

Effect of forest structure on the spatial variation in soil respiration in a Bornean tropical rainforest

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ABSTRACT

This study was undertaken to identify critical and practical factors explaining spatial variations in soil respiration and to estimate stand-scale soil respiration in an aseasonal tropical rainforest on Borneo Island. To this aim, we conducted soil respiration measurements at 25 points in a 40 m × 40 m subplot of a 4 ha study plot between 2002 and 2006, and examined the spatial variation in soil respiration averaged over the 4 years in relation to soil, root, and forest structural factors. In addition, we examined the spatial representativeness of soil respiration measured in the subplot using a specific scaling procedure. Consequently, we found significant positive correlation between the soil respiration and forest structural parameters such as the mean diameter at breast height (DBH), total basal area, and maximum DBH within 6 m of the measurement points. The most important factor was the mean DBH within 6 m of the measurement points, which had a significant linear relationship with soil respiration. Using the derived linear regression and an inventory dataset, we estimated the 4 ha plot-scale soil respiration. The 4 ha plot-scale estimation ($6.0 \mu\text{mol m}^{-2} \text{s}^{-1}$) was nearly identical to the subplot-scale measurements ($5.7 \mu\text{mol m}^{-2} \text{s}^{-1}$), which were roughly comparable to the nocturnal CO_2 fluxes calculated using the eddy covariance technique. In addition, we discuss characteristics of the stand-scale soil respiration at this site by comparing with those of other forests reported in previous literature in terms of the soil C balance. Soil respiration at our site was noticeably greater, relative to the incident litterfall amount, than soil respiration in other tropical and temperate forests probably owing to the larger total belowground C allocation by emergent trees. Overall, this study suggests the arrangement of emergent trees with larger DBH and their belowground C allocation could be primary factors controlling spatial variations in soil respiration in the tropical rainforest.

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1. Introduction

Tropical forests contain about 40% of the global vegetation carbon (C) (Skole and Tucker, 1993) and are responsible for about 50% of terrestrial gross primary production (Grace et al., 2001). Owing to their huge C stock and budget, tropical forests could affect the global C balance, and hence potentially play an important role in climate change, despite the fact that they cover only 12% of the total land surface (FAO, 1993). The eddy covariance method is a widely used technique for determining stand-scale carbon dioxide

(CO_2) fluxes (e.g., Malhi et al., 2002; Baldocchi, 2003; Kumagai et al., 2006) and has advanced our understanding of ecosystem C processes. However, this method provides unreliable measurements for nocturnal CO_2 fluxes under low wind speed conditions (e.g., Goulden et al., 1996; Baldocchi, 2003; Saitoh et al., 2005; Ohkubo et al., 2007). Nocturnal CO_2 fluxes can be used as a proxy for the respiration of the ecosystem; thus, alternative chamber methods for the respiration are still important in estimating ecosystem respiration to understand the processes of C flow in relation to climate change.

The efflux of CO_2 from the soil surface (soil respiration) is one of the major components of the ecosystem C balance and contributes 50–95% of total ecosystem respiration (Law et al., 1999; Xu and Qi, 2001; Janssens et al., 2001; Yuste et al., 2005). Soil respiration is the

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sum of multiple processes, such as root respiration and microbial decomposition (Hanson et al., 2000; Kuzyakov, 2006). It varies significantly in time and space according to small- and large-scale changes in the biological, physical, and chemical properties of the soil (e.g., Xu and Qi, 2001; Reichstein et al., 2003; Hibbard et al., 2005). Previous studies conducted in various types of forest ecosystems reported considerable and variable patterns of spatial variation in soil respiration with changes in moisture (Stoyan et al., 2000), C content (La Scala et al., 2000), litter biomass (Fang et al., 1998), microbial biomass (Scott-Denton et al., 2003), and root biomass (Hanson et al., 1993; Shibistova et al., 2002). Previously reported data suggest the magnitude of the spatial variation in soil respiration is larger in tropical forests than in other forest ecosystems because soil respiration is normally higher in tropical areas (Davidson et al., 2000; Schwendenmann et al., 2003; Sotta et al., 2004; Hashimoto et al., 2004; Ohashi et al., 2007a; Kosugi et al., 2007). Thus the determination of factors affecting the spatial variation in soil respiration are crucial not only for understanding CO₂ dynamics but also for accurately estimating the total amount of soil respiration, which permits a comparison with stand-scale CO₂ fluxes based on the eddy covariance method.

Roots contribute to total soil respiration through root respiration and root litter C decomposition due to fine root turnover and root exudates (e.g., Gower et al., 1996; Ryan et al., 1997; Davidson et al., 2002). Since root respiration and root litter C decomposition depend on belowground C allocation by trees, they can be closely linked to the forest structure in some ecosystems (e.g., Stoyan et al., 2000; Savin et al., 2001; Sørensen and Buchmann, 2005). Therefore, knowledge of the spatial arrangement of trees and canopy structure (i.e., forest structure) can be a practical tool for explain spatial variations in soil respiration in tropical forests, which enable us to extrapolate measurements based on spatially limited sampling to stand-scale estimates. In addition, the use of forest structural factors has advantages over the use of other factors that require special devices and techniques for measurement. However, there is little information on the effects of forest structure on spatial variations in soil respiration in tropical rainforests (e.g., Sotta et al., 2004).

The present study was undertaken to identify factors explaining spatial variations in soil respiration and to estimate stand-scale soil respiration in a primary tropical rainforest on the island of Borneo. Since spatial variations in soil respiration could vary also in time (Ohashi and Gyokusen, 2007b; Ohashi et al., 2009), we averaged 35 soil respiration observations conducted for 4 years at each of 25 sampling points in a subplot and examined spatial variations of soil respiration in relation to soil, root, and forest structures. In addition, we discuss the characteristics of the soil C balance at this site by comparing with those found by previous studies conducted in other tropical and temperate forests.

2. Material and methods

2.1. Study site

The study was carried out in a lowland mixed-dipterocarp forest in the Lambir Hills National Park, Sarawak, Malaysia (4°20'N, 114°02'E), situated about 30 km southwest of Miri, Sarawak (Fig. 1). The mean annual temperature recorded between 1968 and 2001 at Miri airport, 20 km from the study site, was approximately 27 °C with little seasonal fluctuation. The mean annual rainfall at the airport is approximately 2700 mm with some annual rhythm (Gomyo and Kuraji, 2006). The timing of an intra-annual dry spell is unpredictable, and the dry spell has never lasted for more than 1 month in this study period. This means the study site does not have phase-locked dry seasons under maritime influences in contrast to

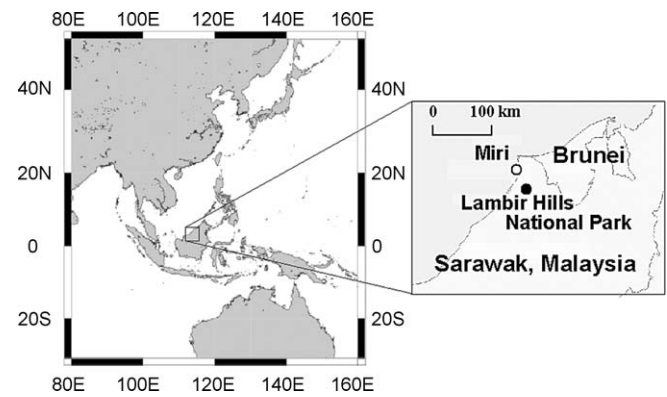


Fig. 1. Location of the Lambir Hills National Park, Sarawak, Malaysia.

Amazonian and African tropical rainforests (Kumagai et al., 2005; Manfroi et al., 2006; Kume et al., 2008).

At this site, the soils are red-yellow podzolic soils (Malaysian classification) or ultisols (United States Department of Agriculture Soil Taxonomy), with high sand content (62–72%), low pH (4.0–4.3), and high porosity (54–68%) (Ishizuka et al., 1998; Sakurai, 1999). A 93 m crane facility was constructed in the park for long-term ecological studies. Using the crane facility, stand-scale CO₂ fluxes have been measured by eddy covariance techniques at a height of 66 m from the ground (e.g., Saitoh et al., 2005; Kumagai et al., 2006). A 4 ha study plot surrounding the crane and comprising 400 subplots of 10 m × 10 m has been established. We established a 40 m × 40 m plot within the 4 ha plot and used the 25 intersections of the 10 m × 10 m square grids as sampling points for this study.

2.2. Forest structure

The park has an area of 6949 ha, 85% of which is covered by lowland mixed-dipterocarp forest. The continuous tree layer is approximately 40 m above the ground, but the height of emergent trees reaches 50 m. The leaf area index (LAI) ranges spatially between 4.8 and 6.8 m² m⁻² with a mean of 6.2 m² m⁻² (Kumagai et al., 2004). Litterfall is evenly distributed through the year (Nakagawa, unpublished data), suggesting little variation in the LAI. In this forest, the mean density of trees with a DBH greater than 10 cm was approximately 700 trees ha⁻¹. The mean total basal area was 43.3 m² ha⁻¹, and total basal area of the trees with a DBH greater than 10 cm accounted for about 90% of the total basal area of the trees with a DBH greater than 1 cm. More complete descriptions of the lowland tropical rainforest were given by Ashton and Hall (1992), Nakagawa et al. (2000), and Manfroi et al. (2004).

2.3. Soil respiration measurements

Soil respiration rates were measured using a commercial respirometer (LI-6400, LI-COR Inc., Lincoln, NE), consisting of an infrared gas analyzer (IRGA) and a small soil chamber (LI-6400-09) 962 cm³ in volume (diameter of 9.5 cm). Measurements were replicated three times at each sampling point and averaged. It took 3–4 min to take the three replicate readings. PVC collars (diameter of 10.4 cm and height of 7.0 cm) were inserted into the forest floor to a depth of ~4 cm at each sampling point in February 2002. Small litter and branches were left in the collar, although large items were removed. All collars were left at the site for the entire study period. Measurements at the 25 points were conducted from February 2002 to October 2006 in 2–3-month intervals in the period between February 2002 and April 2003 and in 2–5-month

intervals thereafter for a total of 35 measurement campaigns. The variable sampling intervals, due to practical reasons, probably have little influence on the soil respiration estimates because of the small seasonal variations in temperature and absence of a well-defined dry season (Ohashi et al., 2009). Each measurement campaign was carried out over 2–3 h in the morning. Additionally, we measured soil temperature and moisture simultaneously during each measurement campaign. Soil temperature at 10 cm depth was measured with a soil temperature probe connected to a soil respirometer (LI6400-09TC). The volumetric soil moisture content at 0–10 cm depth was measured with a handheld moisture sensor (Hydrosense, Campbell Scientific, Utah, USA) at three points very close to each chamber. A more complete description of the sampling procedures for soil respiration was given by Ohashi et al. (2009).

2.4. Soil, root, and forest structural parameters

In October 2006, soil porosity, root density, thickness of the litter layer, and vegetation area index (VAI, leaf area index plus stem area index) were measured at the 25 measurement points. Soil samples (volume of 100 cm³ and at 0–5 cm depth) were collected very close to the 25 measurement points to determine soil porosity and root density. The derived samples were saturated and then dried at 105 °C for 24 h. Soil porosity was determined from the difference between the saturated and dry sample weights. Coarse (diameter > 2 mm) and fine roots (diameter < 2 mm) including both live and dead roots were collected by hand from the dry soil samples sieved with a 2 mm mesh. The thickness of the litter layer was measured at the time of soil sample collection. The VAI was measured at each point using digital non-spherical color photographs (Nikon COOLPIX990). The photographs were taken with the camera pointing upward 1.0 m above the ground on cloudy days to avoid the effect of direct sunlight, and the VAI was determined from the photographs using Gap Light Analyzer software (Frazer et al., 1999).

In June 2005, the DBH and position were measured for all trees with a DBH greater than 10 cm in the 4 ha plot. From these data, we calculated stand structural parameters for the 25 measurement points; that is, the number of trees, total basal area, maximum DBH of trees, and mean DBH of trees within 3–8 m of the measurement point, according to Søe and Buchmann (2005). Litterfall amounts were measured between January 2002 and June 2006 using 0.5 m² litter traps at the 80 points of intersection for 20 m square grids in the 4 ha plot, except for the center of the plot because of the presence of the research crane. Among the 80 points, 9 points were very close to the measurement points. The litter traps were made of 1 mm nylon mesh and placed 1 m above the ground. Litter was collected from the litter traps once or twice each month, oven-dried for 48 h at 50 °C, and weighed.

2.5. Method of analysis

Using correlation analysis, we examined the effects of the soil porosity, root density, litterfall, and forest structure on the soil respiration averaged over 4 years at each point. Although temporal variations were not examined in this paper, our previous study showed low temporal variation in mean soil respiration for the 25 points because of the absence of a well-defined dry season and indistinct seasonal variations in temperature (Ohashi et al., 2009). This means that considering spatial variations in soil respiration is more critical than considering temporal variations in estimating the annual soil respiration on a stand scale.

In addition, we do not consider temporal changes in the spatial distribution of soil respiration (e.g., Xu and Qi, 2001; Søe and Buchmann, 2005; Ohashi and Gyokusen, 2007b) since we use soil

Table 1

Descriptive statistics and linear regressions for soil, root, and stand structural parameters versus soil respiration rate. VAI is the vegetation area index (leaf area index plus stem area index). Num(), BA(), Max(), and DBH() are the number of trees, total basal area, maximum DBH, and mean DBH within a distance in meters given in the parentheses (see Figs. 3 and 4).

Parameter	Unit	Mean	n	R ²
<i>Soil component</i>				
Root density	g C m ⁻²	235.5	25	0.28*
Soil porosity	m ³ m ⁻³	0.69	25	0.10
Thickness of litter layer	cm	5.0	25	0.11
<i>Stand structural component</i>				
Litterfall	g C m ⁻² year ⁻¹	306.8	9	0.13
VAI	m ² m ⁻²	5.76	25	0.03
Num(8) ^a		11.8	25	0.24
BA(6)	cm ² m ⁻²	32.6	25	0.37**
Max(6)	cm	145.0	25	0.38**
DBH(6)	cm	22.0	25	0.60***

* $p < 0.01$.

** $p < 0.005$.

*** $p < 0.001$.

^a Negatively correlated with soil respiration; all other parameters were positively correlated.

respiration data averaged over 4 years. At our study site, spatial variations in soil respiration were significantly different among the measurement campaigns, and the temporal changes in the spatial variations, which can be affected by soil temperature, soil water content, and soil animals, are complicated at our site (Ohashi et al., 2007a, 2009). However, using average values enables us to identify primary factors affecting the spatial variation in soil respiration through the years. Furthermore, this study considered the soil components and stand structural components as shown in Table 1, which changed little throughout the four sampling years.

In this study, to confirm the spatial representativeness of the soil respiration measured in the 40 m × 40 m subplot, we estimated the 4 ha plot-scale soil respiration based on a specific scaling procedure. The 40 m × 40 m subplot-scale measurements were extrapolated for the 4 ha plot-scale estimation using linear regression that can explain well the spatial variations in soil respiration as follows. First, soil respiration rates at the 355 intersections of 10 m × 10 m square grids in the 4 ha plot were estimated using the linear regression derived in the subplot under the assumption that the linear regression derived in the subplot was also applicable across the 4 ha plot. Secondly, we calculated the average and standard deviation of the soil respiration rates for the 355 intersections in the 4 ha plot. In this study, we defined the derived average as the stand-scale soil respiration estimate. In addition, to ascertain the spatial dependence of factors, which can explain well the spatial variations in soil respiration at this site, variogram analysis was performed using GS+ for Windows ver. 7.0J (Gamma Design, Michigan, USA) according to Ohashi and Gyokusen (2007b) and Ohashi et al. (2009).

Using the derived stand-scale soil respiration and litterfall-C measured at the 80 points in the 4 ha plot, we estimated the stand-scale soil C balance. In addition, to clarify the characteristics of the soil C balance at this site, the estimated soil C balance was compared with those reported for other tropical and temperate forests as obtained by Davidson et al. (2002) and Hibbard et al. (2005).

3. Results

3.1. Spatial variability

The frequency distribution of the soil respiration rates averaged over the 4 years at each of the 25 sampling points was skewed with a range of 7.0 μmol m⁻² s⁻¹ (Fig. 2). The mean rate ± standard

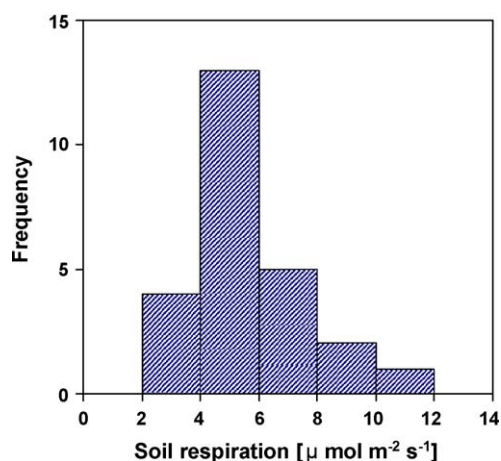


Fig. 2. Frequency distribution of the soil respiration rate measured in the subplot ($n = 25$). The soil respiration rates in this figure were averaged over the 35 measurement campaigns.

deviation and coefficient of variation were $5.7 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 33%. Table 1 shows the relationships between soil, root and forest structure parameters and soil respiration. Soil respiration did not correlate with soil porosity, litterfall, thickness of the litter layer, the VAI, or the number of trees within a distance of 8 m (Num(8)). Root density weakly correlated with soil respiration ($R^2 = 0.28$, $p < 0.01$). We found intermediate to relatively strong correlations in the relationships between soil respiration and forest structural parameters. The total basal area and maximum DBH within a distance of 6 m (BA(6) and Max(6), respectively) moderately correlated with soil respiration ($R^2 = 0.37$, $p < 0.005$; $R^2 = 0.38$, $p < 0.005$). The strongest correlation was found for the relationship between the mean DBH within a distance of 6 m (DBH(6)) and soil respiration ($R^2 = 0.60$, $p < 0.001$). We found a significant linear relationship between DBH(6) and soil respiration (Fig. 3) ($Y = 0.24 \cdot X + 0.42$, where Y is the soil respiration and X is DBH(6)). We also confirmed that the residual of soil respiration estimates (i.e., observed values minus estimates from the regression shown in Fig. 3) was not significantly correlated with other factors in Table 1 ($R^2 < 0.13$; $p > 0.05$) and that multiregression analysis little improved the reproducibility of the soil respiration.

Correlations between the mean DBH, total basal area, maximum DBH and soil respiration showed remarkable variations

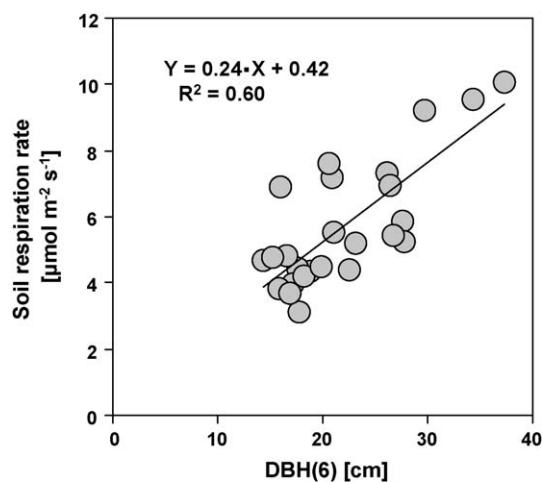


Fig. 3. Relationship between soil respiration averaged over 4 years and the mean DBH of trees within 6 m of the measurement points (DBH(6)). The regression showed a significant linear relationship ($p < 0.001$).

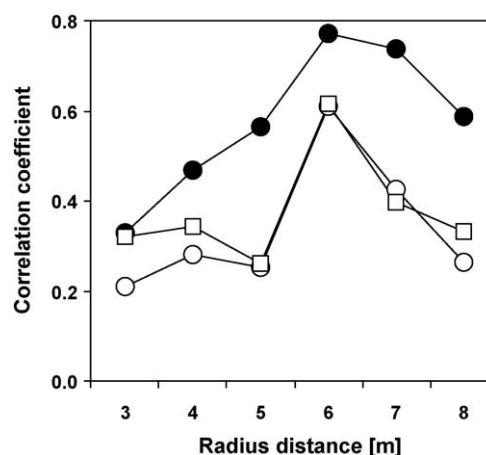


Fig. 4. Correlation between the mean DBH (closed circles), basal area (open circles), and maximum DBH (open squares) within various distances from each measurement point and soil respiration at each measurement point.

depending on the distance from the measurement points (Fig. 4). The maximum correlation (R_{max}) was found at a distance of 6 m for the mean DBH, basal area, and maximum DBH ($R_{max}^2 = 0.60, 0.37, 0.38$, respectively). We also examined the dependence of the correlations among the mean DBH, basal area, maximum DBH, and root density at each measurement point on the distance from the measurement points (Fig. 5). Consequently, R_{max} was found at a distance of 6–7 m for the mean DBH, basal area, and maximum DBH ($R_{max}^2 = 0.37, 0.25$, and 0.38 , respectively).

To understand the meaning of DBH(6), we examined the frequency distribution of the individual DBH within 6 m of the measurement points (data not shown). At the measurement points with smaller values of DBH(6), the DBH ranged between 10 and 40 cm and the frequency distribution of the DBH peaked at about 20 cm. On the other hand, at the measurement points with larger values of DBH(6), the DBH ranged between 20 and 100 cm and the peaks of the frequency distribution of the DBH were insignificant at a DBH of about 20 cm. Further, DBH(6) was weakly related to BA(6) ($n = 25$, $R^2 = 0.26$; $p < 0.01$).

Additionally, we examined the relationships among soil temperature, soil moisture and soil respiration for each measurement campaign. Although strong correlations were found for some measurement campaigns, soil respiration did not correlate significantly with either soil temperature or soil moisture in most measurement campaigns (mean $R^2 = 0.20$ and 0.16 , respectively).

3.2. Stand-scale soil respiration and litterfall-C

We extrapolated the $40 \text{ m} \times 40 \text{ m}$ subplot-scale soil respiration to 4 ha plot-scale soil respiration. Under the assumption that the linear regression between the measured soil respiration rate and DBH(6) as shown in Fig. 3 is also applicable in the 4 ha plot, we estimated soil respiration rates at the 355 intersections of $10 \text{ m} \times 10 \text{ m}$ square grids in the 4 ha plot using the linear regression. The mean soil respiration rate for the 355 intersections in the 4 ha plot was 2265 ± 636 (mean \pm standard deviation) $\text{g C m}^{-2} \text{ year}^{-1}$, which is equivalent to $6.0 \pm 1.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$. This value was nearly identical to that for the $40 \text{ m} \times 40 \text{ m}$ subplot ($2161 \pm 719 \text{ g C m}^{-2} \text{ year}^{-1}$), which is equivalent to $5.7 \pm 1.9 \mu\text{mol m}^{-2} \text{ s}^{-1}$. To confirm the spatial dependence of DBH(6), we performed variogram analysis. Consequently, almost the same frequency distribution of DBH(6) was found for the subplot and 4 ha plot with the peak of DBH(6) at 20–25 cm (data not shown). Further, the semivariance of DBH(6) in the 4 ha plot showed that there was autocorrelation within a separation of about 20 m, and that

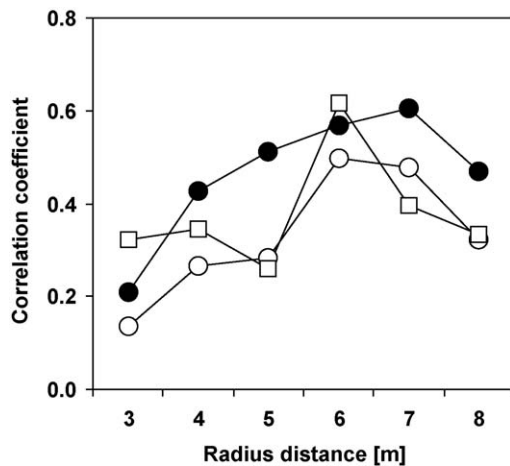


Fig. 5. Correlation between the mean DBH (closed circles), basal area (open circles), and maximum DBH (open squares) within various distances from each measurement point and root biomass at each measurement point.

the spatial dependence was unclear at a separation of greater than 20 m (data not shown).

The mean litterfall-C measured at the 80 points in the 4 ha plot between 2002 and 2006 was $303 \pm 104 \text{ g C m}^{-2} \text{ year}^{-1}$. Fig. 6 shows the relationship between annual litterfall-C and annual soil respiration in various tropical and temperate forest ecosystems with a linear regression based on a global dataset (Davidson et al., 2002). The figure shows that significantly larger litterfall-C and soil respiration were measured in tropical forests than in temperate forests and that the soil respiration measured at our site was the second largest among tropical forests in the Amazon, Costa Rica, and Hawaii and temperate forests (data are cited from Table 1 in Davidson et al., 2002 and Table 2 in Hibbard et al., 2005). On the other hand, the litterfall-C was the smallest among the tropical forests. Consequently, soil respiration at our site is extremely large at a given litterfall-C in terms of the global dataset. We confirmed the same tendency shown in Fig. 6 could be found using the 4 ha plot-scale soil respiration and annual litterfall-C at this site.

4. Discussion and concluding remarks

4.1. Spatial variations in soil respiration and forest structure

This study found significant correlations between soil respiration and forest structural parameters such as the mean DBH, total basal area, and maximum DBH within 6 m of the measurement points (DBH(6), BA(6), Max(6), respectively), and the most critical parameter explaining the spatial variation in soil respiration was DBH(6) (Table 1). Soil respiration at our site increased with increasing DBH(6) (Fig. 3). We confirmed the correlation between soil respiration and the DBH changed remarkably depending on the distance within which measurements were taken, and the maximum correlation was found at a distance of 6 m (Fig. 4). Here, DBH(6) is weakly related to BA(6), and the measurement points with larger values of DBH(6) have trees with $\text{DBH} > 40 \text{ cm}$ whereas measurement points with smaller values of DBH(6) did not. These results suggest larger sized trees are likely to be present within the measurement circle for larger DBH(6) at this site.

Relationships among the mean DBH, basal area, maximum DBH, and root density at each measurement point showed maximum correlation at a distance of 6–7 m (Fig. 5), indicating root density had positive linear relationships with the mean DBH, basal area, and maximum DBH within a distance of 6–7 m. This suggests the root biomass could be larger at the point where larger trees were

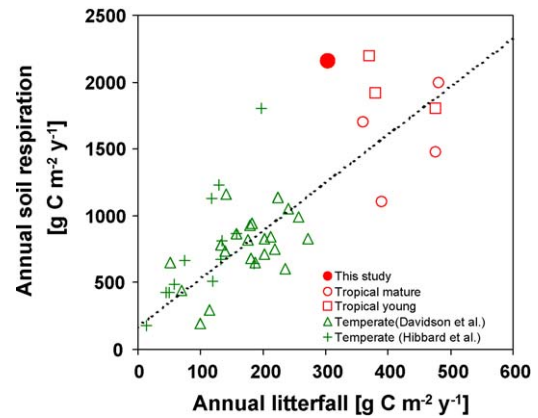


Fig. 6. Regression of annual soil respiration and annual litterfall-C for tropical and temperate forests from the works by Davidson et al. (2002) and Hibbard et al. (2005). The line represents the linear regression based on a global dataset collected by Davidson et al. (2002) and the regression is expressed as soil respiration = $161 + 3.61 \times \text{litterfall-C}$. The closed circle represents the datum for this study. Open circles and open squares represent data recorded for mature and young tropical rainforests, respectively. Open triangles and crosses represent data observed in temperate forests collected by Davidson et al. (2002) and Hibbard et al. (2005), respectively.

present within a distance of 6–7 m. This idea is supported by the measurements of the horizontal root distributions in emergent trees at the site. Roots of Dipterocarpaceae trees with a DBH greater than 60 cm spread 4.0–11.4 m ($n = 8$) from the trees, with a mean distance of 7.1 m (Yamashita et al., 2008). Thus, emergent trees at our site are likely to contribute to soil respiration within about 7 m of the trees, which corresponds well with the distance (i.e., 6–7 m) derived in this study (Figs. 4 and 5). In addition, this idea agrees with the observation by Zinke (1962) that the pattern of a soil property such as the nutrient condition around an individual tree generally develops with radial symmetry and that circles of influence can overlap in a forest ecosystem (Zinke, 1962). On the other hand, a strong correlation was not found directly between root density at 0–5 cm depth and soil respiration (Table 1). Roots deeper than 5 cm possibly contribute to soil respiration and could drive spatial patterns of the soil respiration rate at our site. Thus root sampling being limited to the soil surface in this study could be a reason for the correlation with root density being weaker than that with DBH(6), although it was suggested that surface root biomass in the soil at 0–5 cm depth accounted for about 70% of the root biomass in soil at 0–80 cm depth at our site (unpublished data).

In previous studies conducted in other tropical forests, several factors determining spatial variations in soil respiration have been reported. Sotta et al. (2004) showed that the soil moisture was a major factor in explaining spatial variations in soil respiration in an Amazonian tropical forest. They did not find a significant relationship between the soil respiration and basal area. Schwendenmann et al. (2003) also found a significant correlation between spatial soil respiration and soil moisture, but they found no clear correlations among soil respiration, fine root biomass, soil C content, and phosphorus content in a neo-tropical rainforest in Costa Rica. In a Southeast Asian tropical rainforest, soil moisture and root biomass are major factors determining the spatial variations in soil respiration (Adachi et al., 2006; Kosugi et al., 2007). The most influential factor determining spatial variations in soil respiration in other tropical rainforests is likely to be soil moisture. On the other hand, the impact of soil water on the spatial variation in soil respiration was not significant at our site. Thus key factors controlling the spatial variability of soil respiration vary among tropical rainforests, probably in relation to tree type, soil type, and climate seasonality.

4.2. Spatially extrapolated soil respiration

It is practical to use the stand structural parameter DBH(6) to extrapolate soil respiration spatially because stand-scale measurements of this parameter can be conducted more easily than can measurements of other parameters such as soil moisture, soil temperature, root biomass, and soil porosity. Consequently, this study estimated soil respiration at the 4 ha plot-scale as $6.0 \pm 1.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, which was nearly identical to the soil respiration measured in the subplot ($5.7 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$). This means the distribution pattern of larger sized trees in the subplot ($40 \text{ m} \times 40 \text{ m}$) can represent the whole forest structure in the 4 ha plot. In addition, the variogram analysis ascertained that the $40 \text{ m} \times 40 \text{ m}$ subplot can represent the whole forest structure in the 4 ha plot.

For the study site, spatially integrated CO_2 fluxes during the night were estimated using the eddy covariance technique. Nocturnal CO_2 fluxes have been estimated at between 7.6 and $8.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ through a year using the friction velocity (u_*) to remove data under stable conditions ($u_* < 0.5 \text{ m s}^{-1}$) (Saitoh et al., 2005). Since the nocturnal CO_2 fluxes are considered as being nearly completely ecosystem respiration, it could be expected that the total above-ground respiration (i.e., leaf and woody tissue respiration) is between 1.6 and $2.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ at our site when we consider the 4 ha plot-scale soil respiration of $6.0 \mu\text{mol m}^{-2} \text{s}^{-1}$. Although component measurements of above-ground respiration have not been conducted at our site, the indirect estimation of above-ground respiration was $1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ using the relationship between the LAI and above-ground respiration in tropical forests (Meir and Grace, 2002; Malhi et al., 1999). This value is very close to the range of values that could be expected from the estimated soil respiration and the nocturnal CO_2 flux based on the eddy covariance technique. Note there is little seasonal variation in air temperature at our site (Kumagai et al., 2005; Ohashi et al., 2007a); thus, almost constant ecosystem respiration can be expected normally through a year. Therefore, it can be thought that the soil respiration measured in the 4 ha plot subplot was roughly comparable to the spatially integrated CO_2 fluxes at night, and the soil respiration measured in the subplot could be regarded as representing the stand-scale soil respiration at our site, although the validity of our extrapolation should be examined by further measurements in the other subplots.

4.3. Soil C balance

Annual soil respiration measured in the present study was significantly larger than that expected in worldwide forest ecosystems for a given annual litterfall-C measurement (Fig. 6). This suggests the total belowground C allocation by trees (TBCA), which is defined as the annual soil respiration minus the annual litterfall-C on the basis of an assumption of constant soil C stocks in a steady state (Gower et al., 1996; Raich and Nadelhoffer, 1989; Raich and Schlesinger, 1992; Giardina and Ryan, 2002), at our site is larger than that for other forests. Davidson et al. (2002) summarized previous worldwide literature and showed the ratio of TBCA to litterfall-C (TBCA/LF) was about 3.6 in various forest ecosystems (Fig. 6). TBCA/LF in this study (7.1) was considerably higher when compared with data in the literature and also the highest among tropical forest ecosystems, for which TBCA/LF ranged between 2.8 and 4.7 for mature tropical forests and between 3.8 and 5.9 for young tropical forests (Fig. 6). It has been reported that TBCA for young forests is likely to be greater than that for mature forests, which need to establish and maintain root systems to support the water and nutrient demands of rapidly growing trees (Jipp et al., 1998; Davidson et al., 2002). Our TBCA/LF ratio was larger than the ratios for young tropical forests (Fig. 6), although our site can be categorized as mature forest according to

the age estimates for canopy trees (less than 800 years old) in another Bornean rainforest (e.g., Kurokawa et al., 2003). In addition, root biomass in the soil surface being significantly greater than that for Amazonian forest (Table 1, Trumbore et al., 2006) supports the TBCA being greater at our site.

Furthermore, to characterize the soil respiration at our site, global soil respiration models for the Northern Hemisphere (Raich et al., 2002; Reichstein et al., 2003) were used in this study. A climate-driven model employing temperature and precipitation (Raich et al., 2002) estimated the annual soil respiration at our site as $1772 \text{ g C m}^{-2} \text{ year}^{-1}$ under the condition of there being no water limitation. On the other hand, a modified model that includes the LAI as a surrogate of site productivity in addition to temperature and precipitation (Reichstein et al., 2003) estimated the annual soil respiration at our site as $2381 \text{ g C m}^{-2} \text{ year}^{-1}$, which was close to the actual annual soil respiration (2161 – $2265 \text{ g C m}^{-2} \text{ year}^{-1}$). This suggests that site productivity associating with C assimilation activity is important for soil respiration processes in tropical rainforests as noted by Reichstein et al. (2003).

Root respiration and root litter C decomposition, which originate from TBCA, can be limited by the C assimilation rate in trees. Recent studies pointed out that soil respiration is closely linked to photosynthesis in a forest ecosystem (Ryan and Law, 2005; Höglberg et al., 2001; de Neergaard et al., 2002; Tang et al., 2005). Here, gross C assimilation by photosynthesis is the world's highest in tropical evergreen forests (e.g., Gower, 2003) and photosynthesis in emergent trees is thought to contribute most to gross C assimilation in tropical rainforests (e.g., Carswell et al., 2000; Kumagai et al., 2006). Furthermore, a favorable condition for active photosynthesis can be found throughout the year owing to the absence of a well-defined dry season at our site (Kumagai et al., 2004). These results support the TBCA being the largest contributor to annual soil respiration at our site and emergent trees at our site playing an important role as a source of TBCA. Therefore, it seems the spatial arrangement of emergent trees and canopy structure (i.e., forest structure) strongly affect soil respiration in tropical forests. This idea agrees with our results that forest structural parameters such as DBH(6) are the most critical factors explaining spatial variations in soil respiration in Bornean tropical forest.

It has also been reported that poor nutrient soil can result in larger TBCA in forest ecosystems (Keith et al., 1997; Giardina and Ryan, 2002). Although the nutrient condition at our site is still uncertain, a short-lived and intense storm at our site (Manfroi et al., 2006; Kume et al., 2006) might lead to poor nutrient conditions in the sandy soil owing to rapid surface and subsurface runoff.

This study is the first report showing a significant relationship between soil respiration and forest structure in tropical forests. Literature on soil respiration in tropical forests based on long-term measurements is still limited, as shown in Fig. 6. Therefore, to clarify the generality of forest structure as a critical and practical indicator of spatial variations in soil respiration, further studies focusing on stand structural parameters are needed for tropical rainforests.

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