Effect of Fungus-Growing Termite on Soil CO₂ Emission at Termitaria Scale in Dry Evergreen Forest, Thailand

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1. INTRODUCTION

Carbon dioxide (CO₂) emission from soils (soil respiration) is an important of the carbon balance in terrestrial ecosystems. Soil respiration contributes 50-95% of the total ecosystem respiration (Janssens et al., 2001; Chambers et al., 2004) as well as the second largest terrestrial carbon emission in the forest ecosystems (Solomon et al., 2007). Soil respiration comes from CO₂ production of all living organisms in the soil, including plant roots, soil microbes, and animals (Lavelle and Spain, 2001; Luo and Zhou, 2006). Tropical forests contribute to over a third of net primary productivity in global terrestrial ecosystems (Field, 1998; Roy and Saugier, 2001; Field and Raupach, 2004). According to Bonan (2008) reported that about 45% of global terrestrial carbon stocks were contributed by tropical forests. Consequently, tropical forests could strongly influence future CO₂ concentration in atmosphere.

High variability in soil respiration from tropical forests has been discussed. Although soil microorganisms and roots constitute the dominant contributors of soil respiration, the rate of soil respiration has been shown to change and fluctuate at an unexpectedly large scale (10-90%) (Hanson et al., 2000). It is difficult to explain by known environmental factors, such as soil water content and temperature. According to Ohashi et al. (2007) and

**Termites are one of the major contributors to high spatial variability in soil respiration. Although epigalel termite mounds are considered as a point of high CO₂ effluxes, the patterns of mound CO₂ effluxes are different, especially the mound of fungus-growing termites in a tropical forest. This study quantified the effects of a fungus-growing termite (Macrotermes carbonarius) associated with soil CO₂ emission by considering their nesting pattern in dry evergreen forest, Thailand. A total of six mounds of M. carbonarius were measured for CO₂ efflux rates on their mounds and surrounding soils in dry and wet seasons. Also, measurement points were investigated for the active underground passages at the top 10% of among efflux rates. The mean rate of CO₂ emission from termitaria of M. carbonarius was 7.66 µmol CO₂/m²/s, consisting of 2.94 and 9.11 µmol CO₂/m²/s from their above mound and underground passages (the rate reached up to 50.00 µmol CO₂/m²/s), respectively. While the CO₂ emission rate from the surrounding soil alone was 6.86 µmol CO₂/m²/s. The results showed that the termitaria of M. carbonarius contributed 8.4% to soil respiration at the termitaria scale. The study suggests that fungus-growing termites cause a local and strong variation in soil respiration through underground passages radiating out from the mounds in dry evergreen forest.**
conducted in termitaria of the fungus-growing termites. Consequently, the observation was also their surrounding area has been affected by up to several tens meters. Not only the nest itself but underground passages expanding from the nest center under the effect of termites on soil respiration by considering seasonal tropical forests. Here, this study focuses on the tropical forests.

To date, there is no compelling evidence to support the effect of termites on soil respiration at a large scale, and the results can be applied to tropical forest ecosystems.

2. METHODOLOGY
2.1 Study site
A field study was conducted in the dry evergreen forest (DEF) at Sakaerat Environmental Research Station (SERS) (14°30′N, 101°56′E; approximately 500 m above sea level) in Nakhon Ratchasima Province, northeastern Thailand (Figure 1). According to SERS meteorological station from 2005 to 2015, the mean annual rainfall was 1,083.8 mm with monthly rainfall less than 40 mm during the dry season from November to March and the wet season lasting from May to October. The averages of relative humidity and the annual temperature were 83.8% and 26.7°C (9.1-38.9°C), respectively. The DEF covers an area of 29.5 km², where the dominant tree species are Hopea ferrea and Hopea odorata with canopy trees generally reaching 23 to 40 m high (Kanzaki et al., 1995).

2.2 Field experiments design
Six mounds of M. carbonarius were randomly determined for the mound CO₂ emission with a distance greater than 10 m between each mound. The mounds were chosen at different places in the DEF according to the vegetation, elevation. Mound sizes were measured for the height (base to the top) and circular length of the bottom. A plot (10 m × 10 m) was set up to cover each mound and its surrounding soil. Each plot was divided into 100 grids (1 m × 1 m in each grid). PVC collars were placed on a mound randomly at 5 to 6 points and the center of the grids for 100 points in each mound plot (Figure 2). CO₂ emission rates were measured using a portable infrared gas analyzer (IRGA, EGM-4, PP Systems, Hitchin, UK) with a closed soil CO₂ efflux chamber (SRC-1, PP Systems) (diameter 10 cm) for 1 time per dry season from December 2014 to May 2015, and wet seasons from October 2015 to November 2015. After CO₂ measurement, the soil temperatures and soil moisture contents were measured immediately around each PVC collar at about 10 cm depth by using 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. The measurement was performed one day per plot with starting from 9:00 am until 6:00 pm (3 to 5 minutes per point) without rainfall.
Figure 1. Study site in DEF at Sakaerat Environmental Research Station (SERS), Thailand. (SERS map modified from Trisurat, 2010)

Figure 2. Experimental design for determine CO\(_2\) emission and relative factors from the termitaria of \(M.\) carbonarius.

The high emission rate was determined at top 5% (>6 µmol CO\(_2\)/m\(^2\)/s in dry season), and top 10% (>10 µmol CO\(_2\)/m\(^2\)/s in wet season) of CO\(_2\) emission rates. If the high rate was found on the measurement points in each plot (excepted on mound), this points was examined for active or inactive termitaria by excavating in the depth of 40 cm, such excavated underground passages will be soon repaired about 1 h. by termites. The depth and diameter of underground passages were measured. The distributions of the high rate efflux points were put on the map of the plot scale.

2.3 Statistical analysis

All the raw data were tested for normality by using the Kolmogorov-Smirnov test. Significant differences of CO\(_2\) emission rates between the termite mounds and surrounding soils for the dry and wet seasons were detected by the univariate ANOVA with Tukey's HSD Post-hoc test. The relationship of CO\(_2\) emissions between depth and diameter of underground passages from mounds of \(M.\) carbonarius was tested using linear regression analysis. All statistical calculations were performed in SPSS ver. 20.0.0 for Windows.

3. RESULTS

3.1 CO\(_2\) efflux from termitaria of fungus-growing termite (\(M.\) carbonarius)

The total average of CO\(_2\) emission rates from the termitaria of \(M.\) carbonarius and the surrounding soil was 7.10±4.74 µmol CO\(_2\)/m\(^2\)/s. There was a significant difference among the six plots (Table 1).
CO\textsubscript{2} emission rates from the mounds and surrounding soils were significantly different between dry and wet seasons (Table 2). The annual mean of CO\textsubscript{2} efflux rates from the mounds was 2.94±2.73 µmol CO\textsubscript{2}/m\textsuperscript{2}/s which was 2.5 times significantly lower than the surrounding soils (included the underground passages) of 7.36±4.72 µmol CO\textsubscript{2}/m\textsuperscript{2}/s, with a wide range from 0.91 to 50.00 µmol CO\textsubscript{2}/m\textsuperscript{2}/s (Figure 3). CO\textsubscript{2} efflux from the surrounding soils was higher in the wet season than the dry season (F=436.38, p<0.001), while above mound CO\textsubscript{2} emissions itself were higher in the dry season (3.86±3.35 µmol CO\textsubscript{2}/m\textsuperscript{2}/s) than wet season (2.06±1.52 µmol CO\textsubscript{2}/m\textsuperscript{2}/s).

### Table 1. CO\textsubscript{2} emission rates from six plots of *M. carbonarius* (mound and surrounding soil) with varying mound sizes in dry and wet seasons.

| Plot | Mound area (m\textsuperscript{2}) | CO\textsubscript{2} emission (µmol CO\textsubscript{2}/m\textsuperscript{2}/s±SD) |
|------|----------------------------------|-------------------------------------------------|
|      | Mound (n=6) | Surrounding soil (n=100) | Mound (n=6) | Surrounding soil (n=100) |
| 1    | 0.64 | 5.54 | 3.69 | 1.44 | 10.54 |
| 2    | 0.24 | 3.07 | 2.32 | 3.94 | 8.20 |
| 3    | 1.85 | 2.48 | 5.43 | 1.67 | 12.24 |
| 4    | 1.61 | 1.90 | 7.11 | 1.06 | 9.85 |
| 5    | 3.85 | 6.97 | 7.66 | 2.03 | 10.14 |
| 6    | 2.55 | 3.41 | 4.39 | 2.20 | 8.87 |
| Location average | 3.86±3.35 | 5.10±4.06 | 2.06±1.52 | 9.97±4.24 |
| Season average | 5.03±4.03 | 9.17±4.49 |
| Total average | 1.79 | 7.10±4.74 |

### Table 2. Differences in CO\textsubscript{2} emission between the plot, area (mound and surrounding soil), and season.

| Source of variation | CO\textsubscript{2} emission rate (µmol CO\textsubscript{2}/m\textsuperscript{2}/s) |
|---------------------|-------------------------------------------------|
|                      | df | F   | p    |
| Plot                | 5  | 2.464 | 0.031 |
| Season              | 1  | 9.027 | 0.003 |
| Area                | 1  | 95.130 | 0.001 |
| Plot × Season       | 5  | 2.595 | 0.024 |
| Plot × Area         | 5  | 2.593 | 0.024 |
| Season × Area       | 1  | 48.94 | 0.001 |
| Plot × Season × Area| 5  | 1.984 | 0.078 |

Statistically significant p values are in bold.

As extremely high CO\textsubscript{2} points, the top 5-10% of CO\textsubscript{2} emission rates were considered in each plot. A total number of high CO\textsubscript{2} points were found at 101 points among 1,200 measurement times. These points were examined which consisting of 3 types as active underground passage (Figure 4), lateral root, and normal soil. The termitaria as underground passages were found 69.31% of all the points, the remaining of 26.73% and 3.96% were roots (almost closed to the big tree) and the normal soils, respectively (Table 3). An area of termitaria as underground passages was calculated as 5.83 m\textsuperscript{2} by the number of active underground passages (70) among measurement points (1,200) per plot area (100 m\textsuperscript{2}).

![Figure 3. Box plots of distribution of seasonal variation in CO\textsubscript{2} emission rates from termitaria of *M. carbonarius* in dry and wet season. Box plots indicate the distribution by percentiles. The median is given by horizontal line in the box. A part of bottom and top of the box indicates 25\textsuperscript{th} and 75\textsuperscript{th} percentiles, respectively. The whiskers extend out to the maximum or minimum value of the data. Significant differences are indicated by asterisk on the curly bracket (p=0.001).](image-url)
Figure 4. Active underground passages of *M. carbonarius* mound representing high CO$_2$ emission resources

Table 3. Examination of underground soils on measurement point of high CO$_2$ emission rate

| Examination of underground soil* | Termitaria (underground passage) | Surrounding soil |
|----------------------------------|----------------------------------|------------------|
| Number of high CO$_2$ emission source | 70                               | 27               |
| Average of CO$_2$ emission rate (µmol CO$_2$/m$^2$/s) | 15.97±9.20 | 18.11±5.90 |
|                                   |                                   | 16.99±2.83 |

*Underground passage=active underground passage from the mound of *M. carbonarius*, Root=lateral root/branch root, and normal soil=neither found.

Mean of CO$_2$ efflux rate (±SD) from the underground passages of *M. carbonarius* mounds was 15.97±9.20 µmol CO$_2$/m$^2$/s. Frequency distribution of CO$_2$ efflux rates from the soil around the mounds, and underground passages of the termite mounds is shown in Figure 5. CO$_2$ efflux rates from surrounding soil including the underground passages (7.36±4.72 µmol CO$_2$/m$^2$/s) was significantly higher than soil alone around the mound (6.86±3.92 µmol CO$_2$/m$^2$/s) (p<0.001), whereas CO$_2$ effluxes from the surrounding soils included the high CO$_2$ efflux rates from the flat roots and normal soils, which had mean values of 18.11 and 16.99 µmol CO$_2$/m$^2$/s, respectively.

3.2 Effect of termitaria (*M. carbonarius*) and surrounding soils on soil respiration

As mentioned above, the mean rate of CO$_2$ emission from the underground passages of *M. carbonarius*’s mound was immoderately high. In fact, this rate was not only from the activities of termites but also from the microbe activities by the gas passed through the nearby soils associated with underground tunnels. Thus, the mean CO$_2$ emission rate was 9.11 µmol CO$_2$/m$^2$/s from only the underground passages (5.83 m$^2$) by excluded the mean CO$_2$ emission rate of surrounding soils (6.86 µmol CO$_2$/m$^2$/s). However, CO$_2$ emission rate from above the mound was only 2.94 µmol CO$_2$/m$^2$/s with area of 1.79 m$^2$. The finding in the results showed that the average of CO$_2$ emission from the termitaria (mound and underground passage) of *M. carbonarius* was 7.66 µmol CO$_2$/m$^2$/s with the total area of 7.62 m$^2$. Consequently, the fungus-growing termite (*M. carbonarius*) contributed 8.43% to soil respiration at the termitaria scale (100 m$^2$), consisting of the mounds and the underground passages of 0.76% and 7.67%, respectively (Figure 6). In addition, the relationship between underground passages of *M. carbonarius* and their CO$_2$ emission rates was determined. There was no significant difference in CO$_2$ efflux rates between depth and diameter of underground passages in the dry and wet seasons as an example in Figure 7.
Figure 5. Frequency distribution of CO$_2$ emission rate from surrounding soil and underground passages (activities of termite+natural microbe) of *M. carbonarius* mounds

Figure 6. An aspect of contribution of *M. carbonarius'*s termitaria and surrounding soil on soil respiration at area scale 100 m$^2$

3.3 Changes in soil respiration with soil temperature and soil moisture content

The temporal variation in soil respiration, as well as soil temperature and moisture, showed large variation by the season. Annual respiration of surrounding soil was significantly positively correlated with soil temperature ($R=0.259$, $p<0.001$) and soil moisture content ($R=0.359$, $p<0.001$) (Figure 8). However, the rate of soil respiration tended to drop with soil temperature and moisture tended to high. As the result, there was ambiguity between the effects of soil temperature and soil moisture on the variability of soil respiration, because this result includes both temporal and spatial variation, especially hot spots from the underground passages.
4. DISCUSSION

Our results showed that the mean of the frequency distribution of the respiration rates from surrounding soils alone (6.86 µmol CO₂/m²/s) was determined as respiration rates from soil microbes, roots, and subterranean soil insects or animals at the termitaria scales (100 m²/mound). In the same forest, the rate of soil respiration was widely fluctuations in both dry season (1.3-6.1 µmol CO₂/m²/s) and wet season (3.6-14.5 µmol CO₂/m²/s) where was...
considered by Hasin et al. (2014). The rate of the ground soil respiration in this study was similar to the rate of 6.57 µmol CO$_2$/m$^2$/s in the same site (Boonriam et al., 2021) as well as the rates of 6.05 and 6.76 µmol CO$_2$/m$^2$/s from DEF of northern Thailand which reported by Adachi et al. (2009) and Hashimoto et al. (2004) respectively. It seems that the CO$_2$ emission rate of this study has not much change over the years. In addition, the previous other studies had shown the rate of soil respiration in various tropical forests which were 6.45 µmol CO$_2$/m$^2$/s in Amazon, Brazil (Sotta et al., 2004), 3.96-5.32 µmol CO$_2$/m$^2$/s in Malaysia (Ohashi et al., 2007; Ohashi et al., 2017), and 4.28 µmol CO$_2$/m$^2$/s in Vietnam (Avilov et al., 2019).

In this study, fungus-grower termite (M. carbonarius) has a crucial influence on soil respiration by the total rate of CO$_2$ emissions from their termitaria (7.66 µmol CO$_2$/m$^2$/s), especially CO$_2$ emissions from underground passages (9.11 µmol CO$_2$/m$^2$/s) at termitaria scale in this forest. As results of this study, CO$_2$ emission from above the mounds (2.94 µmol CO$_2$/m$^2$/s) were 2.5 and 3.1 times significantly lower than their surrounding soils (including underground passages) and only underground passages, respectively. Our result showed that the dispersal (transmission) of the CO$_2$ emission from the underground passages of M. carbonarius’s mounds were expressed as at top 5% (>6 µmol CO$_2$/m$^2$/s in dry season), and top 10% (>10 µmol CO$_2$/m$^2$/s in wet season) of CO$_2$ emission rates. There were extremely high at around the surrounding soils as much as the rate of hot spots in Malaysia-tropical rainforest that were suggested by Ohashi et al. (2007). Although Ohashi et al. (2017) determined that the CO$_2$ emission from the termite nest was higher than the surrounding soil in Malaysia-tropical rainforest, the rate was conducted from different types of nests comprising tree base (nests built on a tree base), epigeous and subterranean nests. On the other hand, Song et al. (2013) reported that the termite mound did not affect as hot spot to soil respiration in China-tropical rainforest with the range of 1.63 to 3.71 µmol CO$_2$/m$^2$/s. These mounds were either typical soil-feeding termites (non-fungus grower), or the fungus-growing termites that build a dome-shaped mound with thick walls and several branching underground passages (Inoue et al., 2001).

Mound-building termites construct the nests in sophisticated ways to achieve the thermoregulation and gas exchange (Noirot and Darlington, 2000; Korb, 2003). According to Inoue et al. (2001) conducted in the same DEF, Thailand, the study found that about 4-10 main underground passages radiating out from each M. carbonarius’s mound and build the dome-shaped mounds with a thick wall. The thickness of the mound wall was about 20-40 cm thick. Thus, it was difficult for passing gas through the wall. On the other hand, while the gas exchange was mostly released through the central mound in tropical savanna according to Konate et al. (2003), Brümmer et al. (2009), and Risch et al. (2012). For example in Konate et al. (2003) reported that the mounds of fungus-growing termites emitted about 10-19 µmol CO$_2$/m$^2$/s compared to 5-10 µmol CO$_2$/m$^2$/s from its surrounding soils. However, CO$_2$ emission from termite mounds in savannas contributes less than 1% to total soil respiration (Brümmer et al., 2009; Jamali et al., 2013). In relative hot environments as tropical savannas, fungus-growing termites (Macrotermes species.) built mounds like a cathedral shape to maintain the inside temperature and CO$_2$ concentration for fungus cultivation in the mounds at 30ºC and 0.2-1.0%, respectively (Korb and Linsenmair, 2001). In contrast, the mound architecture in tropical forest relatively cool environments has achieved to maintain the inside temperature (28-30ºC) and CO$_2$ concentration (1.0-1.5%) by building the dome-shaped structure with thick walls (Korb and Linsenmair, 2001). As our results, mound CO$_2$ emission of the fungus-growing termites in tropical forests is quite different from the tropical savannas by the nest pattern and ventilation.

Fungus-growing termite contributions to soil respiration were not only from individual termite activities but also from the nest material (fungus combs). Fungus combs have much higher biomass than termite individuals in mound (Konate et al., 2003; Yamada et al., 2005) and release a high rate of CO$_2$ emissions (Sugimoto et al., 2000). In the same forest, according to Yamada et al. (2005) estimated the fraction of respiration from annual aboveground litterfall, the total amount of respiration rate from fungus combs (7.2%) was six times higher than the population of fungus growers (1.2%), while non-fungus-growing termites respired as 2.8% of carbon in the annual aboveground litterfall. Apparently, fungus-growing termite in a tropical forest has the potential of fungus combs to mound CO$_2$ emissions that mediated by termites as well as a previous study in savannas according to Konate et al. (2003). In addition, the fungus grower, especially M. carbonarius is widely distributed in Southeast Asia such as Thailand, Cambodia, Vietnam, and Malaysia (Roonwal, 1970).
In recent research, the density of *M. carbonarius* was recorded at 33 mounds/ha in the same forest of the DEF of northeast Thailand (Boonriam, 2016).

In general, soil CO$_2$ emission rate increased with increasing soil temperature and soil moisture content (Lloyd and Taylor, 1994; Xu and Qi, 2001; Qi et al., 2002; Reichstein et al., 2002). Nevertheless, this study results seem as if the values of soil temperature and soil moisture content were moving to high point, the soil respiration rates tend to drop. According to Boonriam et al. (2021) implied that soil respiration in the same forest was limited by soil moisture during the dry season, so the increase in soil temperature to a very high degree reduced soil moisture even more, which reduced soil respiration. In addition, precipitation variability can have an effect on soil respiration. A high soil moisture content creates a barrier on the surface of the soil atmosphere, which may inhibit the release of CO$_2$ from the soil. (Sotta et al., 2004; Wood et al., 2013).

In tropical forests, the soil CO$_2$ emission was mainly controlled by soil organic carbon and soil moisture (Pandey and Singh, 2018), while soil temperature was slightly related to soil respiration during the wet season (Intanil et al., 2018). However, CO$_2$ emission rates from the mounds of fungus-growing termites were significantly higher in the dry season than in the wet season resulting in this study. As the expected result, the respiration rate on the termite mound should be very low by little plant litters falling to the top, low microbial activity in the dry season, and the thickness of the mound wall as well. In this case, there was probably due to the relatively hot-dry environments that affected termites to maintain inside to optimal conditions by exchange gases through the thinnest part or dry cracked parts of the mound wall. Perhaps, according to Ashton et al. (2019) found that the termite abundance and activity (included *Macrotermes*) increased during the drought in the tropical forest. Therefore, termite mound needs to control the condition inside the mound to the optimal (Korb, 2003). In Asian zone, Ocko et al. (2017) noted that the active *Macrotermes* mound must be effectively ventilated to remove CO$_2$ and heat with diffusivity through their porous surface and underground passages by contribution of the diurnal wind.

For attractive features of earlier studies, CO$_2$ emissions from termite mounds have confirmed that mounds are important local hot spots, estimated to be between 0.05 and 0.27 µmol CO$_2$/m$^2$/s, representing reach up to 3% of the total estimated ecosystem respiration (Chambers et al., 2004; van Asperen et al., 2021). However, seasonal tropical forests have sometimes a fluctuation of the climate. Consequently, this contribution of mound CO$_2$ emission in terms of fungus-growing termites is one of the best approaches for evaluating soil biological activities in relation to carbon and energy flow in terrestrial ecosystems.

5. CONCLUSION

Overall, the study highlights the termitaria of fungus-growing termite (*M. carbonarius*) was contributed about 8.4% to the soil respiration at termitaria scale. The rate of CO$_2$ emissions from the mound alone was lower than their surrounding soil. However, the high CO$_2$ emissions from the surrounding soil were affected by the underground passage through from the nest/colony of the fungus-growing termite. Future information regarding the total soil CO$_2$ 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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