

CO₂ Emission from Epigeal Mounds of Non-Fungus Growing Termites in a Seasonal Tropical Forest, Thailand

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Abstract

Termites, as main decomposers, are major contributors driving carbon cycle by litter decomposition. Termites were emphasized as one of high CO₂ emission sources of spatial variation in soil respiration. The aim of this study was to compare CO₂ emissions from the epigeal mounds of non-fungus growing termites in dry evergreen forest of Thailand. CO₂ emission was directly measured on mounds and surrounding soils of five termite species ($n = 5$) with a portable infrared gas analyzer connected to PVC pipes during the wet season (October 2015) and the dry season (January 2016). The CO₂ emissions were significantly different between termite species. *Globitermes sulphureus* had the highest nest CO₂ emission ($37.7 \pm 14.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ Mean \pm SD), followed by *Microcerotermes crassus*, *Termes comis*, *Termes propinquus* and *Dicuspiditermes makhamensis*, respectively. CO₂ emissions in termite mounds and their surrounding soil were significantly higher in wet season than dry season. *Globitermes sulphureus* and *M. crassus* mounds produced significantly more CO₂ than surrounding soils but *T. propinquus* and *D. makhamensis* produced significantly less CO₂ than surrounding soils. Therefore, *G. sulphureus* and *M. crassus* are major CO₂ producers among non-fungus growing termites in a tropical forest.

Introduction

Tropical forests significantly impact global climate by regulating greenhouse gas and storing 45-50% of global terrestrial carbon stocks (IPCC, 2007). Soil CO₂ emission (soil respiration) plays an important role in global carbon cycling with contributing more than 50% of the total ecosystem respiration (Janssens et al., 2001; Xu et al., 2001; Chambers et al., 2004). Soil CO₂ emission from tropical forests could strongly influence future concentrations of atmospheric carbon dioxide. However, soil respiration considerably varied with space and time (Boonriam et al., 2021a). Spatial variability in soil respiration from tropical forests remains difficult to assess and it may lead to inaccurate soil respiration estimates at ecosystem level. Consequently, understanding of above and belowground soil activities on carbon cycle in tropical forest is necessary.

Soil respiration comes from CO₂ production of all living organisms in the soil, including plant roots, soil microbes, and animals (Lavelle et al., 2001; Luo and Zhou, 2006). Soil microorganisms and roots are thought to dominate most soil respiration. However, soil respiration rate has been shown to fluctuate unexpectedly (10-90%) at large scales (Hanson et al., 2000). The known environmental factors: soil, water content, and temperature are unable to completely explain this variation. According to Ohashi et al. (2007; 2017), certain areas displayed extremely higher rates of soil respiration (hot spots) and soil macrofauna were focused as a predominant driver in tropical forests. Events were attributed to the undisclosed activities of soil animals,

particularly social insects such as termites. Because it is widely known that termites are superabundant soil insects in seasonal tropical forests (Yamada et al., 2003, 2005; Inoue et al., 2006).

Termites are major structural components of soil partition up to 95% of the total soil insect biomass (Jones and Eggleton 2000) and population density in the tropics could reach up to 1000 termites per m² (Eggleton et al., 1996). Termites are widely distributed along an altitudinal gradient from lowland to mountain (Kayani et al., 1979; Akhtar et al. 1992). Termites are significantly important to drive carbon cycle by litter decomposition as much as half of the primary litter production (e.g. Matsumoto and Abe, 1979; Bignell and Eggleton, 2000; Coleman et al., 2004). Termites can be divided into two major feeding groups, wood/litter feeders (fungus and non-fungus growers) and soil feeders (non-fungus growers) (Wood, 1976; Collins, 1989; Bignell et al., 1997; Bignell and Eggleton, 2000). Fungus growing termites cultivate symbiotic fungi on fungus gardens (fungus combs) consisting of plant litter materials built with partially digested termite faeces (Korb, 2003). Termite CO₂ emissions were estimated to contribute up to 2% of global terrestrial emissions (Sugimoto et al., 2000). Several studies considered epigeal termite mounds as high CO₂ emission point sources. As the epigeal termite mounds in tropical savanna emitted higher CO₂ than surrounding soils with emphasis on fungus growing termite (Macrotermitinae) (Konate et al., 2003; Brümmer et al., 2009; Risch et al., 2012), except in seasonal tropical forest (Boonriam et al., 2021b). Besides, De Gerenyu et al. (2015) reported that termite mounds contributed up to 10% of the total soil respiration in a tropical monsoon forest in Vietnam. Thai-tropical forests also contain various epigeal termite mounds, especially non-fungus growing termites (Termitidae) due to the number of species and nests were higher than fungus growing termites (Yamada et al., 2003). According to Korb (2003), epigeal termite mounds have a different complex architecture to maintain a constant temperature and humidity. While the seasonal tropical forests have sometimes a fluctuation of the climate. Consequently, determining epigeal mound CO₂ emission in terms of non-fungus growing termites is one of the best approaches for evaluating soil biological activities in relation to carbon and energy flow in terrestrial ecosystems.

This study aimed to 1) compare CO₂ emission from epigeal mounds of different non-fungus growing termites in a seasonal tropical forest, 2) compare CO₂ emission from the mounds and their surrounding soils, and 3) determine the relationship between the surrounding soil CO₂ emissions and soil environmental factors in the dry and wet seasons.

Materials and Methods

Study site

A field study was performed in the dry evergreen forest (DEF) at Sakaerat Environmental Research Station (SERS) (14°30'N, 101°56'E; about 500 m above sea level) in Nakhon Ratchasima Province, northeastern Thailand (Fig 1). According to SERS meteorological stations from 2005 to 2015, the mean annual rainfall was 1,084 mm with monthly rainfall less than 40 mm during the dry season from November to April and the wet season started from May to October. The average annual relative humidity and temperature were 83.8% and 26.7°C (9.1-38.9°C), respectively. During the study, the monthly rainfall, temperature, and relative humidity were 189 mm, 25.1°C, and 74.4%, respectively in October 2015 (wet season) and 12.1 mm, 23.7°C, and 71.0%, respectively in January 2016 (dry season). The DEF covers an area of 29.5 km², where the dominant tree species are *Hopea ferrea* and *Hopea odorata* with canopy trees reach generally 23 to 40 m (Lamotte et al., 1998).

Field experiments

Five dominant species of the epigeal mound-building of non-fungus growing termites were selected for this study, namely *Dicospiditermes makhamsensis*, *Globitermes sulphureus*, *Microcerotermes crassus*, *Termes comis*, and *Termes propinquus*. Mound characteristic (e.g. population colony) of the non-fungus growing termites in each species had been preliminarily observed by a cross-section. Morphological characters of termite soldiers and the shape of their mounds were observed (Fig 2).

The five mounds of each termite species were randomly selected with a distance greater than 5 m between

each mound. The mound sizes were measured for the height (base to the top) and circular length of the bottom. Three to five PVC collars (10 cm in diameter and ca. 3 cm in height) were placed at the mound and surrounding soils 10 to 30 cm from the mound at least one day before the measurement to avoid the disturbance of soil activities (Fig 3). The CO₂ emissions of each mound was measured by using a portable infrared gas analyzer (IRGA, EGM-4, PP Systems, Hitchin, UK) with a closed soil CO₂ efflux chamber (SRC-1, PP Systems) (10 cm diameter) one time in October 2015 (wet season) and January 2016 (dry season).

After CO₂ measurement, soil temperature and soil moisture content of the surrounding soils were measured immediately around each PVC collar at about 10 cm depth with a digital thermometer waterproof probe (type H-1 and H-2, Shinwa Co., Ltd., Japan) and soil moisture sensor (SM150, Delta-T Devices Ltd., Cambridge, UK), respectively. However, soil temperature and soil moisture content of the mounds were not measured because to avoid disturbing mound and termite activity. All measurements began from 9:00 am to 6:00 pm (3 to 5 minutes per location) in the day without rain.

Statistical analysis

All the analysis was performed on log-transformed data to transform the skewed data to approximately conform to normality. The Kolmogorov – Smirnov test was used to test for normality. Then, an analysis of CO₂ emission rates for detecting significant differences among the termite mound species was tested by the analysis of variance ANOVA as well as their surrounding soils during the dry and wet seasons. Mean for groups in homogeneous subset among species were evaluated by Tukey HSD's post hoc test. The difference of CO₂ emission from the nest and surrounding soil in each species was tested by t-test. The relationship between CO₂ emission from surrounding soil and the soil environmental factors (i.e. soil temperature and soil moisture content) was determined with the Pearson correlation analysis. All statistical calculations were performed in SPSS ver. 20.0.0 for Windows.

Results

Rate of CO₂ emissions were directly detected on the mounds of 5 dominant termite species (n = 5) during the dry and wet seasons in the DEF at SERS. The characteristic of the selected termite mounds was described as the size, feeding group, and physical and environmental factors (Table 1). The mound CO₂ emissions were widely variable ranging from 0.17 to 55.15 $\mu\text{mol CO}_2\text{m}^{-2} \text{s}^{-1}$, while the range of CO₂ emissions from their surrounding soil was considerably narrower from 0.68 to 14.86 $\mu\text{mol CO}_2\text{m}^{-2} \text{s}^{-1}$. The results showed that the mean of the CO₂ emission rate was significantly different between the termite species ($F = 49.174$ $P < 0.001$) (Table 2).

The highest average of the mound CO₂ emission was from *G. sulphureus* that reached up to $37.7 \pm 14.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ mean \pm SD, followed by *M. crassus*, *T. comis*, *T. propinquus* and *D. makhimensis* which were 15.50 ± 7.84 , 6.45 ± 2.35 , 1.98 ± 1.78 , and $1.79 \pm 0.99 \mu\text{mol m}^{-2} \text{s}^{-1}$ mean \pm SD, respectively. In both locations, CO₂ emission rate was significantly different between the mound and surrounding soil ($F = 35.210$, $P < 0.001$) (Table 2) (Fig 4). While CO₂ emission from the surrounding soil alone was not different between species ($P = 0.657$) (Fig 4).

The mean of the total CO₂ emission from the mounds ($12.68 \pm 15.41 \mu\text{mol m}^{-2} \text{s}^{-1}$ mean \pm SD) was 2.5 times higher than surrounding soils ($5.06 \pm 3.29 \mu\text{mol m}^{-2} \text{s}^{-1}$ mean \pm SD). The overall mean of CO₂ emissions from the mounds was 3.9 and 2.1 times higher than surrounding soils in the dry and wet seasons, respectively (Fig 5). There was a significant difference for both mounds and surrounding soils between the dry season and wet season ($F = 14.957$ $P < 0.001$) (Table 2). In each season, mound CO₂ emissions were significantly different among the species and surrounding soils in the dry season and wet season ($P < 0.001$). The mound CO₂ emissions from *G. sulphureus* and *M. crassus* mounds were significantly higher than surrounding soils in both dry and wet seasons. In contrast, *T. propinquus* and *D. makhimensis* emitted significantly CO₂ less than the surrounding soils (Fig 6).

The average rate of CO₂ emission from surrounding soils was 3.4 times higher in the wet season ($7.83 \pm$

2.33 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ mean \pm SD) than the dry season (2.29 \pm 0.89 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ mean \pm SD). The relationship between the soil CO₂ emissions, soil temperature, and soil moisture content aids in distinguishing seasonal variations. The CO₂ emission rates from surrounding soils were positively correlated with soil moisture contents. (Pearson correlation, $r = 0.804$, $P < 0.001$) (Fig 7). The highest CO₂ emission rates (more than 10 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were found at around 10 to 19% of the soil moisture content. While the relationship between soil temperature and surrounding soil CO₂ emission was not significant (Pearson correlation, $r = -0.024$, $P = 0.768$). The soil temperature had limited variation from 21.8 to 27.5 °C.

Discussions

This study found that the CO₂ emission from the mounds of non-fungus growing termites were different between species and their surrounding soils during both dry and wet seasons in a tropical seasonal forest. The mean annual mound CO₂ emission was 2.5 times higher than surrounding soils. In particular, CO₂ emissions from the mounds of *G. sulphureus* and *M. crassus* were much higher than other termite species and greater than their surrounding soils in both seasons. The high CO₂ emissions were from the mounds from these species because their populations were found ubiquitously in the nest or mound with a thin wall, whereas the other species were found in some part of the nest. Also, most of the nest materials are mixed from the macerated wood and their faeces (Bignell and Eggleton, 2000). Moreover, *G. sulphureus* and *M. crassus* are a group of wood/litter feeders that these species may be consumed directly to organic carbon much more than the soil feeders. Although respiratory rate varied inversely with body weight, the substrates for all feeding groups have an effect on the variations in metabolic rate (Jeeva et al., 1999). In the same forest, these two species were found in high abundance and biomass, especially *M. crassus* was 46% and 36% of the termite abundance and biomass, respectively (Yamada et al., 2003). Therefore, the mounds of *G. sulphureus* and *M. crassus* could potentially drive the high spatial variation in soil CO₂ emission in the tropical seasonal forests.

As a result, the mean CO₂ emission rate from the mound of *G. sulphureus* was higher than the mound of other species in this study. This emission rate was also higher than the mound from the other studies in both non – fungus grower (Brümmer et al., 2009; Jamali et al., 2013; De Gerenyu et al., 2015; Konemann and Kard, 2016) and fungus – grower termites (Konate ´ et al., 2003; Nyamadzawo et al., 2012; Sawadogo et al., 2012; Ohashi et al., 2017) from the different topography, except for some rates of CO₂ emissions from the subterranean nest of termites (e.g. *Hospitalitermes hospitalis*) in a tropical rainforest (Ohashi et al., 2017) (Table 3).

In addition, the other soil organism was proposed as the CO₂ point source such as ants and earthworm (Khalil et al., 1990; Stoyan et al., 2000; Risch et al., 2005; Ohashi et al., 2007). According to Ohashi et al. (2017) reported that the CO₂ emission rate from the subterranean nest of ant *Dinomyrmex gigas* (45.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was higher than the rate in this study. However, the CO₂ emission rate from *G. sulphureus* mound in this study that was higher than soil CO₂ emission which affected by the other ants (Sousa-Souto et al., 2012; Hasin et al., 2014; Fernandez-Bou et al., 2019) and earthworms (Šimek and Pižl, 2010) (Table 3). In term of earthworms, although there were no effect on the emission of CO₂ from soil (Guo et al., 2019), earthworms have increased the carbon content and other nutrients (Lavelle et al., 2001) for enhancing soil respiration by microbial activities.

Meanwhile, the CO₂ emissions from *T. propinquus* , *D. makhamensis* , and *T. comis* mounds were both much lower than *G. sulphureus* and *M. crassus* and were significantly lower than surrounding soils in both seasons (except for *T. comis* which did not differ between surrounding soils in the wet season). However, these three species are categorized as soil-feeder, while *G. sulphureus* and *M. crassus* are wood/litter-feeder (Wood, 1976; Collins, 1989; Bignell et al., 1997; Bignell and Eggleton, 2000). This was probably due to the respiration rate from termite populations of soil-feeders was lower than wood/litter-feeders. According to Yamada et al. (2005) Termite individual contributions to carbon mineralization by the respiration from wood/litter-feeders and soil-feeders were 2.8% and 1.2% of the annual aboveground litterfall in the DEF at SERS, respectively.

Mound structure differences between species may also contribute to variation in mound CO₂ emissions. Nest

construction material as the wood carton (a mixture of faeces and macerated wood) is used for the most wood/litter-feeding group, while many soil-feeders use faeces mixed with topsoil (Bignell and Eggleton, 2000). In addition, the soil feeder epigeal mounds may not contain the entire colony population above the mound because most individuals move below the soil for foraging and to avoid adverse environmental conditions (Fig 8). Moreover, the mound CO₂ emission rates of *T. propinquus*, and *D. makhamensis* were similar to those reported by Song et al. (2013) who reported that the range of CO₂ emission from termite mounds (species: not given) was from 1.63 to 3.71 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and these species did not affect soil CO₂ emission in the tropical rainforest. As the result of Song et al. (2013), mounds were either typical soil-feeding group mounds or similar to the fungus growing termites that build a dome-shaped mound with thick walls (20-40 cm thickness) and several branching underground passages (Inoue et al., 2001).

Previous studies have reported that the mound-builder and subterranean nest of termites emitted significantly higher CO₂ than typical soils (e.g. Konate et al., 2003; Brümmer et al., 2009; Risch et al., 2012; De Gerenyu et al., 2015; Ohashi et al., 2017). Not only CO₂ emission from termite individuals, but their nest also contributed to soil respiration. According to Hu et al. (2017) reported that CO₂ emission from termite nest soil was higher than typical soil, due to termite nest soils had higher dissolved organic carbon concentration and C/N ratio, accelerating for microbial activities. In a tropical savanna, the fungus-growing termite was emitted 10-19 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ from the mound which compared to 5-10 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ from surrounding soils (Konate et al., 2003). In a tropical rain forest, the mean of CO₂ emission from termite mound was reached up to 27.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ that much higher than the surrounding soil (3.96 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Ohashi et al., 2017). An earlier study (Ohashi et al., 2007) indicated that the rate of soil respiration was sometimes extremely high (>10 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) contributing 10% to the total soil respiration in the tropical rainforest. De Gerenyu et al. (2015) showed that the mound CO₂ emission of *Odontotermes* termites (fungus grower) and *G. sulphureus* (non-fungus grower) was 2.0-2.5 times higher than the background soil during both dry and wet seasons. Also, those termite mounds contributed up to 10% of the total soil respiration in a tropical monsoon forest of southern Vietnam, showing the maximum rates of the mound CO₂ emissions were 17 and 20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ from *Odontotermes* and *G. sulphureus*, respectively. On the other hand, mound CO₂ emission rate was 2.5 times lower than the surrounding soil that was affected by termite respiration through their underground passages in the surrounding soil (Boonriam et al., 2021b).

The relationship between soil CO₂ emission and its environmental factors was also observed from only soil around each mound, while soil temperature and soil moisture content were not measured from the mounds to avoid disturbing termite activity at the nest. In this study, soil CO₂ emission rate was 3.4 times higher in the wet season than the dry season. Soil CO₂ emissions showed a consistent relationship with soil moisture content. In addition, soil CO₂ emission rate was started to decrease when soil moisture content peaked more than 18% (Adachi et al., 2009) and 21% (Hasin et al., 2014) in diurnal variation of Thai tropical forest. A previous study reported that the rate started to drop at 27 °C soil temperature and 21% soil moisture content in the same topographical forest (Boonriam et al., 2021a). Although precipitation influences soil microbial activities accelerating soil respiration, high precipitation could inhibit CO₂ emission by a barrier of high moisture content in the soil (Sotta et al., 2004; Wood et al., 2013). This inconstancy within the timing and magnitude of precipitation occasions can influence soil respiration.

Conclusion

The CO₂ emissions from termite mounds were generally higher than surrounding soils. The mound CO₂ emission, *G. sulphureus* and *M. crassus* are major CO₂ producers among the non-fungus growing termites in this tropical forest. The difference in CO₂ emissions among termite mounds may due to the population colony, ventilation, and thickness of the nests. The rate of soil CO₂ emission was increased with increasing soil moisture content. Future information regarding the total soil CO₂ emission and the mound density on large scale as well as their environmental conditions are necessary for evaluating the contribution to the total soil respiration in Thai-tropical forest.

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Author contribution

The experiment was designed by Warin Boonriam, Akinori Yamada, and Pongthep Suwanwaree. Data collection, sampling, and species identification were performed by Warin Boonriam. Statistical analysis and text review were discussed by Warin Boonriam, Pongthep Suwanwaree, and Sasitorn Hasin. All authors discussed and revised the manuscript.

Conflict of interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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