

# Termites and Global Methane – Another Assessment

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**Abstract.** New CH<sub>4</sub> emission data from a number of Northern and Southern Hemispheric, tropical and temperate termites, are reported, which indicate that the annual global CH<sub>4</sub> source due to termites is probably less than 15 Tg. The major uncertainties in this estimate are identified and found to be substantial. Nevertheless, our results suggest that termites probably account for less than 5% of global CH<sub>4</sub> emissions.

**Key words.** Methane, termites, global methane budget.

## 1. Introduction

Methane (CH<sub>4</sub>) is an important trace gas in the global atmosphere, contributing significantly to its longwave opacity, and to the chemistries of both the troposphere, as a sink for hydroxyl radicals and a dominant source of carbon monoxide, and the stratosphere, as a sink for chlorine radicals and a source of water vapour (Logan *et al.*, 1978, 1981). CH<sub>4</sub> has been increasing in concentration in the earth's atmosphere at about 1–2% per year on decadal, or possibly longer, time scales (Rasmussen and Khalil, 1981; Fraser *et al.*, 1984; Rasmussen and Khalil, 1984). Such increases may significantly affect future levels of stratospheric ozone (Owens *et al.*, 1985) and climate (Ramanathan *et al.*, 1985). The identity and magnitude of the major CH<sub>4</sub> sources are uncertain. Recent estimates of the total annual source strength vary from 400 to 1200 Tg (Ehhalt and Schmidt, 1978; Sheppard *et al.*, 1982; Khalil and Rasmussen, 1983a), with the majority resulting from the anaerobic decay of biological material. Consideration of identified CH<sub>4</sub> sinks favors the lower limit of this range (Logan *et al.*, 1981; Crutzen and Gidel, 1983; Fraser *et al.*, 1986). Activities such as rice and cattle production, the mining and use of fossil fuels, biomass burning are believed to be the cause of increasing atmospheric CH<sub>4</sub> levels (Rasmussen and Khalil, 1981; Fraser *et al.*, 1981; Blake *et al.*, 1982), although possibly decreasing levels of atmospheric hydroxyl radical may also be significant (Khalil and Rasmussen, 1985).

Termites produce measurable quantities of  $\text{CH}_4$  (Breznak, 1975). The relative importance of termites as a global source of  $\text{CH}_4$  is a subject of some debate with estimates varying from 2 to 150 Tg per year (Zimmerman *et al.*, 1982; Rasmussen and Khalil, 1983; Zimmerman and Greenberg, 1983; Khalil and Rasmussen, 1983b; Collins and Wood, 1984; Zimmerman *et al.*, 1984; Seiler *et al.*, 1984). New experimental data on  $\text{CH}_4$  production by a variety of termites from the Northern and Southern Hemispheres are presented in this paper, and compared to previous results. The data indicate that while there are large variations in the amount of  $\text{CH}_4$  produced by different species of termites, and possibly in the ratios of biomass consumed to  $\text{CH}_4$  produced, the total  $\text{CH}_4$  source due to termites is probably less than 15 Tg per year, thus making a contribution of less than 5% to global  $\text{CH}_4$  emissions.

## 2. Experimental

Six species of termites were studied, namely *Mastotermes darwiniensis* Froggatt, *Nasutitermes exitiosus* (Hill), *Coptotermes acinaciformis* (Froggatt), *Coptotermes lacteus* (Froggatt), *Zootermopsis angusticollis* (Hagen) and *Coptotermes formosanus* Shiraki. The Australian species (M.d., N.e., C.a., C.l.) were studied at the CSIRO Divisions of Atmospheric Research and Chemical and Wood Technology, where laboratory colonies are maintained for short durations and subsequently used in bioassays in wood preservation and natural durability studies (Gay *et al.*, 1955; Howick and Creffield, 1975; Howick *et al.*, 1975). Damage to timber structures in Australia is largely caused by species of the three genera *Mastotermes*, *Nasutitermes* and *Coptotermes*, the latter being the most economically significant due to its Australia wide distribution (Gay and Calaby, 1970). The Australian termites were originally obtained by CSIRO scientists near Darwin, Northern Territory (12.5°S, 131°E; M.d., C.a.), Seymour, Victoria (37.5°S, 145°E; N.e.) and Canberra, Australian Capital Territory (35°S, 149°E; C.l.). The two remaining species were collected in the United States from Beaverton and Hillsboro, Oregon (45.5°N, 123°W; Z.a.) and Hawaii (20.5°N, 156°W; C.f.), and studied at the Oregon Graduate Center.

All termites and wood masses quoted in this paper are live and dry masses respectively.  $\text{CH}_4$  emissions from the Australian termites were investigated using techniques similar to those developed by Rasmussen and Khalil (1983) for *Z. angusticollis* and subsequently *C. formosanus* (this work). Termites (0.7–0.9 g), typically 200 individuals for *C. lacteus*, *C. acinaciformis*, *N. exitiosus*, 25 individuals for *M. darwiniensis* were placed in glass jars (1.2 l) containing ambient air, moistened filter paper and 200 mg blocks of *Eucalyptus regnans* F. Muell and *Pinus radiata* D. Don. The jars were stored in the dark for at least 24 h to equilibrate at temperatures between 19° and 31 °C. A single set of termites was used for experiments involving the same species of termite at different temperatures. Prior to commencing an experiment, termite activity was monitored periodically, and if assessed to be normal (no mortality, evidence of wood consumption), gas emission experiments were initiated by flushing the jars thoroughly with ambient air before sealing. Air samples (20 ml) were withdrawn through a septum using a gas tight syringe, at times

up to 24 h after the experiments were initiated. These air samples were replaced by identical volumes of ambient air of known  $\text{CH}_4$  concentrations. The linearity of observed  $\text{CH}_4$  emission rates was used to indicate whether  $\text{CH}_4$  production was constant in each experiment.  $\text{CH}_4$  concentrations were analysed in Australia and the U.S.A. using identical flame ionization detector gas chromatographs, calibrated with secondary air standards (Rasmussen and Khalil, 1981; Fraser *et al.*, 1984).  $\text{O}_2$  and  $\text{CO}_2$  measurements were only performed on jar experiments conducted at the Oregon Graduate Center. Duplicate, blank glass jars, containing wet filter paper, wood, ambient air, and no termites, were analysed during each experiment. No changes in  $\text{CH}_4$  concentrations were observed, compared to ambient levels.

A mound of C.I. (basal diameter 1.3 m, height 0.8 m), collected from near Canberra in May 1982, was maintained by the CSIRO Division of Chemical and Wood Technology for wood consumption studies in an Accelerated Field Simulator (AFS) (Johnson *et al.*, 1983). The AFS was operated at 27–28 °C and 85 to 90% relative humidity. The gaseous emissions of this mound colony were investigated in November 1982. The mound, located in a steel tank containing sand and soil, was connected to a feeder box containing three timber species via a *P. radiata* lined PVC tube. To prevent termites from escaping, the tank was fitted with a water filled moat around its top edge. The metal feeder box was complete enclosed, but observation of termite activity was possible through a perspex lid. The arrangement of mound, tank and feeder box is shown in Figure 1.

Wood consumption studies were carried out over a period of two years and average rates of consumption of *P. radiata*, *E. regnans* and *Eucalyptus obliqua* L'Herit were 0.36, 0.19, and 0.04 kg per week respectively. (Creffield, J. W., unpublished data). The termite population was approximately 900 000 ( $\pm 5\%$ ) individuals (3.3 kg), estimated by averaging results from 76 bioassays, using 1 g subsets of mound termites, to determine average consumption rates of *P. radiata* over 1 week periods throughout the two

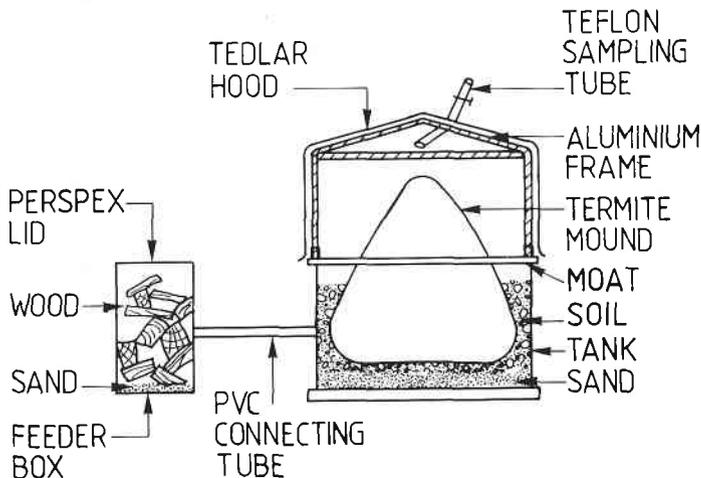


Fig. 1. The arrangement of the holding tank and moat, the feederbox and the Tedlar hood used to study the gaseous emissions of a living termite mound (*C. lacteus*) maintained in the Accelerated Field Simulator of CSIRO, Division of Chemical and Wood Technology (Johnson *et al.*, 1983).

year experiment (Creffield, J. W., unpublished data). This estimated population for the laboratory mound agrees with other estimates of *C. lacteus* mound populations made by direct counting methods in the field (Gay and Greaves, 1940). Average termite weights were obtained from Gay *et al.* (1955). The vitality of the mound was established by the consistency in these long term feeding rates, the visual observation of mound building and wood consumption activity, and by the appearance of juvenile instars, indicating breeding activity.

For the gaseous emission studies the mound was covered by a Tedlar plastic sheeting hood supported by an aluminium frame (see Figure 1). The hood (internal volume 1900 l) was attached to the tank on the outside of the moat with tape, making a gas-tight seal. Air samples were withdrawn at times up to three hours after the hood was put in place over the mound, using a clean metal bellows pump to flush and fill glass (0.5 l) and stainless steel (1.0 l) flasks. CH<sub>4</sub> and CO<sub>2</sub> concentrations were determined using a flame ionization detector gas chromatograph. Ambient laboratory air samples, collected throughout the experiment, showed no change in CH<sub>4</sub> or CO<sub>2</sub> concentrations. The mound temperatures (surface, 28 °C; core 36 °C, intermediate 32 °C) remained constant throughout the experiment. Termite activity was monitored visually throughout the experiment. No changes were observed.

### 3. Results and Discussion

The CH<sub>4</sub> and CO<sub>2</sub> emissions from the living termite mound (*C. lacteus*) are shown in Figure 2, from which fluxes of 0.67 (± 0.2) mg of CH<sub>4</sub> per kg (termite) per hour and 4.7 (± 0.2) g of CO<sub>2</sub> per kg (termite) per hour were derived. The mixing ratios of both CH<sub>4</sub> and CO<sub>2</sub> increased linearly with time, suggesting that the imposition of the hood did not significantly affect their emission rates. Seiler *et al.* (1984) have shown that the ratio of CH<sub>4</sub> to CO<sub>2</sub> emissions is approximately constant for individual termite species, but varies over a range of 10<sup>-4</sup> to 10<sup>-2</sup> for six different genera, presumably related to diet. Fungi cultivating termites show the lowest values, grass consuming termites the highest, and wood and dung consuming termites intermediate values. Despite being a wood consuming termite, the value observed here for *C. lacteus* (1.4 × 10<sup>-4</sup>) falls at the lower end of this range. The average wood consumption rate from the 76 bioassays was approximately 1.1 g per kg (termite) per hour (J. W. Creffield, unpublished data), indicating that *C. lacteus* emit 0.6 mg CH<sub>4</sub> per gram of wood consumed, a factor of 6 lower than found by Zimmerman *et al.* (1982) for *Reticulitermes tibialis* Banks and *Gnathatermes perplexus* (Banks).

The results of CH<sub>4</sub> emission experiments involving termites in sealed glass jars are shown in Figure 3. The capacity of termites to produce CH<sub>4</sub> varies from species to species, within subsets from different mounds or nests of particular species, and also with temperature. The different species studied produce CH<sub>4</sub> at rates that range over more than two orders of magnitude, while variability within a species, e.g. *C. acinaciformis* from five different mounds (Creffield *et al.*, 1985) or *Z. angusticollis* from three different nests, can differ by as much as a factor of 40. *M. darwiniensis* produced CH<sub>4</sub>

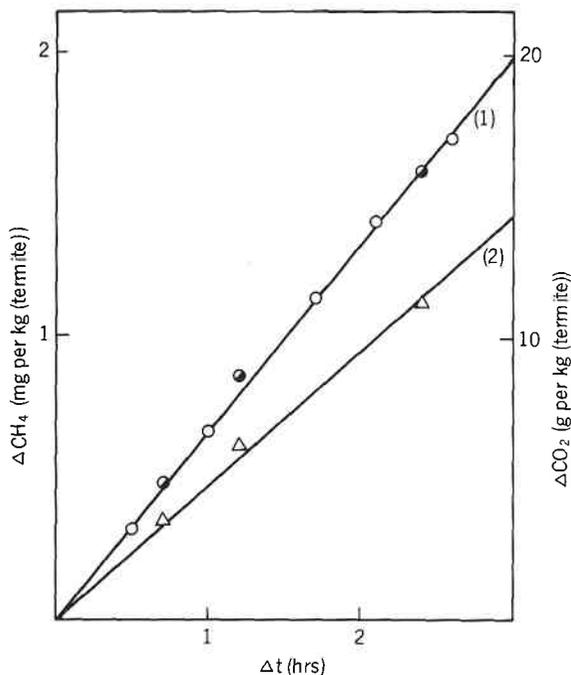


Fig. 2. Observed  $\text{CH}_4$ (1) and  $\text{CO}_2$ (2) emissions from a mound of *C. lacteus* containing approximately  $0.9 \times 10^6$  termites (3.3 kg). Air samples were collected in glass (○) and stainless steel (●, Δ) flasks. Solid lines are linear regressions through origin:  $\Delta\text{CH}_4 = 0.67 (\pm 0.02) \Delta t$ ;  $\Delta\text{CO}_2 = 4.7 (\pm 0.2) \Delta t$ .

at approximately 8 and 12 mg per kg (termite) per hour at 28° and 31 °C respectively, the latter being the highest  $\text{CH}_4$  flux yet recorded for any termite species. *C. formosanus* yielded 0.06 mg  $\text{CH}_4$  per kg per hour at 25 °C, confirming the very low flux measured by Breznak (1975) for this ubiquitous and very destructive termite. The causes of this considerable range of variability are not well known. Certainly diet (Breznak, 1975; Seiler *et al.*, 1984) and habitat temperature (Zimmerman and Greenberg, 1983) appear to be significant factors.

The average  $\text{CH}_4$  flux measured from the living mound in the AFS (0.7 mg  $\text{CH}_4$  per kg (termite) per hour) is lower than the flux inferred from the glass jar experiments involving workers from the same mound (1.1 mg  $\text{CH}_4$  per kg (termite) per hour at 28°C). This could be a response to the different environments experienced by the termites in the mound versus the glass jars, or due to partial consumption of mound termite emitted  $\text{CH}_4$  by mound microorganisms, a possibility that has been discussed elsewhere (Seiler *et al.*, 1984). Considering the range of  $\text{CH}_4$  emissions measured from species to species (two orders of magnitude in this study), the agreement between mound and jar experiments for *C. lacteus* is encouraging and suggests that jar experiments may be used to obtain approximate estimates of  $\text{CH}_4$  emissions from termites in the field.

The environmental conditions such as light levels, humidity, temperature,  $\text{CO}_2$  and  $\text{O}_2$  concentrations, experienced by termites in these glass jar experiments are not unlike

those of a termite mound or nest in the field. Termites prefer the absence of solar radiation, an immobile atmosphere, stable saturated or near saturated relative humidities (usually in excess of 90%) and high, stable temperatures (Becker, 1970; Bouillon, 1970;

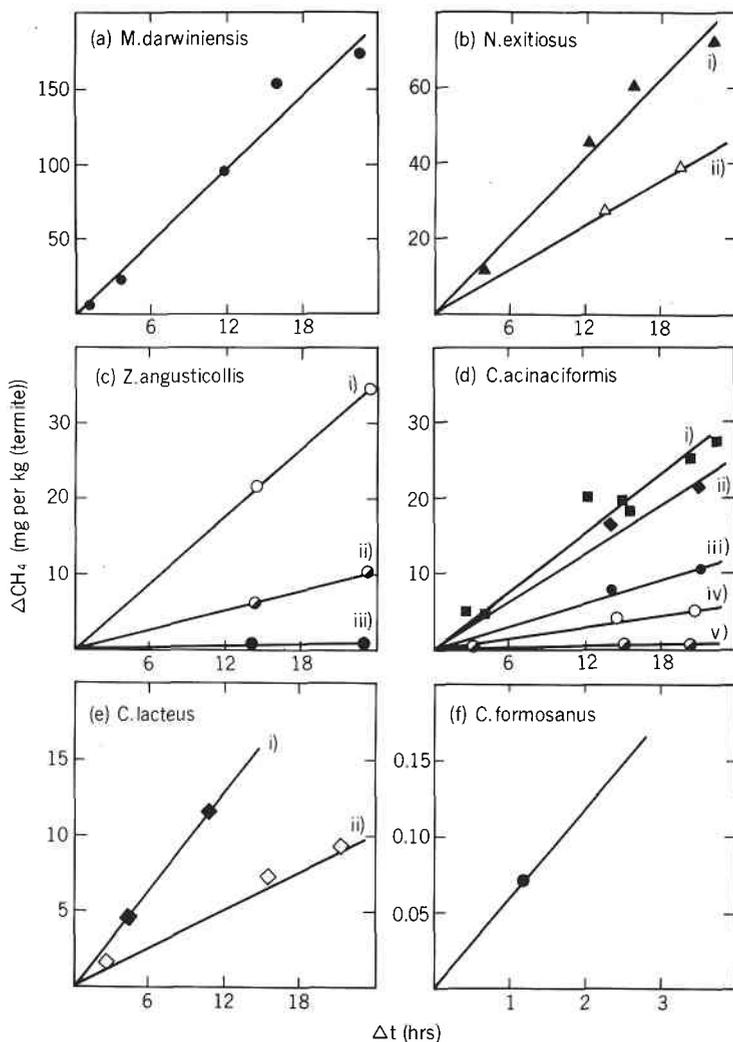


Fig. 3. The increase ( $\Delta\text{CH}_4$ ) in  $\text{CH}_4$  mass (mg) per kg (termite) with respect to laboratory air blanks as a function of  $\Delta t$ , time after initiation of experiment, for: (a) *M. darwiniensis* workers, experiment conducted at 28 °C; (b) *N. exitiosus*, workers, (i) 28 °C, (ii) 23 °C; (c) *Z. angusticollis*, workers, 19.5 °C from three different nests at (i) Beaverton, Oregon, (ii), (iii) from Hillsboro, Oregon; (d) *C. acinaciformis*, workers, (i)–(v) five subsets (from different mounds) 23 °C; (e) *C. lacteus*, workers from the laboratory mound maintained by CSIRO, Division of Chemical and Wood Technology; (i) 28 °C, (ii) 23 °C; (f) *C. formosanus*, 25°, workers from Hawaii.

Solid lines are linear regression through origin,  $\Delta\text{CH}_4 = k (\pm 1\sigma)\Delta t$ ,  $k$  (mg ( $\text{CH}_4$ ) per kg (termite) per hr) = (a) 8.0 ( $\pm 0.8$ ); (b) (i) 3.5 ( $\pm 0.4$ ), (ii) 2.0; (c) (i) 1.5, (ii) 0.44 (iii) 0.04; (d) (i) 1.3 ( $\pm 0.3$ ), (ii) 1.09, (iii) 0.51, (iv) 0.26, (v) 0.03 ( $\pm 0.02$ ); (e) (i) 1.1, (ii) 0.42 ( $\pm 0.02$ ); (f) 0.06.

Noirot, 1970; Lee and Wood, 1971), conditions which are reproduced in these simple experiments. Nest and mound  $\text{CO}_2$  concentrations are generally in the range 1–5% (Day, 1938; Noirot, 1970; Peakin and Josens, 1978), and there is even the suggestion that termites prefer elevated levels of  $\text{CO}_2$  (Bouillon, 1970), although nest design is such as to prevent the build-up of excessive  $\text{CO}_2$  concentrations (Peakin and Josens, 1978).  $\text{CO}_2$  levels in the glass jar experiments described here did not exceed 0.6%, and the levels attained in the mound experiment were about 1%. Thus, conditions in our experiments did not approach the  $\text{CO}_2$  and  $\text{O}_2$  levels that begin to stress termites, and the relatively constant  $\text{CH}_4$  and  $\text{CO}_2$  production rates we observed (Figures 2 and 3) suggest that the termites were not affected by the small changes in  $\text{CO}_2$  and  $\text{O}_2$  levels that occurred during these experiments. However there may be other unidentified environmental factors that could influence the results and may invalidate their extrapolation to approximate termite emissions in the field. In this paper we have assumed that these factors are negligible.

The five sets of *C. acinaciformis*, which showed  $\text{CH}_4$  emitting rates that varied from 0.03 to 1.28 mg  $\text{CH}_4$  per kg (termite) per hour (Figure 3), were collected from five, free standing mounds (1.5 m basal diameter, 1.5 m high), containing between 1.2 and 2.9 kg of termites ( $0.3 \times 10^6$  –  $0.8 \times 10^6$  termites) (Creffield *et al.*, 1985). Wood consumption

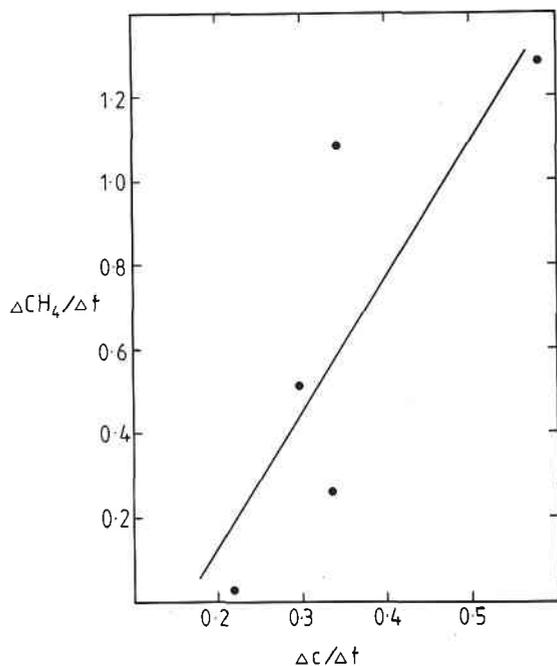


Fig. 4. The  $\text{CH}_4$  emission rate ( $\Delta \text{CH}_4/\Delta t$ : mg per kg (termite) per hr) as a function of rate of wood consumption ( $\Delta C/\Delta t$ : g (wood) per kg (termite) per hr) for five sets of *C. acinaciformis* from five different mounds. The solid line is a linear regression:  $\Delta \text{CH}_4/\Delta t = -0.5 (\pm 0.5) + 3.2 (\pm 0.1) \Delta C/\Delta t$ ,  $r^2 = 0.67$ .

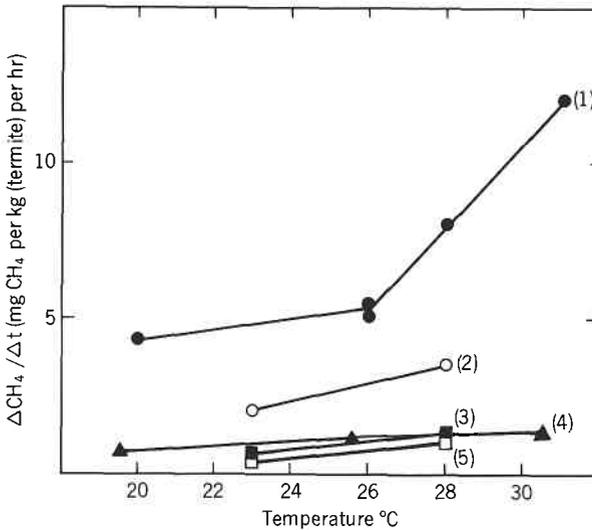


Fig. 5. Average CH<sub>4</sub> fluxes (mg CH<sub>4</sub> per kg (termite) per hr) as a function of temperature for workers of (1) *M. darwiniensis*, (2) *N. exitiosus*, (3) *C. acinaciformis*, (4) *Z. angusticollis*, (5) *C. lacteus*. *C. acinaciformis* at 23° is the average (0.6 ± 0.5) of the C.a. fluxes detailed in Figure 3 (d), (i)–(v); at 28°C, the average of the five subsets was 1.3 (± 1.0). *Z. angusticollis* at 19.5°C is the average (0.7 (± 0.7)) of the 3 subsets detailed in Figure 3 (c), (i)–(iii); at 25.5° and 30.5°C the averages were 1.2 and 1.4 respectively.

experiments involving samples of *P. radiata*, *E. regnans* and *Ceratopetalum apetalum* D. Don, also showed a range of results from 0.2 to 0.6 gm (wood) per kg (termite) per hour (J. W. Creffield, unpublished data). A positive correlation between wood consumed and CH<sub>4</sub> emitted is observed (Figure 4), with the average being 3.2 (± 0.1) mg CH<sub>4</sub> per gm of wood. Thus, from the results presented here, *C. acinaciformis* produces five times more CH<sub>4</sub> per gm of wood consumed than does *C. lacteus*.

The effect of temperature on CH<sub>4</sub> fluxes for a number of termite species is shown in Figure 5. Raising the temperature by 5°C within each species preferred temperature range (Table I) caused a 30–110% increase in measured CH<sub>4</sub> emissions for the termites studied. The specific CH<sub>4</sub> emission enhancement factors, when the temperature was raised by 5°C, obtained by linear interpolation of the data in Figure 5, are 2.4 (*M. darwiniensis*), 2.1 (*C. acinaciformis*), 2.6 (*C. lacteus*), 1.8 *N. exitiosus* and 1.3 *Z. angusticollis*. Larger factors (2.0, for 20° to 25°C; > 10, for 20° to 30°) have been reported for *Z. angusticollis* and *T. tibialis* respectively (Zimmerman and Greenberg, 1983). An average emission enhancement factor, for a 5°C rise in habitat temperature, of 2 is assumed in Table I, if the relevant experimental data are not available, to correct CH<sub>4</sub> emissions measured at a particular temperature to the corresponding mean habitat temperature.

Since CH<sub>4</sub> is produced by termites during the breakdown of cellulose, increased food consumption at higher temperatures probably contributes to these enhanced CH<sub>4</sub> releases. Becker (1970) has shown that for a number of termite species food consumption doubles

**Table I.** A summary of the classification, distribution, habitat, habitat temperature range and measured CH<sub>4</sub> emission rates of various northern and southern hemispheric, tropical and temperate termites studied in this work and elsewhere

Species	Family	Distribution	Habitat	Temp. <sup>b</sup>	Ref.	$\Delta\text{CH}_4/\Delta t$ <sup>c</sup>	Ref.
<i>Mastotermes darwiniensis</i> (Froggatt)	Masto- termitidae	10°–23° S N. Australia	Subterranean; trees	a. 24–28 m. 31–35	1	15	
<i>Nasutitermes exitiosus</i> (Hill)	Termitidae	25°–35° S E. & S. Aust.	Mound, 0.5m	a. 16–21 n. 26–31 m. 21–26	1,2	2.3	
<i>Coptotermes acinaciformis</i> (Froggatt)	Rhino- termitidae	15°–38° S N. & S. Aust.	Mound, 2m; trees	a. 14–26 n. 33–38 m. 20–32	1,2	1.0 <sup>d</sup> (± 85%)	
<i>Coptotermes lacteus</i> (Froggatt)	Rhino- termitidae	25°–38° S E. Aust.	Mound, 2m; trees	a. 14–21 n. 32–36 m. 23–29	1	0.8	
<i>Zootermopsis angusticollis</i> (Hagen)	Hodo- termitidae	50°–28° N W. U.S.A.	Damp wood	a. 4–21 p. 18–22 m. 11–22	3,4	0.6 <sup>e</sup> (± 100%) 2.5 <sup>f</sup>	8,9
<i>Zootermopsis nevadensis</i> (Hagen)	Hodo- termitidae	47°–32° N W. U.S.A.	Damp wood	a. 4–20 p. 18–22 m. 11–21	3,6	6.5 <sup>g</sup>	9
<i>Reticulitermes tibialis</i> (Banks)	Rhino- termitidae	46°–23° N central S.W. U.S.A.	Subterranean	a. 2–16 p. 24–28 m. 13–22	3,4	0.6 <sup>h</sup> (± 40%)	10
<i>Gnathamitermes perplexus</i> (Banks)	Termitidae	38°–23° N S.W. U.S.A.	Subterranean; trees	a. 7–16 m. 14–23	4,5	1.4 <sup>i</sup> (± 20%)	10
<i>Reticulitermes flavipes</i> (Kollar)	Rhino- termitidae	44°–23° N E. U.S.A.	Subterranean	a. 10–17 p. 24–28 m. 17–23	3,4	0.4 <sup>j</sup> (± 80%)	11
<i>Coptotermes formosanus</i> (Shiraki)	Rhino- termitidae	35°–10° N, 32° S S. U.S.A. S. Japan S. China S. Africa Pac. Islands	Subterranean; trees	a. 13–27 p. 26–30 m. 20–29	3,4,7	0.06 (± 120%)	11
<i>Cryptotermes brevis</i> (Walker)	Kalo- termitidae	32° N–32° S Caribbean Central & S. Africa N., Central & S. America	Dry wood	a. 18–24 p. 26–30 m. 22–27	3,4	0.2 <sup>k</sup>	10

<sup>b</sup> °C; *a* = annual mean ambient temperature appropriate to distribution; *n* = average nest temperature; *p* = preferred temperature from laboratory studies; *m* (mean habitat temperature) = (*a* + *n*)/2 or (*a* + *p*)/2 if *n* not available; or *a* + 7° is *n*, *p* not available.

<sup>c</sup>  $\Delta\text{CH}_4/\Delta t$  (mg CH<sub>4</sub> per kg (termite) per hour) at temperature *m* (mean habitat range), obtained by

linear interpolation of data in Figure 5, unless otherwise indicated.

d  $\pm 1$  standard deviation based on variability shown in Figure 3d.

e  $\pm 1$  s.d. based on Figure 3c.

f Assuming 50 mg per termite,  $\Delta\text{CH}_4/\Delta t = 2.5$  (20 °C and below)<sup>9</sup>.

g Assuming 50 mg per termite,  $\Delta\text{CH}_4/\Delta t = 6.5$  (20 °C and below)<sup>9</sup>.

h Assuming 3 mg per termite,  $\Delta\text{CH}_4/\Delta t = 5.9$  (30 °C)<sup>10</sup>, 0.6 (20 °C and below)<sup>9</sup>.

i Assuming 3 mg per termite,  $\Delta\text{CH}_4/\Delta t = 5.5$  (30 °C)<sup>10</sup>, 1.4 (20 °C and below), assuming a 5 °C temperature enhancement factor of 2 (see text).

j  $\pm 1$  s.d., wood diet<sup>11</sup>;  $\Delta\text{CH}_4/\Delta t = 0.8$  (25 °C), 0.4 (20 °C and below), assuming a 5 °C temperature enhancement factor of 2.

k At 25 °C.

#### References:

1. Gay and Calaby (1970)
2. Lee and Wood (1971)
3. Becker (1970)
4. Weesner (1970)
5. Peakin and Josens (1978)
6. Wood and Sands (1978)
7. Harris (1970)
8. Rasmussen and Khalil (1983)
9. Zimmerman and Greenberg (1983)
10. Zimmerman *et al.* (1982)
11. Breznak (1975)

for a 5° rise in habitat temperature. *N. exitiosus* and *M. darwiniensis* also consume wood at 25–35% higher rates when their habitat temperature is raised from 26° to 32 °C over an eight week test period (Howick *et al.* 1975; Howick and Creffield, 1979). However, for *M. darwiniensis*, CH<sub>4</sub> production rises by a factor of 2.4 over this temperature range (Figure 5), and it would appear that the relationships between food consumption, CH<sub>4</sub> production and ambient temperature are not directly proportional. This is not unexpected since many other factors may be involved (e.g. availability of food, effect of temperature on respiration).

An attempt has been made to infer, from these and other laboratory measurements, the contribution made by termites to the global CH<sub>4</sub> budget. Table I presents a summary of habitat, habitat temperature range, and measured CH<sub>4</sub> emission rates (mg CH<sub>4</sub> per kg (termite) per hour), adjusted to mean habitat temperatures, for termites studied in this work and others as reported in the literature. An estimate of the global production of CH<sub>4</sub> due to termites is given in Table II. There are numerous uncertainties involved in arriving at the final figure of 14 Tg per year. Some idea of the magnitude of these uncertainties are shown in Table 2. Generally speaking the uncertainties ( $\pm 1$  standard deviation) associated with the biomass densities and CH<sub>4</sub> production rates per kg (termite) for each ecological region are approximately 100%. Thus the resulting uncertainty in CH<sub>4</sub> production per ecological region is 200%, giving an upper limit per region which is a factor of three greater than the mean. Assuming a lower limit to be a factor of three smaller than the mean, an uncertainty range for the global annual CH<sub>4</sub> source due to termites of approximately 6–42 Tg is calculated.

However there are other uncertainties in this calculation of a global CH<sub>4</sub> flux due to termites that cannot be quantified with the data currently available. For example no CH<sub>4</sub> emission data, in the form of mass of CH<sub>4</sub> per mass of termites per unit time, have

Table II. Termite biomass densities, CH<sub>4</sub> production rates for various ecological regions, and global CH<sub>4</sub> production due to termites.

Ecological Region	Area <sup>a</sup> (10 <sup>12</sup> m <sup>2</sup> )	Biomass <sup>b</sup> density (g m <sup>-2</sup> )	ΔCH <sub>4</sub> /Δt <sup>e</sup> (mg per kg (termite) per hr)	Annual CH <sub>4</sub> production (10 <sup>12</sup> g = Tg)	Possible <sup>j</sup> range
Tropical forest (wet and dry)	18.5	5.6 (± 90%) <sup>c</sup>	5.4 (± 150%) <sup>f</sup>	4.9	2–15
Temperate forest wood/scrubland	20.5	3.0	1.8 (± 120%) <sup>g</sup>	0.9	< 1–3
Savannah (wet and dry)	18.5	4.5 (± 100%)	8.0 (± 120%) <sup>h</sup>	5.8	2–17
Temperate grassland	9.0	d	d	0.4	< 1–1
Cultivated land	11.9	7.8 (± 120%)	d	1.3	< 1–4
Desert scrub	18.0	3.1 (± 100%)	1.0 (± 40%) <sup>i</sup>	0.5	< 1–2
TOTAL	96.4	4.37 × 10 <sup>14</sup> g (biomass)		14	6–42

<sup>a</sup> Zimmerman *et al.* (1982)

<sup>b</sup> Wood and Sands (1978)

<sup>c</sup> 1 standard deviation

<sup>d</sup> assume same as temperate forests

<sup>e</sup> from Table I

<sup>f</sup> mean (± 1 s.d.) of *M. darwiniensis*, *C. acinaciformis*, *C. brevis*

<sup>g</sup> mean (± 1 s.d.) of *C. acinaciformis*, *C. lacteus*, *C. formosanus*, *Z. angusticollis*, *Z. nevadensis*, *R. flavipes*, *N. exitiosus*

<sup>h</sup> mean (± 1 s.d.) of *M. darwiniensis*, *C. acinaciformis*

<sup>i</sup> mean (± 1 s.d.) of *R. tibialis*, *G. perplexus*, *C. acinaciformis*

<sup>j</sup> upper limit = production × 3, lower limit = production ÷ 3 (see text)

been published for tropical forest termites. In making the estimate of approximately 5 Tg per year for tropical forest termites, the assumption has been made that *M. darwiniensis*, *C. acinaciformis* and *C. brevis* are representative of tropical forest termites. Clearly this may not be the case and the same applies for termites from each of the ecological regions. According to Table II tropical forest and savannah termites contribute approximately 80% of global termite emissions and data from only three species (*M. darwiniensis*, *C. acinaciformis* and *C. brevis*) are used to arrive at these numbers. Clearly more work is required in quantifying emissions from representative tropical forest and grassland termites.

It has been shown in this paper that for one species of termite (*C. lacteus*) the experiments in glass jars give reasonable estimates of CH<sub>4</sub> fluxes from living termite mounds, perhaps over estimating fluxes by 40%. Whether this assumption is true for other species of termites is, at present, unknown. Probably glass jar experiments, as detailed in this

paper, in general over estimate  $\text{CH}_4$  fluxes due to termites because of the presence of  $\text{CH}_4$  destroying microorganisms in termite mounds and nests (Seiler *et al.*, 1984).

The results presented in this paper suggest that  $\text{CH}_4$  production by termites approximately doubles for a  $5^\circ\text{C}$  rise in habitat temperature (Figure 5). The magnitude of the estimate of  $\text{CH}_4$  emissions due to termites is significantly dependant on the assumptions made concerning average termite habitat temperature. From field and laboratory studies it seems that many termites prefer temperatures in excess of  $10^\circ\text{C}$  above the ambient air temperatures determined by their geographical distribution. However, the thermal properties of nests vary considerably (Lüscher, 1961), with thin walled nests being maintained at ambient outside temperatures while thick walled nests achieve a considerable temperature elevation. Not all termites live their entire lives within the nests, either moving along extended galleries or surfacing above ground in search of food. This is why the assumption was made (Table I) that the mean temperature experienced by termites ( $m$ ) is an average of the annual average ambient temperature ( $a$ ) and their nest or preferred temperature ( $n$  or  $p$ ), the difference between  $m$  and  $n$  or  $p$  being about  $6\text{--}7^\circ\text{C}$ . If the assumption were made that termites, on average, experience temperatures much closer to their nest or preferred values then the estimates of  $\text{CH}_4$  production due to termites could conceivably double.

Zimmerman *et al.* (1982) estimated a global annual  $\text{CH}_4$  source due to termites of 150 Tg, with an uncertainty range of 75–310 Tg. They based this estimate on the ability of termites to convert biomass to  $\text{CH}_4$ , as measured in the laboratory, and used annual estimates of biomass consumed by termites to deduce this annual  $\text{CH}_4$  release. They assumed digestive processes amongst different termite species to be similar so that, on average, approximately 0.8% of carbon ingested was readmitted as  $\text{CH}_4$ . This assumption of constant conversion efficiency was based on experiments with *R. tibialis* and *G. perplexus* (Zimmerman *et al.*, 1982) and later confirmed for *Z. angusticollis* (Zimmerman and Greenberg, 1983).

Their calculation has been criticised by other researchers. Rasmussen and Khalil (1983) estimated a global  $\text{CH}_4$  production due to termites of about 50 Tg per year, based on laboratory measurements of  $\text{CH}_4$  emissions per termite, and estimates of the global termite population. They suggested that the global  $\text{CH}_4$  source calculated by Zimmerman *et al.* (1982) implies  $\text{CH}_4$  emission rates per termite that are 3–4 times higher than those measured in the laboratory.

Collins and Wood (1984) suggest that the Zimmerman *et al.* (1982) estimate of biomass consumed by termites per year ( $33 \times 10^{15}$  g) is at least an order of magnitude too high, due essentially to the lack of global representativeness of the various species of termites studied in the laboratory. They also suggested that the termite species studied by Zimmerman *et al.* (1982), on which their biomass to  $\text{CH}_4$  conversion factor was based, are also globally unrepresentative and would lead to  $\text{CH}_4$  emission estimates that are too large.

Seiler *et al.* (1984) estimated global  $\text{CH}_4$  emissions due to termites of 2–5 Tg per year, based on the lower estimates of biomass consumed by termites from Collins and Wood (1984), and biomass to  $\text{CH}_4$  conversion efficiencies that are approximately 4–5 times lower than those employed by Zimmerman *et al.* (1982).

The hypothesis of a constant efficiency for biomass to CH<sub>4</sub> conversion by termites needs to be tested further. An exception to this generalization is *C. formosanus*, a successful, wide-spread and very destructive termite, which has been shown by two independent laboratories to produce virtually no CH<sub>4</sub> (Table I). Table III draws together data from the literature that suggest that CH<sub>4</sub> production efficiencies could in fact vary considerably from species to species. Calculated values of  $\Delta\text{CH}_4/\Delta\text{C}$  (mg CH<sub>4</sub> per g (carbon in diet)) vary by approximately two orders of magnitude, with species such as *M. darwiniensis* and *Z. angusticollis* producing near 20 mg of CH<sub>4</sub> per g (carbon) consumed, while *C. formosanus* and *Reticulitermes flavipes* (Kollar) yield less than 1 mg of CH<sub>4</sub> per g (carbon). These data (Table III) must contain considerable uncertainties, for they are largely derived from separate experiments. Nevertheless, the data suggest that CH<sub>4</sub> production by termites may not be a constant function of carbon consumed, and the variability in  $\Delta\text{CH}_4/\Delta\text{C}$  (Table III) is essentially due to the large (two orders of magnitude) interspecies variability in CH<sub>4</sub> emissions ( $\Delta\text{CH}_4/\Delta t$ ),  $\Delta\text{C}/\Delta t$  being relatively constant, varying by a factor of three over the species studied to date.

Some support for a lower estimate of biomass consumed by termites, compared to that calculated by Zimmerman, can be obtained from Tables II and III, where the total

Table III. CH<sub>4</sub> produced per g of diet carbon consumed for different species of termites.

Species	diet	temp. (°C)	$\Delta\text{C}/\Delta t$ <sup>b</sup>	References	$\Delta\text{CH}_4/\Delta t$ <sup>d</sup>	$\Delta\text{CH}_4/\Delta\text{C}$ <sup>h</sup>
<i>M. darwiniensis</i>	wood	26	0.2–0.4	1, 2	5.3	18
<i>N. exitiosus</i>	wood	26	0.2–0.3	1–4	2.9	12
<i>C. acinaciformis</i>	wood	26	0.1–0.4	2, 5–7	1.0	4
<i>C. lacteus</i>	wood	26	0.2–0.5	2, 7, 8	0.8	2
<i>Z. angusticollis</i>	wood	26	0.2	2	3.5 <sup>e</sup>	18
<i>R. tibialis</i>	wood		0.4 <sup>c</sup>		3.3 <sup>f</sup>	8 <sup>i</sup>
<i>G. perplexus</i>	manure		0.3 <sup>c</sup>		3.3 <sup>g</sup>	11 <sup>i</sup>
<i>R. flavipes</i>	wood	<sup>a</sup>	0.6	9	0.4	0.7
<i>C. formosanus</i>	wood	<sup>a</sup>	0.4	9	0.06	0.2

<sup>a</sup> assume 25 °C

<sup>b</sup> g (carbon in diet) per kg (termite) per hr, assuming diet is 45% carbon

<sup>c</sup> from  $(\Delta\text{CH}_4/\Delta t)/(\Delta\text{CH}_4/\Delta\text{C})$

<sup>d</sup> mg CH<sub>4</sub> per kg (termite) per hr, adjusted to 26 °C (Table I, Figure 5)

<sup>e</sup> average of this work and (10)

<sup>f</sup> assuming 3 mg per termite,  $\Delta\text{CH}_4/\Delta t = 5.9$  (30 °C)<sup>11</sup>, 0.6 (20 °C)<sup>10</sup>, adjusted to 26 °C

<sup>g</sup> assuming 3 mg per termite,  $\Delta\text{CH}_4/\Delta t = 5.5$  (30 °C)<sup>11</sup>, 2.8 (25 °C)<sup>10</sup>, adjusted to 26 °C

<sup>h</sup> mg CH<sub>4</sub> per g (carbon in diet), from  $(\Delta\text{CH}_4/\Delta t)/(\Delta\text{C}/\Delta t)$

<sup>i</sup> from (11)

#### References:

1. Howick *et al.* (1975)
2. Wood (1978)
3. Howick and Creffield (1979)
4. Watson *et al.* (1978)
5. Howick and Creffield (1980)
6. Creffield *et al.* (1985)
7. J. W. Creffield (unpublished data)
8. Lenz *et al.* (1980)
9. Haverty (1976)
10. Zimmerman and Greenberg (1983)
11. Zimmerman *et al.* (1982)

biomass of termites is estimated to be  $4.4 \times 10^{14}$  g and biomass consumption rates vary from 0.1 to 0.6 g (carbon) per kg (termite) per hour, resulting in a range of biomass consumed per year of  $1 - 5 \times 10^{15}$  g, assuming biomass is 45% carbon. This figure is an order of magnitude lower than that calculated by Zimmerman *et al.* (1982), and essentially the same as that deduced by Collins and Wood (1984) of  $3.4 \times 10^{15}$  g per year.

#### 4. Conclusion

This paper reports new CH<sub>4</sub> emission data from a number of termite species from tropical and temperate regions of the Northern and Southern Hemisphere, using laboratory experiments. For one species (*C. lacteus*) these laboratory experiments are shown to give CH<sub>4</sub> fluxes that are in reasonable agreement with that measured from a living termite mound maintained in the laboratory. From the data presented here a global annual CH<sub>4</sub> source due to termites of approximately 14 Tg is calculated. However the major uncertainties in this estimate are identified and found to be very substantial, resulting in a possible range of 6–42 Tg. Assuming global CH<sub>4</sub> emissions due to all sources are around 400 Tg per year suggests that termites contribute less than 5% of the global CH<sub>4</sub> source budget.

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