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

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Abstract

1. 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.
2. The annual flux from termite mounds and surrounding soil was dominated by CO₂ with large variations among sites. On a 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.
3. 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.
4. 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 past) would result in errors of more than 5-fold for CH₄ and 3-fold for CO₂.
5. 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. Consequently, there is no

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generic relationship that will allow for the prediction of CH₄ fluxes from termite mounds of all species.

1 Introduction

Savannas cover 20% of global land surface and produce almost 30% of global net primary production (Hutley and Setterfield, 2008; Grace et al., 2006), thus playing an important role in the global carbon cycle. An important component of the carbon and greenhouse gas balance of savanna ecosystems is the exchange of the greenhouse gas 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., 2011c). 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 lead 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; MacDonald et al., 1998; Sanderson, 1996; Jamali et al., 2011a–c) because of their significant contribution to the CH₄ balance of savanna ecosystems as compared to their negligible contribution to savanna CO₂ balance. However, the general assumption that CH₄ is the largest emitted greenhouse gas from termites may not be realistic. For example, in an African savanna, mound CH₄ emissions measured

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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). However, in carbon dioxide equivalents (CO₂-e), termite mound emissions of CH₄ ($\sim 7 \text{ kg CO}_2\text{-e ha}^{-1} \text{ yr}^{-1}$) were an order of magnitude smaller than termite emissions of CO₂ ($\sim 73 \text{ kg CO}_2\text{-e ha}^{-1} \text{ yr}^{-1}$) (Brümmer et al., 2009). Therefore, it is important to investigate and highlight the relative contribution of CH₄ and CO₂ emissions to net greenhouse gas emissions from termites and the savanna landscape.

There is a general consensus that termite mounds are a large point source of CH₄ and CO₂ when compared to adjacent soils (Jamali et al., 2011a; Brümmer et al., 2009; Seiler et al., 1984; Khalil et al., 1990; MacDonald et al., 1998), 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. (2011b) demonstrated that CH₄ and CO₂ emissions from a termite species, *M. nervosus*, were a strong function of termite biomass. Therefore, we hypothesize a good correlation between CH₄ and CO₂ emissions from termites and termite mounds, which 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 (Khalil et al., 1990). If valid, the advantage of this method is that it takes into account the proportion of CH₄ produced inside

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a mound by termites that is not emitted to the atmosphere due to both the gas diffusion barrier imposed by mound wall and CH₄ oxidation by methanotrophs in mound wall material (Sugimoto et al., 1998). However, it is not clear if the relationship between mound CH₄ flux and CH₄ concentration inside a mound is consistent among different species, as assumed by Khalil et al. (1990). The same approach may also be used to predict mound CO₂ fluxes. 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.

Objectives of this 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 concentration 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 × 50 m plots, one each in four savanna locations near Darwin in the Northern Territory, Australia:

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Site 1 was located at CSIRO's Tropical Ecosystems Research Centre (TERC) on the outskirts of Darwin city and is dominated by *Eucalyptus miniata* Cunn. Ex Schauter and *E. tetrodonta* F. Muell. trees over an understorey of annual/perennial C4 grasses with a thick litter layer. TERC, with a tree basal area of $16.8 \text{ m}^2 \text{ ha}^{-1}$ (Table 1), has been protected from fires for > 20 yr (R. Eager, personal communication, 2009). Total termite mound basal area at this site was $18.4 \text{ m}^2 \text{ ha}^{-1}$, 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 m^3 .

Site 2 was established at Charles Darwin National Park (CDNP), located ~ 5.5 km east of Darwin city with the same dominate vegetation as TERC and has not been burnt for over 10 yr (Paul, personal communication, 2009). Tree basal area was $10.9 \text{ m}^2 \text{ ha}^{-1}$ 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 $8.5 \text{ m}^2 \text{ ha}^{-1}$. 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. Average mound size of *T. pastinator* was 0.02 m^3 .

Site 3 was located 21 km south-east of Darwin at Howard Springs (HS-savanna) and was also a savanna open-forest similar to Sites 1 and 2, but with a smaller tree basal area of $4.2 \text{ m}^2 \text{ ha}^{-1}$ 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 $18.1 \text{ m}^2 \text{ ha}^{-1}$ 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 repeat-measured from five mounds of *T. hastilis* at this

site. 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 m^3 .

Site 4 was an ephemeral wetland (HS-wetland) with low trees basal area of $1.5 \text{ m}^2 \text{ ha}^{-1}$ comprising mainly of *Eucalyptus polyciada* (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 2 in every 3 yr. All termite mounds at this site were of *Amitermes meridionalis* covering a total mound basal area of $6.2 \text{ m}^2 \text{ ha}^{-1}$ (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 m^3 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. Chamber bases were permanently fixed around selected mounds throughout the measurement campaign and were connected to chamber tops of the same circumference. Flux of CH₄ and CO₂ was measured in a closed dynamic set up (non-steady state) by connecting each chamber in turn to a fast greenhouse gas analyzer (Los Gatos Research, Mountain View, CA, USA) using an inlet and outlet gas line with Swagelok™ push-fittings, as described by Jamali et al. (2011b).

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2.3 Internal mound CH₄ and CO₂ concentration

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. These gas samples were injected into the FGGA to analyse for the concentrations of CH₄ and CO₂.

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. 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

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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, 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. Simple linear regression was used to analyse the relationship between mound CH₄ flux and CO₂ concentration inside mound.

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 “measured” month preceding and nearest “measured” month antecedent.

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 × 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 × 50 m site. The soil area (A_{soil} ; m² ha⁻¹) was

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calculated as:

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

where A_{site} is 50 × 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 flux was 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 was more than two fold greater than

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that measured for *T. hastilis* and *A. meridionalis* (Fig. 1). Mound CO₂ flux of *M. nervosus* was significantly positively correlated to soil water content ($p \leq 0.05$; $R_{Adj}^2 = 0.61$) (Table 3). Mound CO₂ fluxes from *T. pastinator* showed a positive linear relationship with soil water content ($p \leq 0.05$; $R_{Adj}^2 = 0.66$) but a greater proportion of flux variability could be explained when both soil water content and mound temperature were included in the model ($p \leq 0.001$; $R_{Adj}^2 = 0.98$) (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 uptake and emission in different seasons, ranging between $+8.3 \pm 18.2$ and $-11.7 \pm 8.8 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$ (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 $+82.1 \pm 130.3 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$ in different months of measurement, with emissions occurring when the water table was within 5 m 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 ($p \leq 0.001$; $R_{Adj}^2 = 0.40$), and the coefficient of determination was slightly greater when both soil water content

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and mound temperature were included in the regression model ($p \leq 0.001$; $R_{Adj}^2 = 0.44$; 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, and a significant ($p \leq 0.01$) relationship with soil water content at all three sites (Fig. 2). Soil CO₂ flux at TERC was greatest and similar to that at CDNP, ranging between 45 ± 6 and 268 ± 20 mg CO₂-C m⁻² h⁻¹, and smallest at HS-wetland site ranging between 15 ± 5 and 98 ± 8 mg CO₂-C m⁻² h⁻¹ (Fig. 3). Soil CO₂ flux showed 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 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 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 μg of CH₄-C is emitted for every 1 mg of CO₂-C. Mann–Whitney U

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tests confirmed that 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 concentration 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 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 two 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

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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). 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-folds greater than those at HS-savanna and HS-wetland site (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 combined annual CO₂-e emissions of CH₄ and CO₂ from termite mounds at TERC, CDNP and HS-savanna sites were greater than HS-wetland site which corresponds to the mound basal area (Table 1) 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., 2011c). We did not test this relationship for non-wood-feeding species. The smallest annual CO₂-e emissions from termite mounds were at HS-wetland site probably because the seasonally wet conditions only suit *A. meridionalis* (Anderson et al., 2005). This coupled with a smaller contribution

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from microbial respiration because of saturated soil conditions inhibiting microbial activity, litter accumulation and woody vegetation growth. 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 (Holt, 1987; Brümmer et al., 2009; Jamali et al., 2011a) and is derived primarily from the seasonal population dynamics of termites that inhabit mounds (Jamali et al., 2011b). The aseasonal pattern observed in CH₄ fluxes from the mounds of *T. hastilis* (Fig. 1c) suggests that population dynamics for this species may differ from that of other species.

4.2 CH₄ and CO₂ fluxes from soil

Annual soil fluxes were dominated by CO₂ at all sites with soil CH₄ fluxes contributing ≤ 0.2 % to the combined soil flux of CH₄ and CO₂. Soil CH₄ fluxes at TERC and HS-savanna resulted in a net CH₄ uptake, while fluxes at CDNP and HS-wetland sites produced net soil CH₄ emissions. Soil CH₄ emissions from 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, annual soil CH₄ flux was actually a net emission of +2.9 kg CO₂-e ha⁻¹ yr⁻¹ because individual chambers were a CH₄ source indicating subterranean termite activity which shifted the annual CH₄ flux estimate to being a net emission (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 given the highly patchy distribution of subterranean termite activity.

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4.3 Relationship between mound CH₄ and CO₂ flux

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. This inconsistency arises because the termite species that produced greatest CH₄ per unit mound were not the same that produced the greatest CO₂ (Table 5). For example, mounds of *M. nervosus* had the smallest CH₄ fluxes but greatest CO₂ fluxes compared to other species. A similar observation was made by Khalil et al. (1990) who reported that CH₄ emissions from the mounds of *Amitermes laurensis* 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 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 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 population among the mounds of five Australian termite

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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 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 concentration 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 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 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 and a specific equation will have to be developed for each mound-building termite species.

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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. 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 type 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 emission is clearly required.

5 Conclusions

This study established that termite mounds are a greater source of CO₂ as compared to CH₄ on an annual CO₂-e basis. Our results also 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, e.g. a measurement of CO₂ flux can be used to predict the CH₄ flux for mounds of the same termite species. However, all these relationships had different slopes for different species and were therefore species specific. Using the regression function of one species to predict CH₄ fluxes for

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the mounds of other species would result in large errors. These species-specific relationships are linked to the different processes that determine mound CO₂ or CH₄ concentration and mound CO₂ and CH₄ flux. Differences in mound wall thickness, diffusivity and methanotrophic activity as well as differences in mound microbial composition and activity and termite CH₄ production and respiration all influence the magnitude and flux of the two gases. Our results clearly indicate that the large variability between the different termite species does result in different relationships between internal mound concentration and fluxes and that generic equations cannot and should not be applied, as they would result in large errors.

Acknowledgements. The study was funded by the AusAID and the Australian Research Council Linkage Project LP0774812. We are thankful to Gus Wanganeen, Tracey Dawes, Garry Cook and other staff at CSIRO, Darwin for their support throughout this study. We are also thankful to Donna Giltrap of Landcare Research, New Zealand for her constructive comments on the manuscript. We would also like to thank many students who helped us in field data collection during this study.

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

Site	Family	Species	
TERC	Termitidae	<i>Amitermes darwini</i>	
		<i>Ephelotermes melachoma</i>	
		<i>Ephelotermes taylora</i>	
		<i>Macrognathotermes errator</i>	
		<i>Macrognathotermes sunteri</i>	
		<i>Microcerotermes nervosus</i>	
		<i>Nasutitermes eucalypti</i>	
		<i>Nasutitermes longipennis</i>	
		Rhinotermitidae	<i>Coptotermes acinaciformis</i>
			<i>Schedorhinotermes actuosus</i>
CDNP	Termitidae	<i>Amitermes germanus</i>	
		<i>Drepanotermes septentrionalis</i>	
		<i>Ephelotermes melachoma</i>	
		<i>Macrognathotermes sunteri</i>	
		<i>Microcerotermes nervosus</i>	
		<i>Microcerotermes serratus</i>	
		<i>Nasutitermes eucalypti</i>	
		<i>Nasutitermes longipennis</i>	
		<i>Tumulitermes pastinator</i>	
		Rhinotermitidae	<i>Schedorhinotermes actuosus</i>
HS-savanna	Termitidae	<i>Microcerotermes nervosus</i>	
		<i>Tumulitermes hastilis</i>	
		Unidentified species	
HS-wetland	Termitidae	<i>Amitermes meridionalis</i>	

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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^2_{adj}	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 ($\mu\text{g CO}_2\text{-C m}^2\text{ h}^{-1}$)					
<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.

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

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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 (kg CO ₂ -e m ⁻² 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

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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

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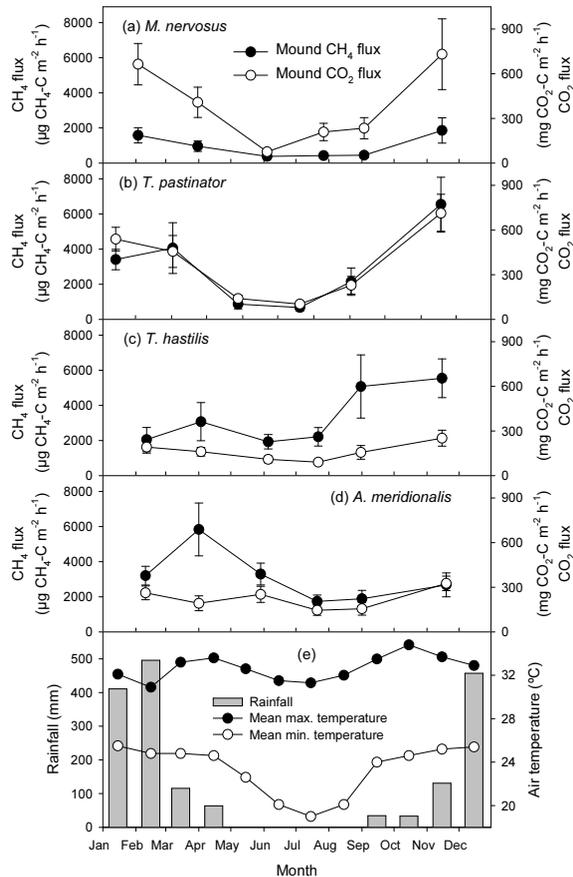


Fig. 1. Mean fluxes of CH₄ and CO₂ repeat-measured from mounds ($n = 5-7$) of four termite species at four different savanna sites; error bars are standard error of the mean; **(e)** shows 2009 monthly climate data for Darwin Airport (Bureau of Meteorology, Australia).

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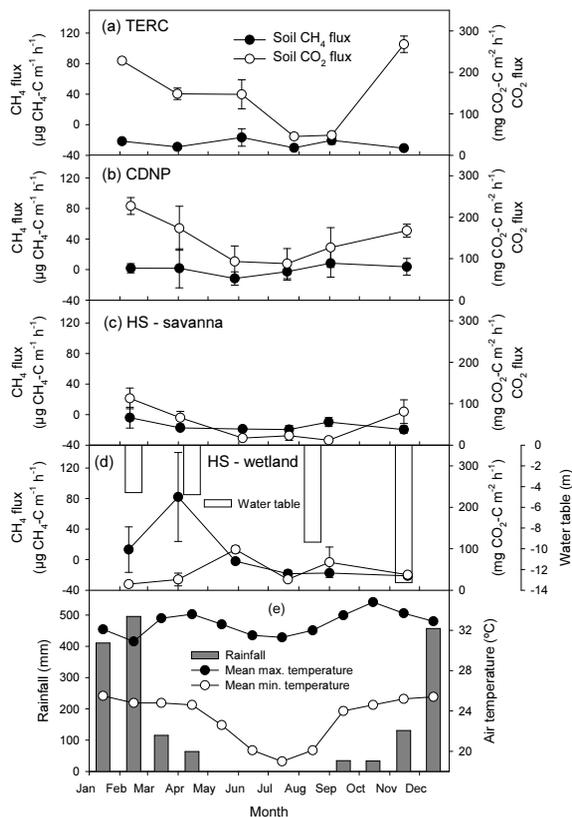


Fig. 2. Mean soil fluxes ($n = 5$) of CH₄ and CO₂ measured at four different sites; error bars are standard error of the mean; **(e)** shows the climate data of 2009 from the Darwin Airport meteorological station of the Bureau of Meteorology, Australia.

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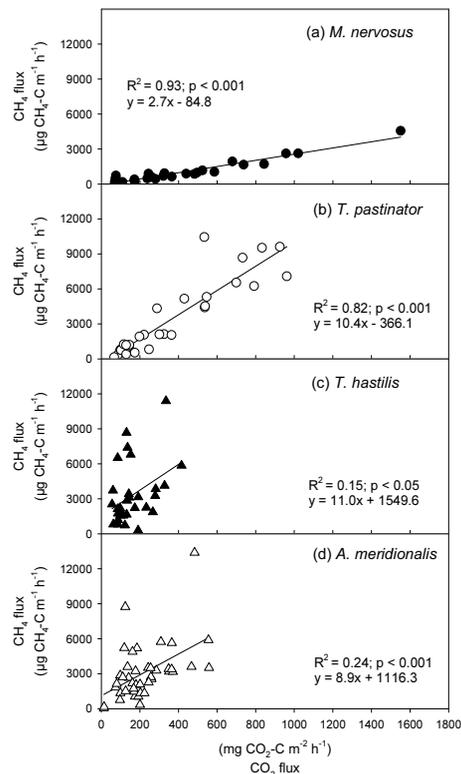


Fig. 3. Simple linear regression analysis between CH₄ and CO₂ fluxes from the mounds of four termite species. Mann-Whitney U test showed that slope of *M. nervosus* mounds was significantly different from the mounds of *T. pastinator* ($p \leq 0.01$), *T. hastilis* ($p \leq 0.01$) and *A. meridionalis*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

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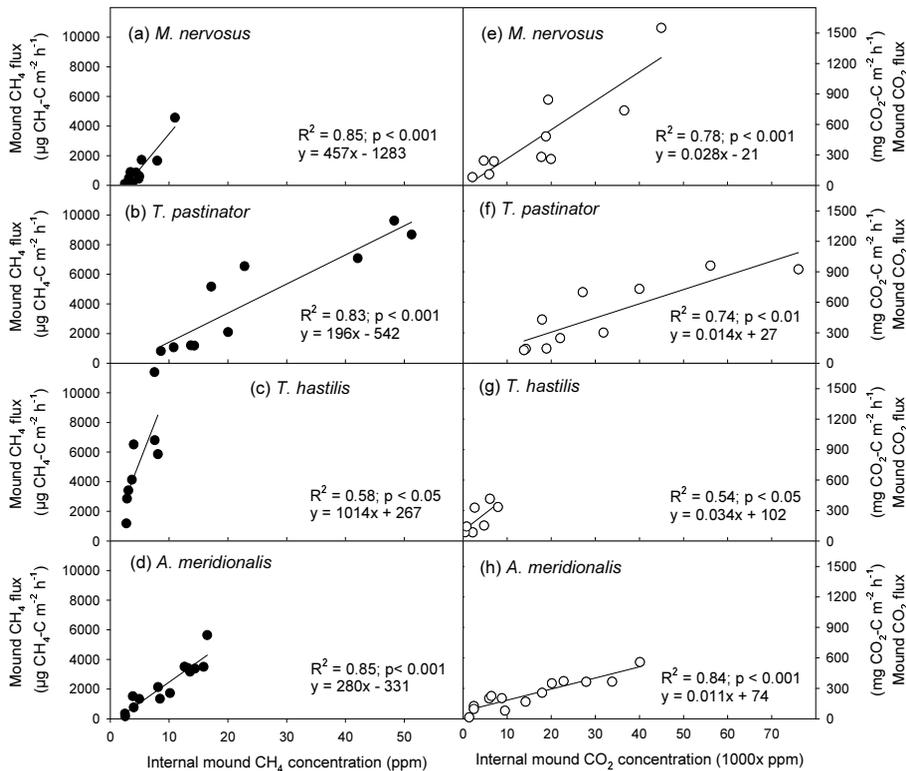


Fig. 4. Relationship of CH₄ and CO₂ internal mound concentrations with respective CH₄ and CO₂ mound fluxes.

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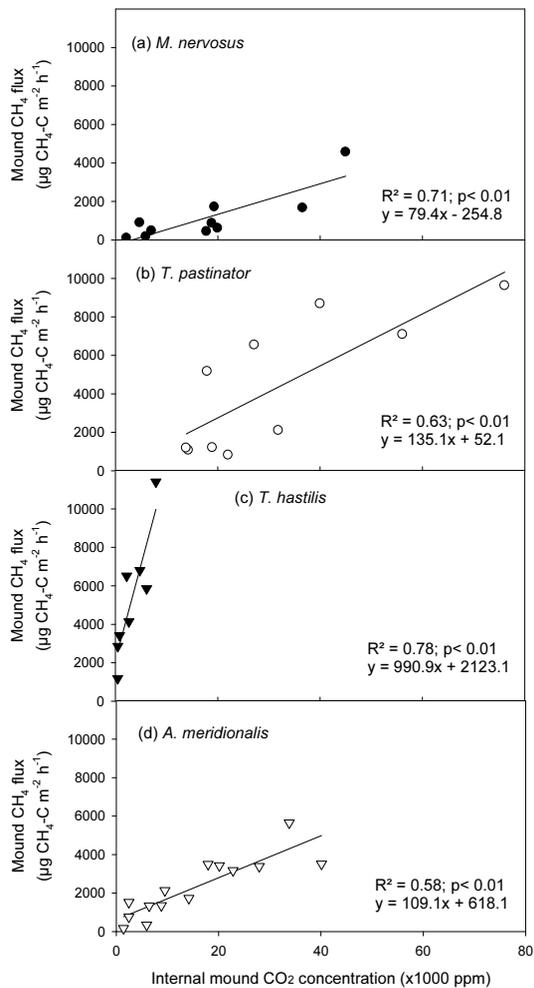


Fig. 5. Relationship of mound CH_4 flux and CO_2 concentration inside mound.

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