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RASMUSSEN AND KHALIL REPLY— Zimmerman and his colleagues have claimed that termites release 150 Tg of methane into the Earth's atmosphere every year[1]. We show in our paper[2] that this estimate is likely to be too high by at least a factor of 3. The source of our disagreement is the method for extrapolating limited laboratory data to the global environment.

Zimmerman and Greenberg are concerned about high CO_2 levels in our jar studies[2], however, their use of an open flow-through system may add more uncertainties to measurements of emission rates (or consumption ratios) than a closed jar system. Termite mounds and galleries in the natural environment contain high levels of CO_2 and humidity depending on the types of termites involved and their habitats. Indeed, species such as *Nasutitermes exitiosus* (Hill) and *Coptotermes acinaciformis* (Froggatt) build thick-walled mounds to preserve water vapour and thus CO_2 and CH_4 as well. Peakin and Josens[3] show that CO_2 concentration inside the nests of many termite species ranges from 0.4% to 4 or 5% and in certain conditions up to 15%. By comparison atmospheric CO_2 concentration is ~0.03%, and CO_2 measurements in our jar studies were 0.5–1.5%. Thus, a flow-through system may not be representative of the natural environment.

Zimmerman and Greenberg are critical of our equation (3) which was constructed to represent Table 2 of their paper[1]. ϵ_i, m_{b_i} and A_i are defined by the colums in Table 2 so that their product $\epsilon_i m_{b_i} A_i$ is the "total termite consumption"[1] $= T_i$ in the i th ecological region. When multiplied by δ, the ratio of CH_4 produced to biomass consumed, one obtains δT_i or the "annual CH_4 production (10^{12} g)" in the i th ecological region (Table 2 of ref. 1). Zimmerman and Greenberg state that they calculated T_i by the product $d_i C_i A_i$ where d_i = termite density in the i th ecological region in "Termites per square metre"[1], C_i = average biomass consumption (g), and A_i is the area of the region as before (m^2). The two formulae are equivalent means for arriving at T_i, except that the average consumption C_i is not given in Table 2 of ref. 1, whereas all the variables of our formula are in the table. We wrote equation (3) to show that T_i is a product of several variables, each subject to errors which propagate to produce larger errors in estimating T_i. We also wanted to point out that δ, which is the ratio of CH_4 produced to grammes of carbon (biomass) consumed, is assumed to be the same for all ecological regions, all types of diets, and all species of termites. Moreover, it is assumed that δ measured in a few laboratory studies can be safely extrapolated to the varied global environment. Equation (3) may be rewritten as $p_G = \sum_{i=1}^{N} T_i \delta_i$, which shows that the global production of CH_4 by termites (p_G) is the sum of the methane production in each ecological region (p_i). p_i is the production of CH_4 in the i th ecological region expressed as the product of "total termite consumption"[1] (of biomass), T_i and δ_i, the emission yield per gramme carbon ingested which varies from one ecological region to the next. The errors in T_i and δ_i over some 11 ecological regions produce large uncertainties in the calculated p_G. These points regarding error propagation and uncertainty analysis are not affected by the means chosen to calculate T_i (as $\epsilon_i M_{b_i} A_i$ or $d_i C_i A_i$). Due to lack of data the true magnitude of the uncertainty in the calculation of p_G cannot be gauged at present, but it is likely to be substantially more than "a factor of 2", which is stated but neither derived nor adequately justified in ref. 1.

This brings us to the crux of the disagreement between us and Zimmerman *et al.* We use measured emission rates ($\bar{p} = \mu g\ CH_4$ per yr per termite) to estimate global production as $p_G = \bar{p} N_\infty$ where N_∞ is the total number of termites in the world[2]. Zimmerman *et al.*[1] use measured ratios (δ) of CH_4 emission per gramme carbon ingested and estimate global production as $p_G = \delta T$, where T is the world "total termite consumption" of biomass. With this synopsis of our work and Zimmerman *et al.*'s paper[1], it is clear that claims of one method being superior to the other are difficult to justify since each has its advantages and disadvantages. Is the extrapolation of laboratory measurements of average CH_4 production by termites to global scales any better or worse than extrapolation of laboratory measurements of average CH_4 emission ratio δ to global scales? Is the world population of termites (N_∞) known any more or less accurately than the total biomass consumed (T) by the world's termites? Even if the laboratory measurement of one of the two variables, $\bar{p}$ or δ, is more accurate than the other, do not the enormous uncertainties in N_∞ and T offset any such advantage and still make the two types of estimates equally unreliable?

The claim by Zimmerman and Greenberg that δ is "... much more uniform among various termite species than emission rates" is not only unsupported by scientific studies but may in fact be untrue. For instance, *Coptotermes formosanus* (Shiraki) are a widespread subtropical species which consume enormous amounts of wood (0.98 g (wood) per kg termite per h)[4], yet produce practically no methane, as shown by Breznak[5] and in our own experiments ($\bar{p} \sim 0.03\ \mu g$ per termite per day). Wood[6] has shown that laboratory colonies of *Mastotermes darwiniensis* (Froggatt), *Zootermopsis angusticollis* (Hagen), *Coptotermes acinaciformis* (Froggatt), *Coptotermes lacteus* (Froggatt) and *Nasutitermes exitiosus* (Hill) comsume 0.48, 0.42, 0.74, 0.51 and 0.48 g (wood) per kg (termite) per h, respectively. These same termites produce 15, 0.5–0.9, 12, 0.7 and 2.3 mg CH_4 per kg (termite) per h respectively (P. J. Fraser and R. A. R. unpublished data). This amounts to a ratio of δ' of 31, 1–5, 21, 1 and 5 mg CH_4 per kg wood consumed, respectively.

Therefore, Zimmerman *et al.*'s extrapolation of few data for δ to estimate gobal CH_4 production by termites may be no more reliable than extrapolation of emission rates. In our opinion, the measurement of δ in the natural environment is also more complex and unreliable than an analogous measurement of $\bar{p}$. Field measurement of δ requires an estimate of biomass consumption and termite density, whereas field measurement of $\bar{p}$ requires only an estimate of the number of termites in the colony.

Finally, Zimmerman *et al.*[1] estimate that there are 2.4×10^{17} termites in the world producing 151.6 Tg CH_4 yr^{-1}, or an average of 1.7 μg per day per termite; yet average emissions from the five colonies they studied[1] show emission rates of 0.2–0.6 μg per day per termite or 3–8 times less than required to achieve 150 Tg yr^{-1}. We agree that termites produce methane, however, at present we find no reason to believe that this source amounts to a worldwide production of 150 Tg yr^{-1}.

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