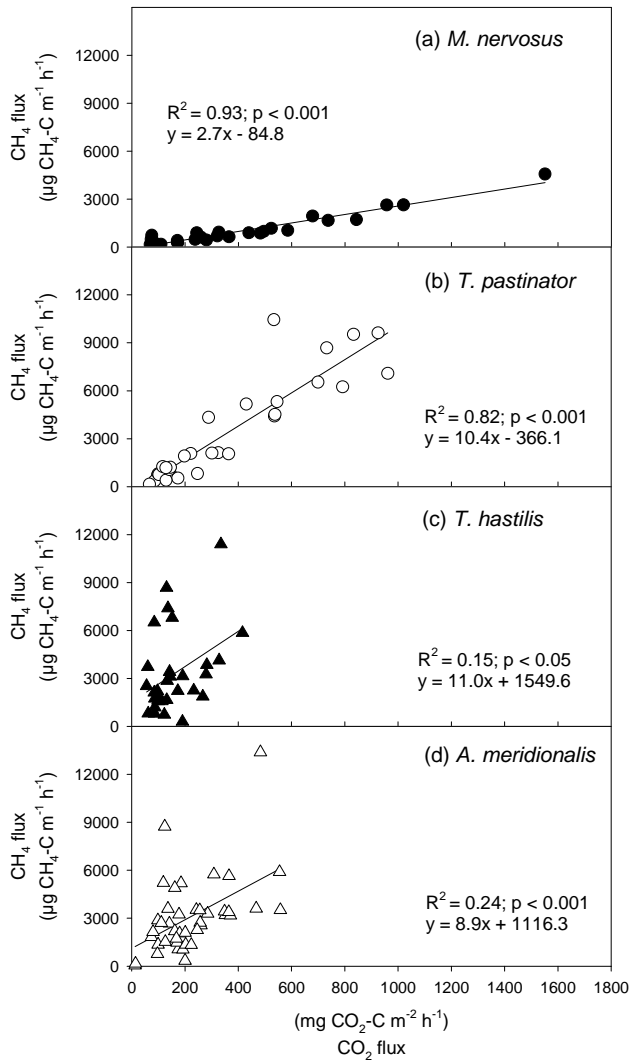


Fig. 3. Simple linear regression analysis between CH₄ and CO₂ fluxes from the mounds of four termite species. The Mann–Whitney *U* test showed that slope of *M. nervosus* mounds was significantly different from the mounds of *T. pastinator* ($p \leq 0.01$), *T. hastilis* ($p \leq 0.01$) and *A. meridionalis* ($p \leq 0.01$).

the equation developed for one species to predict mound fluxes from another termite species, as suggested by Khalil et al. (1990), could have resulted in errors of more than 5-fold for CH₄ and 3-fold for CO₂ in our study. Similarly, CO₂ concentration inside a mound may be used to predict mound CH₄ flux from the same mound using our regression models. However, again, using a generic relationship of CO₂ concentration inside a mound to predict mound CH₄ flux may result in 13-fold errors in predicted fluxes. Consequently, there is no generic relationship between gas mound concentration and flux amongst different species; however, given the limited datasets available on termite fluxes, this method may still be used, but with caution, where direct measurement of mound CH₄ fluxes is difficult.

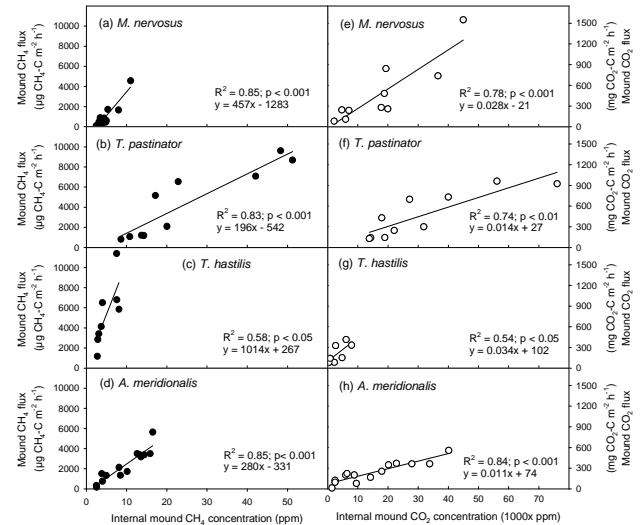


Fig. 4. Relationships of CH₄ and CO₂ internal mound concentrations with respective CH₄ and CO₂ mound fluxes.

The contribution of CH₄ and CO₂ emissions from termite mounds to the total CH₄ and CO₂ emissions from termite mounds and soil in CO₂-e was at maximum less than 1%. Termite mound density and basal area is a significant determinant of plot-scale emissions. Sites used in this study are representative of high rainfall savanna ecosystems (1600–1700 mm annual rainfall). However, north Australian savanna spans an area of some two million km² with rainfall ranging from 600 mm to 2000 mm, and termite density is highly variable across this range. Lower rainfall savanna areas can be populated by far higher mound densities than observed in this study (J. Russel-Smith, personal communication, 2012). Emissions of CO₂ and CH₄ from termites in these semi-arid savannas may be significant given higher densities, although fluxes may be offset by the lower rainfall, soil moisture and vegetation productivity. As such, scaling to regional or biome scales is problematic and further investigation of emission rates from a wider range of savanna types across north Australia is required, especially given emerging interest in GHG abatement projects in tropical savannas involving manipulation of fire regimes to early dry season fire regimes (Russell-Smith et al., 2009). Such a shift reduces fire related GHGs, but the resultant woody thickening and less severe fire occurrence may result in enhanced termite density and therefore GHG emissions, partially offsetting the carbon gains from the change in fire management. Further understanding of the interaction of climate, soil type, fire regime, biomass productivity and termite density, and termite derived GHG emissions is clearly required.

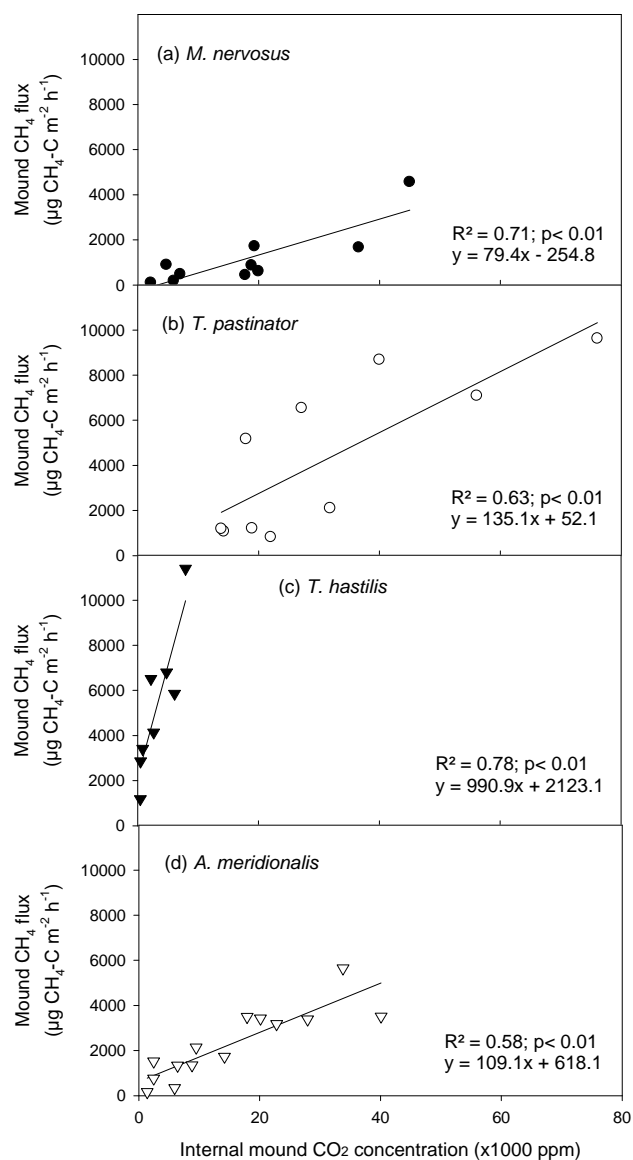


Fig. 5. Relationships of mound CH₄ flux and CO₂ concentration inside mound.

5 Conclusions

This study confirmed that termite mounds are a greater source of CO₂ as compared to CH₄ on an annual CO₂-e basis. However, CH₄ and CO₂ emissions from termite mounds contributed less than 1% to the total CH₄ and CO₂ emissions from mounds and soil combined in CO₂-e. Our results indicate that there is no easy way to measure, or indirectly determine, the CH₄ flux for a variety of termite species. There were significant relationships between CH₄ concentration and CH₄ flux and also significant relationships between mound CH₄ and CO₂ flux. However, all these relationships had different slopes for different species and were therefore species specific. Using the regression function of one species

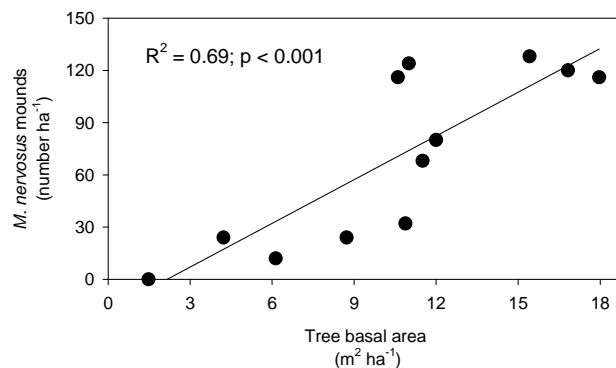


Fig. 6. Relationship between tree basal area and number of *M. nervosus* mounds based on surveys of 50 m × 50 m plots ($n = 12$).

to predict CH₄ fluxes for the mounds of other species would result in large errors. However, given the paucity of data on CH₄ fluxes from termites, the above methods may still be used with caution where direct flux measurements cannot be made. These species-specific relationships may be linked to the different factors and processes that determine mound CO₂ or CH₄ concentration and mound CO₂ and CH₄ fluxes (such as mound wall thickness), and need further investigation. Our results clearly indicate that the large variability among different termite species results in different relationships between internal mound concentrations and fluxes, and that such methods should only be used where unavoidable and with great caution to avoid large errors.

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