Effect of Fungus-Growing Termite on Soil CO_2 Emission at Termitaria Scale in Dry Evergreen Forest, Thailand

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ABSTRACT

Termites are one of the major contributors to high spatial variability in soil respiration. Although epigeal termite mounds are considered as a point of high CO_2 effluxes, the patterns of mound CO_2 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 CO_2 emission by considering their nesting pattern in dry evergreen forest, Thailand. A total of six mounds of *M. carbonarius* were measured for CO_2 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 CO_2 emission from termitaria of *M. carbonarius* was 7.66 µmol $CO_2/m^2/s$, consisting of 2.94 and 9.11 µmol $CO_2/m^2/s$ from their above mound and underground passages (the rate reached up to 50.00 µmol $CO_2/m^2/s$), respectively. While the CO_2 emission rate from the surrounding soil alone was 6.86 µmol $CO_2/m^2/s$. 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.

1. INTRODUCTION

Carbon dioxide (CO_2) 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 CO_2 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 CO_2 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

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Ohashi et al. (2017), extremely higher rates of soil respiration as hot spots (>10 µmol $CO_2/m^2/s$) were observed in the tropical forest of Southeast Asia and suggested that soil macrofauna were the main causes in a tropical forest. Thus, the phenomena were proposed to be attributed to un-revealed activities of soil animals, especially social insects such as termites, because it is well known that termites are superabundant soil animals in seasonal tropical forests (Yamada et al., 2003; Yamada et al., 2005).

Termites play an important role in litter decomposition processes as much as half of the primary litter production (Matsumoto and Abe, 1979; Bignell and Eggleton, 2000; Coleman et al., 2004). They have caused interest in their respiratory gas exchanges associated with soil respiration at niche differentiation. Mound building termites, especially fungus-growing termites (Macrotermitinae) cultivate symbiotic fungi on fungus gardens (fungus combs) that consist of plant litter materials built by using their partially digested faeces (Korb, 2003). A termite colony built the nest ranges from small belowground chambers to large aboveground mounds with the underground passages for its foraging behavior, called termitaria. In tropical savanna, several studies reported that a part of the epigeal termite mound emitted higher CO_2 than its surrounding soils (Konate et al., 2003; Brümmer et al., 2009; Risch et al., 2012). In the tropical forest, according to Lopes de Gerenyu et al. (2015) reported that termite mounds contributed up to 10% of the total soil respiration in southern Vietnam. On the other hand, there was no significant effect of termite mounds on soil CO_2 emission in the tropical rainforest, China (Song et al., 2013). However, the mounds have a complex architecture that allows for the constant environment in temperature and humidity. To evaluate how much CO_2 efflux by underground passages from the mound where could lead to high spatial heterogeneity of soil respiration in the tropical forests.

To date, there is no compelling evidence to support the effect of termites on soil respiration in seasonal tropical forests. Here, this study focuses on the effect of termites on soil respiration by considering their nesting pattern. Numerous termite nests have underground passages expanding from the nest center to up to several tens meters. Not only the nest itself but also their surrounding area has been affected by termite activities. Consequently, the observation was conducted in termitaria of the fungus-growing termites in order to depict the effects 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 26.7ºC (9.1-38.9ºC), respectively. The DEF covers an area of 29.5 km^2, 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 CO_2 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). CO_2 emission rates were measured using a portable infrared gas analyzer (IRGA, EGM-4, PP Systems, Hitchin, UK) with a closed soil CO_2 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 CO_2 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.

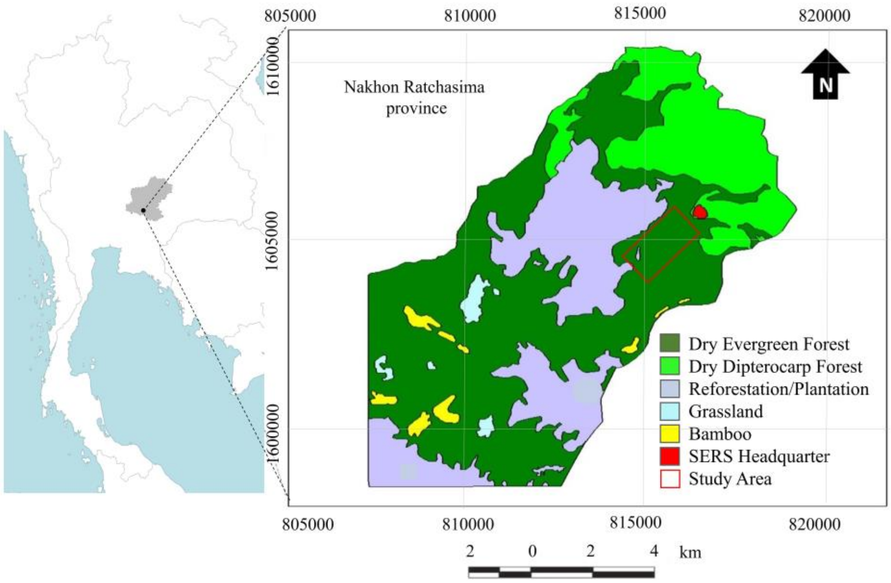

Figure 1. Study site in DEF at Sakaerat Environmental Research Station (SERS), Thailand. (SERS map modified from Trisurat, 2010)

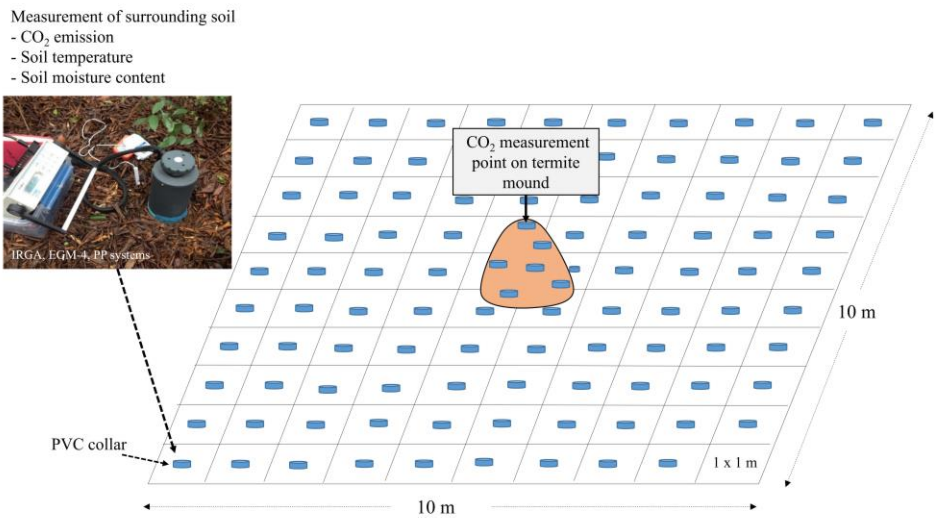

Figure 2. Experimental design for determine CO_2 emission and relative factors from the termitaria of *M. carbonarius*.

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_2 emission rates from the mounds and surrounding soils were significantly different between dry and wet seasons (Table 2). The annual mean of CO_2 efflux rates from the mounds was 2.94±2.73 µmol $CO_2/m^2/s$ which was 2.5 times significantly lower than the surrounding soils (included the underground passages) of 7.36±4.72 µmol $CO_2/m^2/s$, with a wide range from 0.91 to 50.00 µmol $CO_2/m^2/s$ (Figure 3). CO_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_2 emissions itself were higher in the dry season (3.86±3.35 µmol $CO_2/m^2/s$) than wet season (2.06±1.52 µmol $CO_2/m^2/s$).

Table 1. CO_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^2)	CO_2 emission (µmol $CO_2/m^2/s$±SD)			
		Dry season		Wet season	
		Mound (n=6)	Surrounding soil (n=100)	Mound (n=6)	Surrounding soil (n=100)
1	0.64	5.34	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			

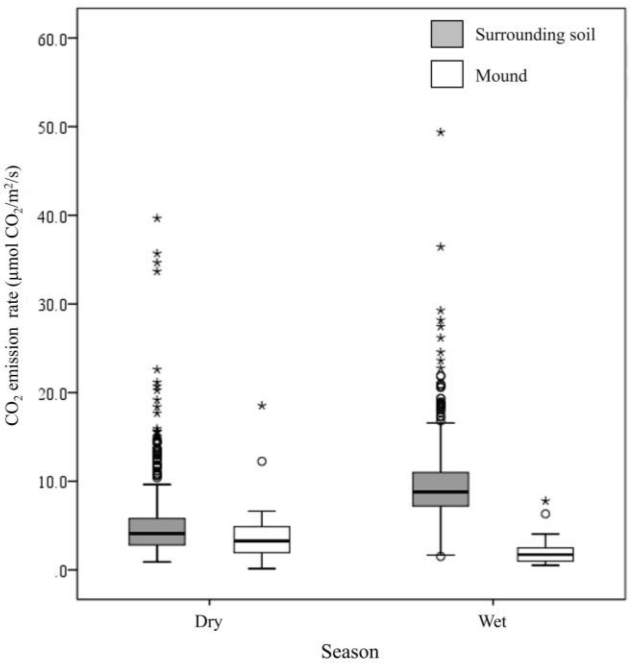

Figure 3. Box plots of distribution of seasonal variation in CO_2 emission rates from termitaria of *M. carbonarius* in dry and wet season. Box plots indicate the distribution by percentiles. The median is given by horizontal line in the box. A part of bottom and top of the box indicates 25th and 75th 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 ($p=0.001$).

Table 2. Differences in CO_2 emission between the plot, area (mound and surrounding soil), and season.

Source of variation	CO_2 emission rate (µmol $CO_2/m^2/s$)		
	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_2 points, the top 5-10% of CO_2 emission rates were considered in each plot. A total number of high CO_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^2 by the number of active underground passages (70) among measurement points (1,200) per plot area (100 m^2).

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	
		Root	Normal soil
Number of high CO_2 emission source	70	27	4
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.

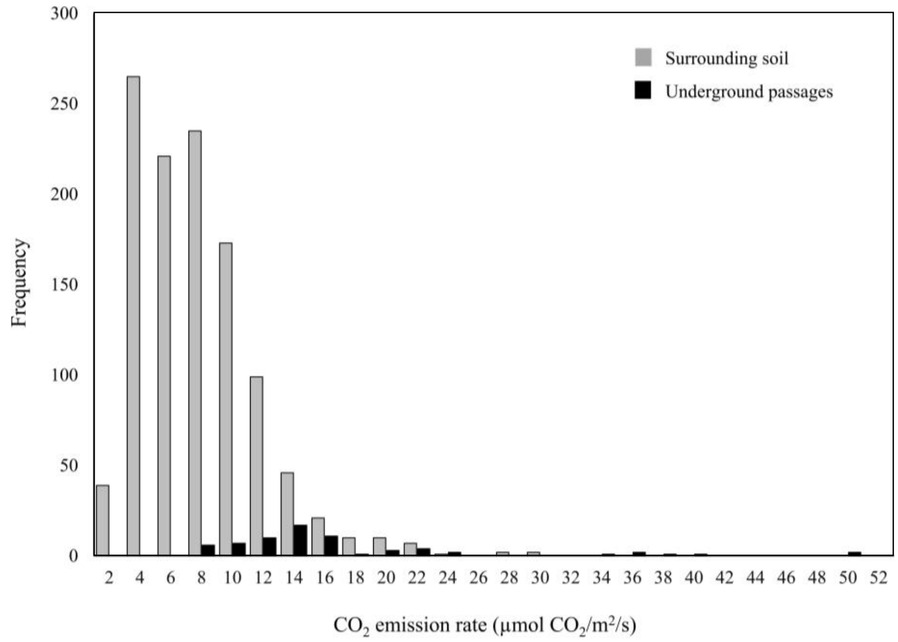

Figure 5. Frequency distribution of CO_2 emission rate from surrounding soil and underground passages (activities of termite+natural microbe) of *M. carbonarius* mounds

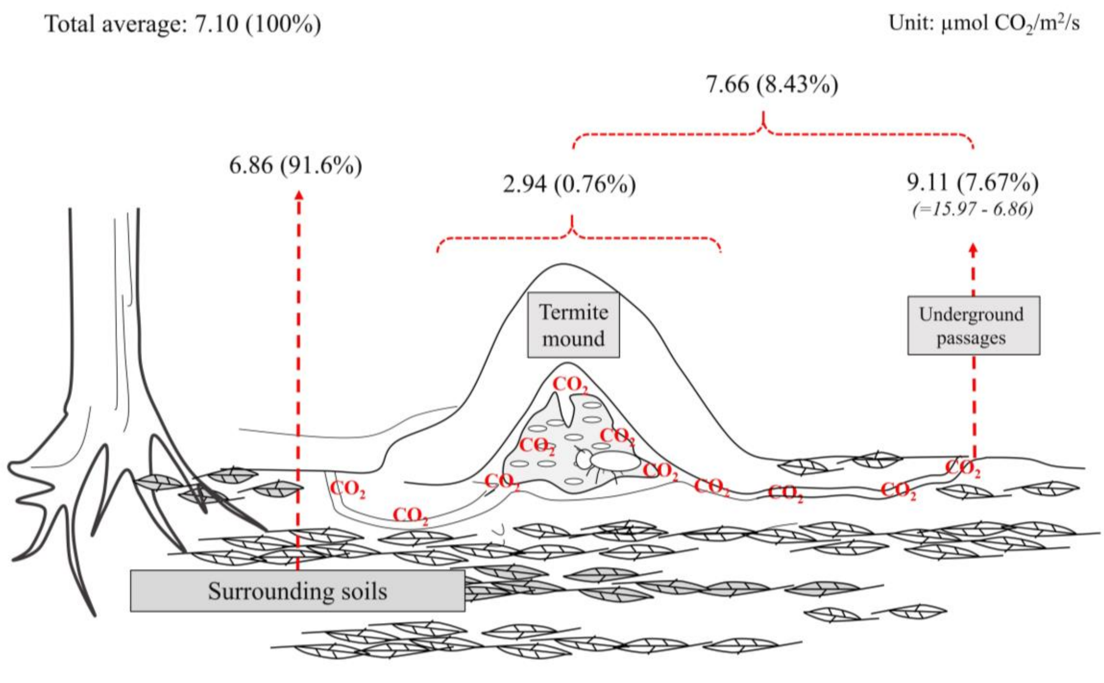

Figure 6. An aspect of contribution of *M. carbonarius*'s termitaria and surrounding soil on soil respiration at area scale 100 m^2

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.

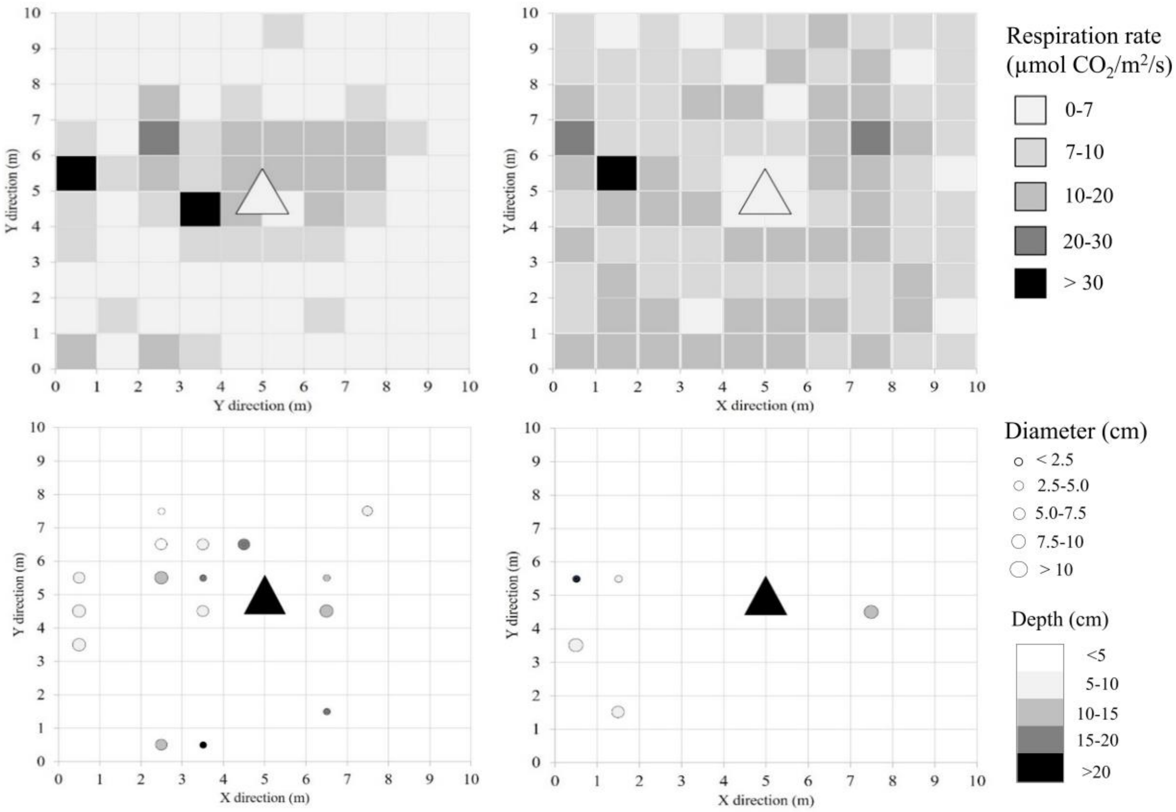

Figure 7. An example of distribution maps of CO_2 emission rate (top row) and underground passage (bottom row) with the diameter and depth from a mound (triangle) of *M. carbonarius* in dry season (left) and wet (right) seasons

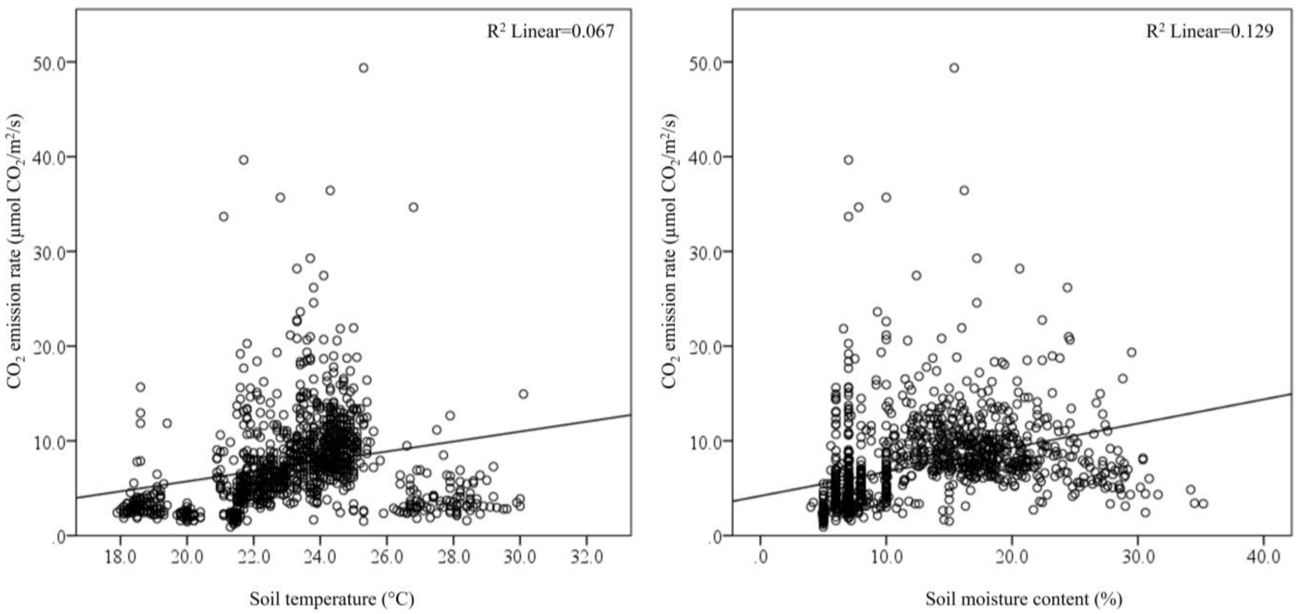

Figure 8. The relationship between soil respiration and soil temperature and moisture.

4. DISCUSSION

Our results showed that the mean of the frequency distribution of the respiration rates from surrounding soils alone (6.86 µmol $CO_2/m^2/s$) was determined as respiration rates from soil microbes, roots, and subterranean soil insects or animals at the termitaria scales (100 m^2/mound). In the same forest, the rate of soil respiration was widely fluctuations in both dry season (1.3-6.1 µmol $CO_2/m^2/s$) and wet season (3.6-14.5 µmol $CO_2/m^2/s$) 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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