

Characteristics of soil CO₂ efflux variability in an aseasonal tropical rainforest in Borneo Island

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Abstract Although soil carbon dioxide (CO₂) efflux from tropical forests may play an important role in global carbon (C) balance, our knowledge of the fluctuations and factors controlling soil CO₂ efflux in the Asian tropics is still poor. This study characterizes the temporal and spatial variability in soil CO₂ efflux in relation to temperature/moisture content and estimates annual efflux from the forest floor in an aseasonal intact tropical rainforest in Sarawak, Malaysia. Soil CO₂ efflux varied widely in space; the range of variation averaged 17.4 μmol m⁻² s⁻¹ in total. While most CO₂ flux

rates were under 10 μmol m⁻² s⁻¹, exceptionally high fluxes were observed sporadically at several sampling points. Semivariogram analysis revealed little spatial dependence in soil CO₂ efflux. Temperature explained nearly half of the spatial heterogeneity, but the effect varied with time. Seasonal variation in CO₂ efflux had no fixed pattern, but was significantly correlated with soil moisture content. The correlation coefficient with soil moisture content (SMC) at 30 and 60 cm depth was higher than at 10 cm depths. The annual soil CO₂ efflux, estimated from the relationship between CO₂ efflux and SMC at 30 cm depth, was 165 mol m⁻² year⁻¹ (1,986 g C m⁻² year⁻¹). As this area is known to suffer severe drought every 4–5 years caused by the El Nino-Southern Oscillation, the results suggest that an unpredictable dry period might affect soil CO₂ efflux, leading an annual variation in soil C balance.

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Introduction

Tropical forests contain nearly 40% of the carbon (C) in the terrestrial biosphere and are responsible for almost 40% of terrestrial net primary productivity (Montagnini and Jordan 2005). Owing to the huge C stocks, loss of tropical forests could affect global C

balance, leading to various climate changes, such as global warming. Micrometeorological measurements that are used to determine stand-scale carbon dioxide (CO₂) fluxes have significantly advanced our understanding of whole ecosystem C processing (Grace et al. 1995; Malhi et al. 1998; Saleska et al. 2003; Miller et al. 2004). However, despite these advances, difficulties in estimating total respiration and in clarifying its sensitivity to environmental changes still remain. Component-scale measurements are important to increase the accuracy of ecosystem respiration estimates, to understand the processes of C flow and to estimate current and future C balance of the ecosystem against climate changes (Pattey et al. 2002; Chambers et al. 2004).

The efflux of CO₂ from soil surface (soil respiration) is one of the major components of ecosystem C cycling, contributing 50–95% of total ecosystem respiration (e.g., Law et al. 1999; Xu et al. 2001; Janssens et al. 2001; Wang et al. 2004; Yuste et al. 2005). The main sources of CO₂ are considered to be root and soil microbial respiration (Hanson et al. 2000; Kuzyakov 2006). Physical and chemical conditions of soil are also related directly and indirectly to CO₂ behavior in soil, increasing the complexity of CO₂ emission processes (Sitaula et al. 1995; Fang and Moncrieff 1998; Bain et al. 2005). As a result, soil CO₂ efflux fluctuates widely in space and time according to changes in various factors, such as temperature, moisture, carbon content, root biomass, pH, cation exchange capacity and soil air porosity (Sitaula et al. 1995; Fang et al. 1998; Davidson et al. 1998; Kiese and Butterbach 2002; La Scala Jr et al. 2000; Lou et al. 2004). Since the effects of these limiting factors vary for each ecosystem, topographic feature, location and time scale, detailed information is necessary to determine soil CO₂ efflux correctly at an ecosystem scale. However, our knowledge in tropical forests, especially in Asian tropics, is still very poor due to the lack of research facilities in this area.

Spatial variation of soil respiration is important not only for understanding CO₂ dynamics but also for suitable sampling design for estimates of mean soil respiration and the response to environmental changes. Published data suggests that the magnitude of spatial variation in soil CO₂ efflux could be larger in a tropical forest (Sotta et al. 2004; Ishizuka et al. 2005; Kosugi et al. 2007) than in other forest

ecosystems (Rayment and Jarvis 2000; Xu and Qi 2001) because CO₂ efflux rate is normally higher in tropical areas (Raich and Potter 1995). Recently, Ohashi et al. (2007b) found hot-spots of soil CO₂ efflux in a Bornean tropical rainforest, whose impact was 10% of total C efflux from soil. One of the factors causing the high variability and complexity could be root distribution (Schwendenmann et al. 2003; Ishizuka et al. 2002). Effects of soil moisture, texture (sandy or clay soil) and topographical position were also observed in a tropical rainforest (Sotta et al. 2006; Kosugi et al. 2007). Furthermore, recent studies in temperate and boreal forest ecosystems reported that nests of soil animals, such as ants, could be a point-source of CO₂ (Risch et al. 2005; Ohashi et al. 2007a), which might also increase spatial variation.

Temporal variation in soil CO₂ efflux is mostly driven by changes in soil temperature and moisture. Temperature is normally a stronger controlling factor than moisture content in temperate and boreal forest ecosystems (e.g., Ohashi et al. 1999; Pumpanen et al. 2003). On the other hand, moisture content could cause seasonal variation in soil CO₂ efflux in tropical forests due to low seasonality in temperature and a phase-locked dry period (e.g., Davidson et al. 2002; Fernandes et al. 2002; Hashimoto et al. 2004; Kosugi et al. 2007). However, in tropical aseasonal rainforests, where both temperature and moisture are favorable all year round, it is difficult to distinguish a clear temporal pattern (Medina et al. 1980; Schwendenmann et al. 2003) and the correlation between soil CO₂ efflux and environmental factors is almost unknown.

This study aimed to characterize spatial and temporal variations in soil CO₂ efflux in relation to temperature and moisture in an aseasonal intact tropical rainforest in Southeast Asia, Sarawak, Malaysia, where the climate is hot and humid with no phase-locked dry period. Annual CO₂ efflux from this forest floor was estimated using these data. Spatial differences in soil CO₂ efflux were studied not only to characterize spatial variation but also to obtain a suitable sampling design for a representative value of soil CO₂ efflux in the ecosystem. The temporal variation in soil CO₂ efflux was obtained from irregular observations over 22 months. Also, for the first time, variation in soil CO₂ efflux within a day in an Asian tropical forest was reported. The diurnal

variation was measured using an automatic open/close soil CO₂ efflux chamber. The preliminary results may be valuable in discussing the magnitude of variation in soil CO₂ efflux at different time scales (short- vs. long-time interval).

Materials and methods

Study site

The study was carried out in a natural tropical rainforest in Lambir Hills National Park (4°12' N, 114°02' E), 30 km south of Miri City, Sarawak, Malaysia (Fig. 1). It was undertaken as part of a project 'Research and observation on the atmosphere and ecosphere interaction in tropical forest canopy' of JST (Japan Science and Technology Agency) (Nakashizuka et al. 2001). One of the goals of the project is to clarify carbon and water cycling of a lowland dipterocarp forest in Southeast Asian humid tropics and to estimate the response to current and future climate change (Kumagai et al. 2004a). An experimental site of 4 ha was established for this project. The site was at an altitude of ~200 m and an 80-m tall canopy crane, constructed in the center of this site, was used to measure the forest C budget using eddy covariance techniques.

The mean annual rainfall at Miri Airport, 20 km from the study site, for the period 1968–2001 was ~2,740 mm. The mean annual temperature was ~27°C, with little seasonal variation (Kumagai et al. 2005). This rainforest was a mixed dipterocarp forest, containing various dipterocarp species

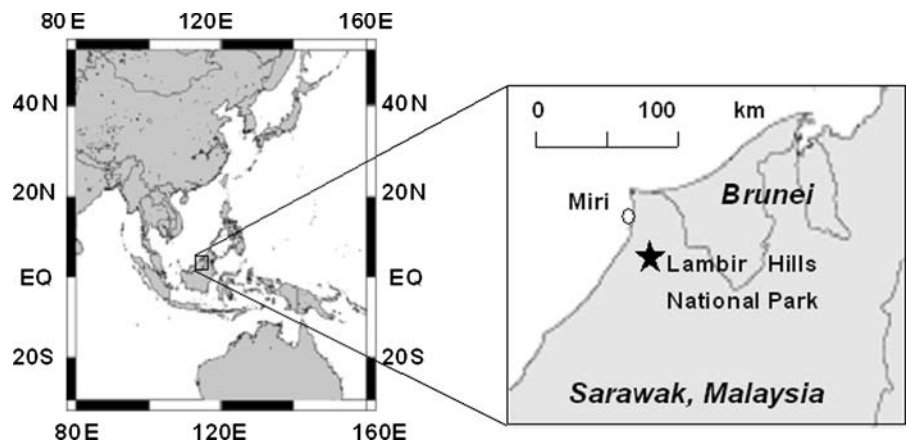
covering 85% of the total park area. A more detailed description of the vegetation of this area is to be found in Ashton (2005). The continuous canopy height of the forest was about 40 m, but the height of emergent trees reaches 50 m. The mean leaf area index (LAI) was 6.2 m² m⁻², ranging from 4.8 to 6.8 m² m⁻² (Kumagai et al. 2004b). The soils consist of red–yellow podzonic soils (Malaysian classification) or ultisols (USDA 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).

At the crane site, a 40 × 40-m plot was established and 25 sample locations selected at the intersections of a 10 × 10-m square grid on the plot. Three intersections were arranged randomly to establish two subplots for each intersection (six subplots in total). Each subplot was constructed from the selected intersection to next one, which was also chosen randomly (Fig. 2). There were six sample locations for each subplot, which were arranged in a row, changing the distance from the base intersection (36 points in total in the six subplots).

Sampling procedure

Spatial variation in soil CO₂ efflux, temperature and moisture content were measured separately from the temporal variation experiments. Spatial differences in soil CO₂ efflux were determined from 61 sample locations, i.e., at 25 intersections of the grid in the main plot and 36 additional points in the six subplots. All 61 measurements were conducted between 09:00 and 15:00 h and repeated four times, on 3 and 4

Fig. 1 Location of Lambir Hills National Park (LHNP), Sarawak, Malaysia



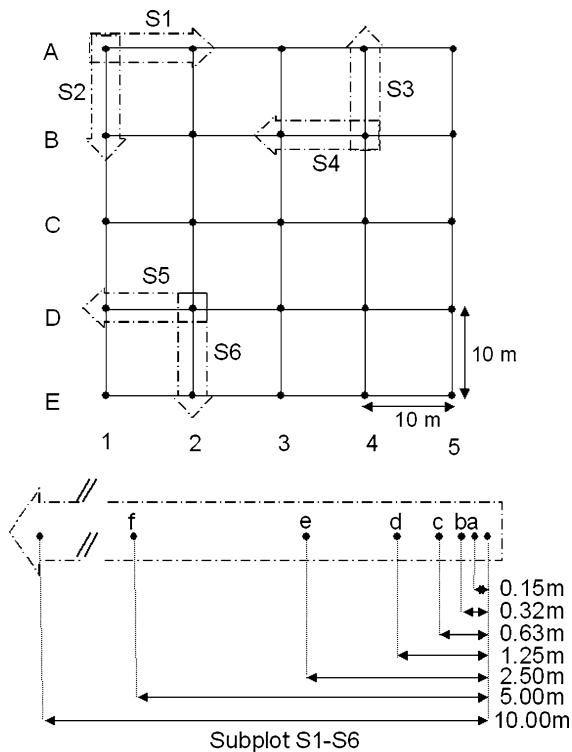


Fig. 2 Sampling design. The 40 × 40 m main plot was established near an 80-m tall canopy crane, constructed for eddy covariance measurements. Filled circle indicates the measurement points of soil CO₂ efflux. A total of 25 intersections were measured to examine spatial and seasonal variation in soil CO₂ efflux. A total of 36 additional points in subplot S1–S6 (six points in each subplot) were measured to examine spatial variation in soil CO₂ efflux

November and 7 and 8 December 2002. The 25 sample locations in the main plot were conducted first, then the six subplots were measured; the total time was nearly 4 h for all 61 measurements. Spatial differences in soil temperature at 10 cm depth and volumetric moisture content at 0–10 cm depth were determined with the CO₂ efflux measurements at the 25 sample locations in the main plot. Temporal fluctuation in soil temperature and moisture content during the measurement periods was monitored at the same depths every 10 min at a fixed location in the main plot. The fluctuation in soil temperature at 10 cm depth was small ($0.93 \pm 0.24^\circ\text{C}$, mean and SD) during the soil CO₂ efflux measurements ($n = 4$). Precipitation during the same periods was also recorded. There was no rainfall on 3 November or on 7 and 8 December. 5 mm rainfall occurred from 12:00 to 13:00 h on 4 November, but soil moisture

content (SMC) at 0–10 cm depth in the main plot did not change (20%) before and after the rainfall. These results suggest that there was little effect of temporal variation in environmental factors on the measurement of spatial differences in soil CO₂ efflux and that the variation in environmental factors probably occurred via site specific conditions at each location.

Temporal variation in soil CO₂ efflux was determined by the mean of the 25 intersections measured from May 2002 to February 2004 (Ohashi et al. 2007b). Measurements were conducted at 2–3 months intervals for the first year (May 2002–April 2003) and at half-yearly intervals thereafter. The 25 samplings were repeated 1–4 days at each time (20 sampling days in total). It took 2–3 h for the 25 measurements, conducted between 09:00 and 15:00 h. Air (77 and 1.5 m above forest floor) and soil (10, 20 and 50 cm depth) temperature profiles were monitored during the measurement period (1 May 2002–29 February 2004). Precipitation and SMC profiles (10, 30 and 60 cm depth) were recorded at the same time. The temperature and moisture content data were collected every 10 min and an hourly mean calculated. There was no rainfall during each measurement for seasonal variation in soil CO₂ efflux. The fluctuation in soil temperature at 10 cm depth was $0.20 \pm 0.26^\circ\text{C}$ during the measurement ($n = 20$), suggesting little effects of temperature change on CO₂ efflux samplings.

Soil CO₂ efflux was also measured every 15 min over two periods, 1 and 2 March 2003 (start 00:00 h, end 02:00 h) and 2–4 March 2003 (start 15:00 h, end 03:00 h), at a location 20 m away from the main plot in order to determine its diurnal variation. Precipitation, hourly changes in air temperature at 77 and 1.5 m above the ground and soil temperature at 10, 20 and 50 cm depth were recorded from 1 to 4 March 2003 to examine the effect of environmental condition on the diurnal variation in soil CO₂ efflux.

CO₂ efflux measurement

Spatial and temporal variation in soil CO₂ efflux was measured using a commercial respirometer (LI-6400; LI-COR Inc., Lincoln, NE, USA), consisting of an infrared gas analyzer (IRGA) and a small soil chamber (LI-6400-09) of 962 cm³ in volume (72 cm² in area). Measurements were replicated three times at each sampling point and then averaged. It took 3–4 min to

take the three replicate readings. PVC collars (7 cm height and 85 cm² area) were inserted into the forest floor to a depth of ~4 cm at each point to minimize soil disturbance during the measurement. Small litter and branches were left in the collar, although large items those size was bigger than the collar were removed. All collars were left on site for the entire study period.

Diurnal variation in soil CO₂ efflux was monitored by an automatic open/close chamber based on a non-steady-state flow-through chamber system (Rochette et al. 1997). It consisted of an iron rectangular parallelepiped chamber 3,600 cm³ in volume (225 cm² in area), a pump, air-flow controller, IRGA (LI-820, LI-COR Inc., Lincoln, NE, USA) and tubes for air circulation between the IRGA and chamber. For the measurement, the top of the chamber closed for 5 min; thereafter, it was automatically opened for 10 min by a motor after each measurement. Air-flow rate through the chamber was controlled at 1.0 m s⁻¹. Air was withdrawn from the upper part of the chamber, passed through the IRGA and returned to the chamber through a tube ring with a manifold hole, which was attached at the base of the chamber to mix the sample air with the air in chamber. Since air movement inside the respiration chamber could disrupt the high laminar boundary layer over the forest floor (Le Dantec et al. 1999) and increase the pressure heterogeneity inside the chamber (Davidson et al. 2002), a fan was not used (LI-COR 1997). CO₂ concentration data were logged with a Handy Logger (LG-C1A, LOG Electronics, Tokyo, Japan) every 10 s and the soil CO₂ efflux rate was determined from the changes in CO₂ concentration inside the chamber. The soil CO₂ efflux measured with the automatic chambers was not significantly different from those made with the commercial respirometer (LI-6400), which was used for the other CO₂ efflux measurements under laboratory and field conditions (paired *t*-test, *df* = 2, *t* = 1.045, *P* = 0.406). To prevent litter-fall into the chamber during the measurements, a plastic net with 1.5 cm squares (size 0.3 × 0.3 m) was spread over the chamber using four wooden sticks of 1 m long.

Measurement of environmental factors

Spatial differences in soil temperature at 10 cm depth were determined at the 25 intersections in the main plot with a soil temperature probe connected to the

soil respirometer (LI-6400-09TC). Temporal changes in air temperature at 77 and 1.5 m above forest floor were monitored by temperature sensors with data-loggers (H0803208 and RS1, Onset, Pocasset, MA, USA) arranged on the crane. Temporal changes in soil temperature at 10, 20 and 50 cm depth were monitored and logged at a fixed location in the main plot using copper-constantan thermocouples and the CR10X micrologger (Campbell Scientific, Logan, UT, USA).

Spatial differences in volumetric SMC at 0–10 cm depth were determined at the 25 intersections with a time domain reflectometry (TDR) sensor (Hydrosense, Campbell Scientific, Logan, UT, USA). Temporal changes in the volumetric moisture content during the measurements of spatial differences were monitored at the fixed location in a main plot using a TDR sensor (CS615, Campbell Scientific) and microloggers (CR23X, Campbell Scientific). Soil moisture profiles at 10, 30 and 60 cm depths were taken during the temporal measurement at a meteorological tower in the park, located 540 m southwest of the crane site, using TDR sensors (CS615) and a CR10X micrologger. Rainfall was recorded using a Tipping-Bucket Rain Gage (Ota Keiki Seisakusyo, No. 34-T) at the meteorological tower.

The relative extractable water in the soil (REW; m³ m⁻³) was calculated using the weighted mean volumetric moisture content in the 0–60-cm soil layer (SMC; m³ m⁻³) as $REW = (SMC - RWC) / (SWC - RWC)$, where SWC and RWC are the saturated and residual water contents averaged in the 0–60 cm layer, respectively. The SMC was weighed and averaged according to the soil depth, as $SMC = (20SMC_{10} + 25SMC_{30} + 15SMC_{60}) / 60$, where SMC₁₀, SMC₃₀ and SMC₆₀ are volumetric SMC at depths of 10, 30 and 60 cm, respectively. The SWC and RWC were taken as the maximum and minimum SMC during the experimental period (1 May 2002–29 February 2004). The REW ranges from zero (soil dry) to one (soil saturated).

Data analysis

Descriptive statistics (maximum, minimum, mean and median values, range) were used to express characteristics of the spatial variation of soil CO₂ efflux. Variogram computation was also performed to ascertain the strength and scale of the spatial

dependence of soil CO₂ efflux. It was evaluated by semivariance, which is defined as:

$$\gamma(h) = \left[\sum \{z(x_i) - z(x_i + h)\}^2 \right] / 2N(h) \quad (1)$$

where $\gamma(h)$ is the semivariance at separation distance h , $N(h)$ is the number of lag pairs at distance interval h and z is the value of variable at location x_i and $x_i + h$. Plotting $\gamma(h)$ against h gives the semi-variogram, which either exhibits purely random behavior or some systematic behavior described by theoretical models (linear, spherical, gaussian and power law models). All soil CO₂ efflux data was log-transformed prior for analysis to normalize the distribution (Gamma Design 2004). We used variable h value at distances less than 2.5 m. These intervals corresponded to the distances between the measurements in the subplots (Fig. 2). For greater distances you used uniform intervals of 2.0 m. We conducted not only isotropic but also anisotropic analyses in order to see a direction-dependent trend in the data. These calculations were performed using GS+ for Windows ver. 7.0J (Gamma Design, MI, USA).

When spatial dependencies were not present, the minimum number of samples (n) required to estimate the mean soil CO₂ efflux of this plot with a given probability level α , was estimated using the following equation (Davidson et al. 2002):

$$n = \{T_{\alpha} s / dm\}^2 \quad (2)$$

where T is the Student's statistic tabulated for the desired confidence interval level and degrees of freedom of the sample, d the relative error considered acceptable, m and s are the mean and standard deviations of soil CO₂ efflux in each measurements. Normality of the data distribution was examined using a Kolmogorov–Smirnov test prior to this calculation with 95% confidence level.

Temporal variation in soil CO₂ efflux were determined and compared over time using the general linear model repeated measures analyses. Sampling dates were specified within-subject factors. Pairwise comparisons with Bonferroni corrections were used for comparing means when interactions were statistically significant among sampling dates. The statistical test was performed using SPSS 13.0.1 (SPSS, Cary, IL, USA).

Regression analyses were used to determine the effect of temperature and moisture content on spatial differences in soil CO₂ efflux. It was also applied to assess the relationship between temporal variation (long and short time intervals) in soil CO₂ efflux and temperature and moisture content (including REW) profiles. Non-linear regression curve was fitted for the factor which could estimate the changes in soil CO₂ efflux at long-time interval best to calculate annual soil CO₂ efflux.

Results

Spatial differences

Soil CO₂ efflux was highly variable in space, showing upto 17.6-fold differences between the 61 sample locations (Table 1). The range of variation averaged 17.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in total, which was larger in December (21.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in average) than in November (13.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in average). While most CO₂ fluxes were under 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$, extremely high fluxes, over 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$, were observed (Fig. 3). Hot-spots of CO₂ effluxes were found at between two and five locations and the locations, except S3-b, varied from 3 November to 8 December. The changes in CO₂ efflux in subplot S3 indicate that the hot-spots observed at location S3-b

Table 1 Spatial variation in soil CO₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$)

Date	n	Max	Min	Mean	Median	Range	SD	CV (%)	Location of hot-spots ^a
03/11/02	61 (59)	17.1	1.8	5.7 (5.4)	5.4 (5.3)	15.2 (8.0)	2.3 (1.7)	41 (31)	S3-b, S6-d
04/11/02	61 (56)	13.9	1.6	5.3 (4.6)	4.4 (4.3)	12.3 (7.1)	2.8 (1.7)	52 (36)	B2, C3, E3, E5, S3-b
07/12/02	61 (58)	22.9	1.3	5.3 (4.8)	4.7 (4.5)	21.6 (8.1)	3.2 (1.7)	59 (35)	A5, B2, S3-b
08/12/02	61 (58)	22.3	1.9	5.3 (4.6)	4.4 (4.3)	20.5 (6.9)	3.3 (1.6)	62 (34)	A5, B2, S3-b

SD and CV are standard deviation and coefficient variation, respectively. Numbers in parentheses are data in which CO₂ hot-spots (<10 $\mu\text{mol m}^{-2} \text{s}^{-1}$) were excluded

^a See Fig. 2 for the name of location

occurred in a limited area with a diameter <0.5 m (Fig. 4). Mean CO₂ efflux decreased by 13% when CO₂ hot-spots were excluded. High correlation was found in soil CO₂ efflux rates without hot-spots between 3 and 4 November ($r = 0.78$, $n = 54$, $P < 0.001$) and between 7 and 8 December ($r = 0.80$, $n = 54$, $P < 0.001$), indicating that spatial patterns were similar between the 2 days. However, the correlation coefficient between values in November and those in December decreased ($r = 0.44$ – 0.68 , $n = 54$, $P < 0.001$) relative to those between the values measured on the subsequent days, suggesting

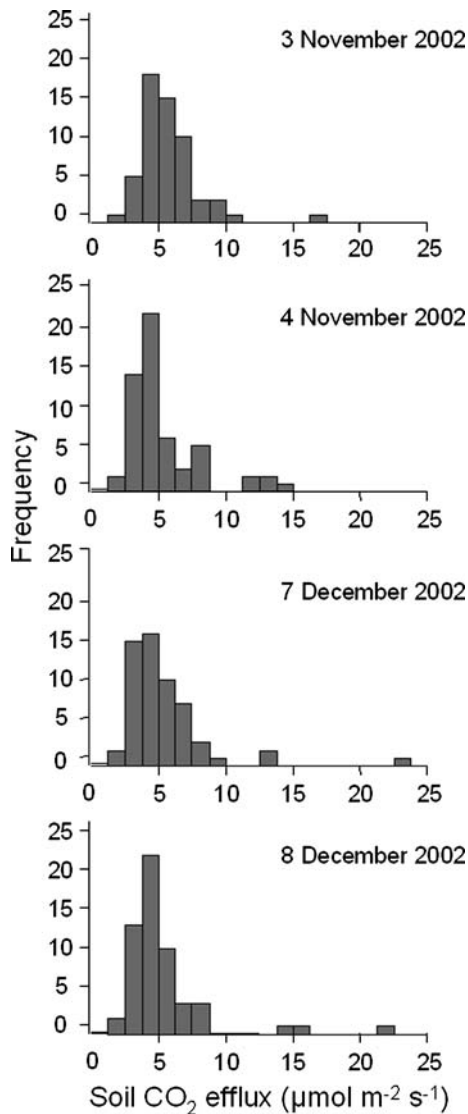


Fig. 3 Frequency distribution of soil CO₂ efflux between sampling points in the main plot and subplots ($n = 61$)

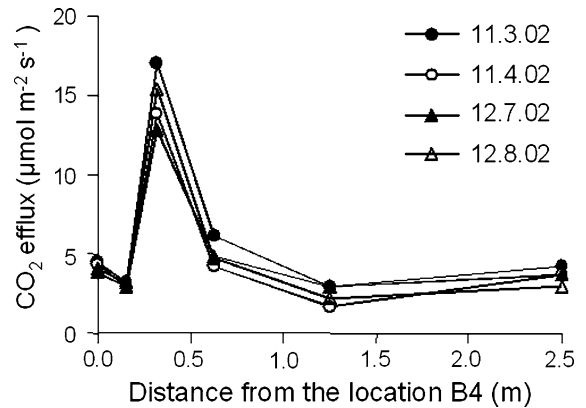


Fig. 4 Changes in soil CO₂ efflux with distance from B4 to A4 in subplot S3. See Fig. 2 for the number of plot and locations

changes in spatial pattern of soil CO₂ efflux over 1 month.

The semivariogram revealed no clear autocorrelation in the spatial variation of soil CO₂ efflux (Fig. 5). We find no directional trend in the data. The minimum number of samples necessary to estimate the mean value of the plot, within 15% of the actual value at 95% confidence level, was calculated from the data, which excluded hot-spots to meet normal distribution. The estimated number of samples averaged 20 and ranged from 17 to 23.

Soil temperature and moisture varied greatly among the 25 sample locations (Table 2). Soil temperature at 10 cm depth positively correlated with the spatial differences in soil CO₂ efflux on 3 and 4 November, but no correlation was observed on

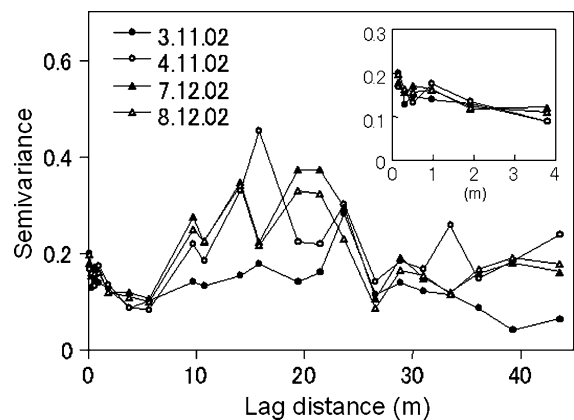


Fig. 5 Semivariogram of log-transformed soil CO₂ efflux. The inset is the variogram when lag distance is < 4 m

Table 2 Ranges of spatial variation in soil temperature at 10 cm depth, volumetric SMC at 0–10 cm depth, and the relationship of each variable with soil CO₂ efflux (correlation coefficient)

Date	<i>n</i>	Temperature (°C)			Moisture (m ³ m ⁻³)			Correlation coefficient	
		Max	Min	Mean ± SD	Max	Min	Mean ± SD	Temperature	Moisture
03/11/02	25	26.2	25.3	25.6 ± 0.3	0.41	0.10	0.22 ± 0.07	0.69*** (0.54**)	-0.31 (-0.31)
04/11/02	25	26.3	25.3	25.7 ± 0.3	0.33	0.12	0.22 ± 0.07	0.75*** (0.58**)	-0.37 (-0.51**)
07/12/02	25	27.3	25.0	25.5 ± 0.4	0.37	0.08	0.24 ± 0.07	0.26 (0.29)	-0.07 (-0.22)
08/12/02	25	26.5	25.3	25.7 ± 0.3	0.33	0.09	0.20 ± 0.07	0.38 (0.20)	-0.15 (-0.27)

, * Significance levels of $P < 0.01$ and $P < 0.001$, respectively. Numbers in parentheses are data in which CO₂ hot-spots (<10 μmol m⁻² s⁻¹) were excluded

7 and 8 December. The correlation coefficient in November decreased when hot-spots were excluded. Effect of moisture content was uncertain, but a negative relationship was observed in 4 November when hot spot data were excluded.

Temporal variation

Although temporal variation in soil CO₂ efflux, air temperature and precipitation showed no clear pattern (Fig. 6), CO₂ efflux varied among sampling days ($F = 5.214$, $df = 4.52$, $P < 0.001$). In particular, soil CO₂ was significantly lower on 2–4 March 2003 than on most of the other measurement days ($P < 0.05$). Temperature had no correlation with the temporal variation in soil CO₂ efflux (Table 3). On the other hand, the variation in soil CO₂ efflux over time corresponded to that of SMC (Fig. 7). There was a positive correlation between soil CO₂ efflux and SMC at every depth and high correlation coefficient was observed in SMC at 30 and 60 cm depth (SMC₃₀ and SMC₆₀). REW (relative extractable water in the soil) also showed a good correlation with soil CO₂ efflux, although the correlation coefficient was less than that of SMC₃₀ and SMC₆₀. Since Fig. 7 indicates that SMC₃₀ had a wider range than SMC₆₀, we used the relationship between temporal variation in soil CO₂ efflux (SR) and that in SMC₃₀ in order to estimate annual soil CO₂ efflux:

$$SR = 0.209 SMC_{30} + 0.7429 \quad (n = 18) \quad (3)$$

The daily and annual mean soil CO₂ efflux estimated from Eq. 3 and daily mean SMC₆₀ from May 2002 to February 2004 were 0.45 mol m⁻² day⁻¹ (5.344 g C m⁻² day⁻¹) and 165 mol m⁻² year⁻¹ (1,986 g C m⁻² year⁻¹), respectively.

Soil CO₂ efflux fluctuated widely in daytime and was stable during night (Fig. 8). The pattern of fluctuation was variable: while soil CO₂ efflux

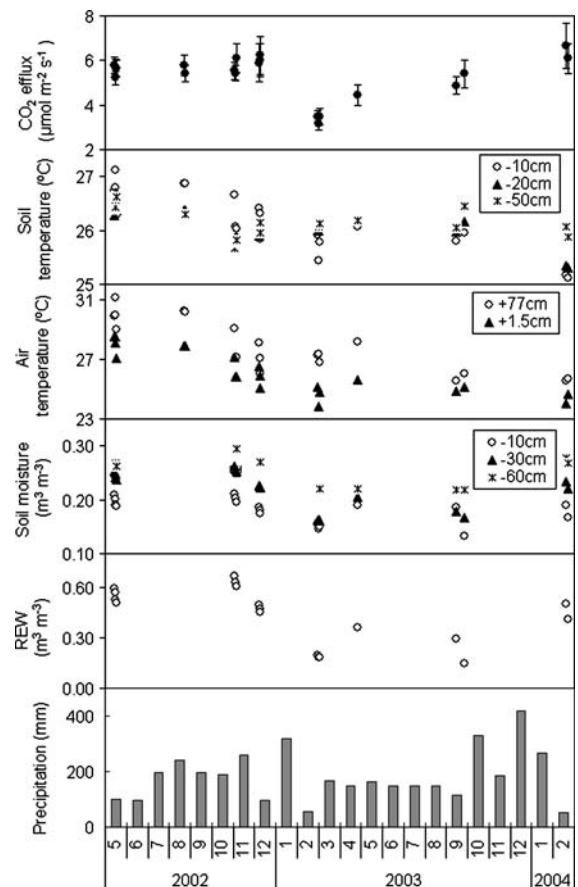


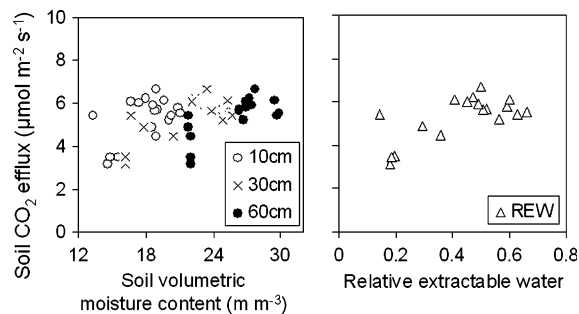
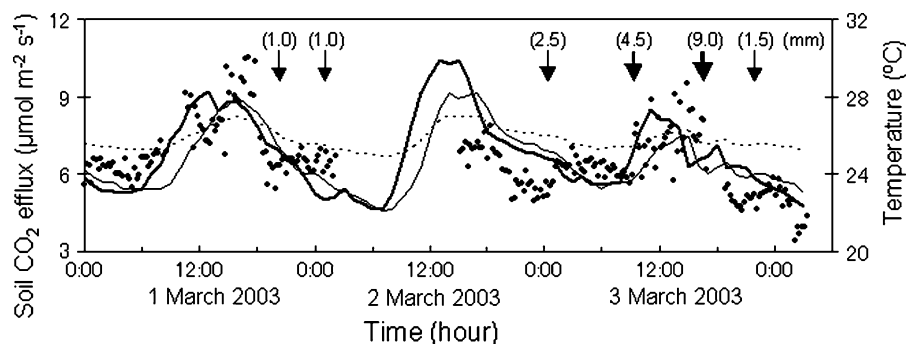
Fig. 6 Seasonal variation in soil CO₂ efflux and environmental factors during the measurement period. *Negative* and *positive* values in the legends indicate sampling height above the ground and depth of below ground level. The *error bar* denotes standard errors ($n = 25$)

Table 3 Correlation coefficients between soil CO₂ efflux and environmental factors

Profile (m) ^a	Correlation coefficient
Temperature (<i>n</i> = 20)	
+77	0.02
+1.5	0.31
-0.1	0.17
-0.2	-0.22
-0.5	-0.06
Moisture content (<i>n</i> = 18)	
-0.1	0.53*
-0.3	0.74***
-0.6	0.75***
REW	0.70**

^a Positive and negative values mean the height above and below ground level

*, **, *** Significance levels of $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively

**Fig. 7** Relationships between soil CO₂ efflux, and SMC at 10, 30, 60 cm depth and REW**Fig. 8** Diurnal variation in soil CO₂ efflux and temperature for the period 1–4th March 2003. *Thick solid, thin solid and dotted lines*, respectively, indicate hourly mean temperature in the air 77 and 1.5 m above the ground and in soil at 10 cm depth.

increased from 6 to 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the former period (1–2 March), it fluctuated unpredictably in the latter period (2–3 March). The high precipitation (4.5 and 9.0 mm) might have disturbed the soil CO₂ efflux, but the small amount of nocturnal precipitation (<2.5 mm) did not affect soil CO₂ efflux at night. Soil CO₂ efflux significantly correlated with air temperature at 77 m ($r = 0.64$, $n = 62$, $P < 0.001$) and 1.5 m ($r = 0.55$, $n = 62$, $P < 0.001$) above the ground and soil temperature at 10 cm depth ($r = 0.49$, $n = 62$, $P < 0.001$). In the former and latter periods, the range of the diurnal fluctuations was 29 and 44% wider than the seasonal fluctuations, respectively. Mean soil CO₂ efflux at night-time (from 18:00 to 06:00 h) was 22% lower than daytime (from 06:00 to 18:00 h).

Discussion

Spatial variation

Spatial variation in soil CO₂ efflux, observed in this study, was higher than either seasonal or diurnal variation. It is difficult to compare our results directly with other studies because the differences in experimental design, such as sampling number, size of soil CO₂ efflux chamber and area of experimental plot, can affect results (Davidson et al. 2002; Yim et al. 2003; Fang et al. 1998). Despite the differences in the plot size (1,600 vs. 570–10,800 m²), sample number (25 vs. 5–80) and chamber size (72 vs. 70–310 cm²), the range of variation in this study (17.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)

Arrows indicate the occurrence of precipitation. The *boldness of arrows* changes according to the amount of precipitation, which is indicated in *parentheses*. Efflux measurements were made every 15 min

was much larger than that reported in other studies for tropical rainforests ($5.4\text{--}7.0 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Sotta et al. 2004, 2006; Ishizuka et al. 2002). This suggests high spatial variation in soil CO_2 efflux in this ecosystem compared to other tropical forests.

The decrease of spatial variation after the removal of extremely high CO_2 effluxes ($>10 \mu\text{mol m}^{-2} \text{s}^{-1}$) suggests that the high spatial variation was attributable to CO_2 hot-spots. In the same forest, Ohashi et al. (2007b) reported that soil CO_2 hot-spots contributed to 10% of total CO_2 efflux, which was similar to our results. Ohashi et al. (2007b) also found that the occurrence of hot-spots varied in time and space, suggesting that mobile factors, such as nests of termites and ants, might be a reason for CO_2 hot-spots. We also observed that most hot-spots disappeared over a month and that they can be formed in very limited areas, less than 0.5 m in diameter. These results support the idea that the respiration chamber might have detected enormous CO_2 emissions originating from nesting and foraging activity of termites and/or ants. Since underground nests/bivouacs of termites and ants are very common in Asian tropical forests, it is highly probable that soil respiration has been measured immediately above or close to a colony (Ohashi et al. 2007b). However, other explanations, such as root distribution (Schwendenmann et al. 2003; Ishizuka et al. 2002) or changes in soil texture (Sotta et al. 2006), are also possible explanations. Stoyan et al. (2000) reported that variation in CO_2 fluxes was dependent on spatial variation of roots and plant debris that varied at scales of centimeter-level, suggesting these factors could cause point sources of soil CO_2 fluxes. Further research is necessary to determine the process of high CO_2 efflux.

Temperature explained 48–57% of the spatial heterogeneity in soil CO_2 efflux in November. Although temperature is frequently mentioned as the main factor controlling soil CO_2 efflux, it mostly explains temporal variation (e.g., Xu and Qi 2001; Sotta et al. 2004). This study found that spatial variation in soil CO_2 efflux is related to local spatial differences in temperature. The unevenness of canopy structure and underground vegetation might generate heterogeneity in the sun's radiation reaching the forest floor, leading to patchiness in temperature in the litter and soil surface layers. Temperature heterogeneity would affect biological activity in the soil, such as

created by microbes and roots. It is also expected that temperatures would be higher at the nests of termites and ants than in the surrounding soil owing to the thermoregulation ability of these insects (Petal 1978; Korb and Linsenmair 2000). However, the decrease in correlation coefficient during December suggests that the other limitation factors were more important than the effect of temperature in this month. The negative effect of soil moisture content, which probably caused a decrease of CO_2 diffusion rates in soil (Schwendenmann et al. 2003), was observed only on 4 November when hot-spot data were excluded. These results indicate that spatial differences in soil CO_2 efflux might have been controlled by multiple factors whose effects vary with time. This idea is also supported by the lower correlation coefficient between months than between days.

Temporal variation

The seasonal pattern of soil CO_2 efflux was unclear because of the low sampling frequency. However, our results showed soil CO_2 efflux has significantly decreased in March 2003 with the decrease in soil moisture content. Previous studies in other tropical regions have also reported a strong effect of SMC and negligible temperature effect. However, most of these studies were conducted in tropical forests, where precipitation was highly seasonal and/or a clear phase-locked dry period could be observed (e.g., Davidson et al. 2002; Hashimoto et al. 2004; Sotta et al. 2006; Kosugi et al. 2007). On the other hand, central Southeast Asia, where our study site was established, has a tropical maritime climate with monsoon rains from the Pacific Ocean and from the Indian Ocean, which is one of the wettest and most aseasonal climates of any tropical region (Roubik 2005). We found that temporal differences in soil CO_2 efflux in the central Asian tropics are still sensitive to soil moisture conditions, even though the climate is stable, warm and humid throughout the year. Schwendenmann et al. (2003) also observed ambiguous and little variation in seasonal soil CO_2 efflux in old-growth neotropical forest in Costa Rica but found that moisture content could explain the variation. While the relationships between CO_2 efflux and moisture content were described by a parabolic function, we found a positive and linear relationship between the two variables.

Although our results indicate a strong effect of soil moisture content, we also observed no decrease in soil respiration in the similar dry period in late September 2003. This suggests that dryness might be not the only reason for the decrease in soil respiration. Since soil temperature was lower in March 2003 than in September 2003, another factors such as decrease in soil temperature might be also important for causing low soil respiration.

Recent research has revealed that, although seasonality (i.e., dry and wet seasons) does not occur, there are some unpredictable intra-annual dry spells in Southeast Asian tropical rainforests (Kumagai et al. 2004b; Harrison 2005). Kumagai et al. (2004b) studied the effect of intra-annual dry spells on canopy conductance, which mainly depends on the physiological behavior of the plant, in the same study site and observed lower canopy conductance in dryer than in wetter periods. They defined three specific periods of moisture condition using REW as: medium dry (0.24–0.33), heavy dry (0.05–0.09), and wet periods (0.47–0.66). In this study, REW varied from 0.15 to 0.66 during measurements and the lowest CO₂ efflux was observed in March 2003, when REW (0.18) was intermediate between medium and heavy dry periods. The coincidental decrease in soil CO₂ efflux and canopy conductance during dry periods suggests that changes in plant physiological conditions, related to dryness, might have caused a reduction in root respiration at our site. As discussed by Kumagai et al. (2004b), the ultisol in this site, which is classified as an argillic soil, might act like sand and clay at low and high tensions in terms of water movement, respectively, resulting in a very low available water capacity during dry periods. Furthermore, our results showed that the correlation coefficient was high between soil CO₂ efflux and moisture content at 30 and 60 cm depth. This suggests that root systems distributed in 30–60 cm range might be responsible for the long-term temporal variation in soil CO₂ efflux. Since root respiration is affected by photosynthetic supply by trees (Högberg et al. 2001), large trees that have deep root systems might depend on water from deeper soil and accordingly play a significant role in the relationship between CO₂ flux and water content. However, additional experiments about the spatial distribution of root systems and phenology of root respiration are necessary to clarify the importance of root respiration in soil respiration in this forest.

Diurnal variation in soil CO₂ efflux correlated with air temperature better than soil temperature at 10 cm depth. This means that short-term temporal variation in soil CO₂ efflux could be driven by changes in metabolic activity in soil surface layer where temperature could be more changeable responding to the air temperature. The observation by Sotta et al. (2004), that diurnal variation in soil CO₂ efflux was mainly controlled by metabolic activity at ~5 cm depth in a tropical forest in Amazon, supports this possibility. Diurnal changes in photosynthetic supply by trees, which co-vary with air temperature, might also caused the diurnal variation in soil CO₂ efflux. However, diurnal variation in soil surface temperature could vary from day to day and place to place due to shading by tree crown, angle of sunlight and the presence/absence of clouds. In this study, we measured diurnal variation at only one location. Further information at various times and locations is necessary to clarify the diurnal variation in soil CO₂ efflux. Our result also suggests that diurnal variation in soil CO₂ efflux could be disturbed by rainfall. A similar phenomenon has been reported in other ecosystems, but the results are controversial. Sotta et al. (2004) reported soil CO₂ efflux was reduced 30% immediately after rainfall, whereas Lee et al. (2002) observed a sudden increase in soil CO₂ efflux with rainfall after dry periods. Since the effect of rainfall is determined by various relationships between the physical and biological properties of soil (e.g., soil compactness, clay content and microbial activity) and rainfall condition (e.g., time, intensity and amount), its effect is complex and could differ among ecosystems. In this study, our data were insufficient to clarify the effect of rainfall on soil CO₂ efflux.

Annual CO₂ efflux

Since there was no spatial dependence in soil CO₂ efflux, the sampling interval of 10 m was considered sufficient to obtain statistically independent samples for CO₂ efflux. The 25 sample locations in the main plots could give an estimation of mean value within 15% of the actual mean with 95% confidence. The annual soil CO₂ efflux, estimated from the SMC at 30 cm depth (1,986 g C m⁻² year⁻¹), was close to reported figures for a primary tropical forest in eastern Amazon (2,000 g C m⁻² year⁻¹; Davidson

et al. 2000) and a tropical monsoon forest in Thailand ($2,560 \text{ g C m}^{-2} \text{ year}^{-1}$; Hashimoto et al. 2004). On the other hand, our results exceeded the range reported for tropical moist/humid forests ($890\text{--}1,520 \text{ g C m}^{-2} \text{ year}^{-1}$) by Raich and Schlesinger (1992). A possible reason of the higher values in this study could be the underestimation of annual soil CO_2 efflux using soda-lime techniques in previous reports (Davidson et al. 2000). The other possibility is an overestimation of nocturnal soil CO_2 efflux in our study. Our results showed soil CO_2 efflux decreased 22% at night-time, with a decrease in temperature, compared to daytime. Similarly, Sotta et al. (2004) reported that night-time efflux was 17% lower than daytime flux in central Amazon. However, Davidson et al. (2000) reported little diurnal change in soil CO_2 efflux in eastern Amazon, while Medina et al. (1980) reported an increase in soil CO_2 efflux at night in Amazonian rainforests of the Rio Negro Basin. These conflicting results suggest that nocturnal soil CO_2 efflux could vary with the ecosystem. More information is needed to ascertain the characteristics of nocturnal soil CO_2 efflux in this study site.

Even though it is assumed that the 22% decrease in night CO_2 efflux is a representative value for this forest, the corrected estimation ($1,767 \text{ g C m}^{-2} \text{ year}^{-1}$) is still higher than that reported by Raich and Schlesinger (1992) and those of many other tropical forests ($820\text{--}1,480 \text{ g C m}^{-2} \text{ year}^{-1}$), where modern techniques using IRGA or gas chromatography were used for soil CO_2 efflux measurements (Ishizuka et al. 2002; Chambers et al. 2004; Fernandes et al. 2002; Priess and Fölster 2001; Schwendenmann et al. 2003; Keller et al. 1986). This means our study site might have a higher soil CO_2 efflux than the average reported for tropical forests. One possible explanation for the high CO_2 efflux is the large volume of root-derived respiration. Davidson et al. (2000) suggested that the strong seasonality in precipitation from the eastern Amazon, where rainfall is $<250 \text{ mm}$ during the 5-months dry season, required a large below ground allocation of carbon to a large root biomass to obtain sufficient water from a deep soil profile during the dry season. This suggestion could also explain the high emission value in Asian tropical seasonal forests reported by Hashimoto et al. (2004), where there was $<100 \text{ mm}$ of precipitation during the 6-months dry season. The relationship between soil CO_2 efflux and REW in this study suggests a significant contribution from root

respiration in this ecosystem. Katayama et al. (unpublished data) estimated that total belowground carbon allocation by trees would be larger in this forest than that in other tropical forests. However, since our study site does not have such severe periodic dry periods, the high CO_2 efflux might possibly come from another source. Ohashi et al. (2007b) suggest that soil animal activity could be a reason of the CO_2 hot-spots in this ecosystem. The potential role of soil animals has not been taken into account in most studies on soil C emission. Our results indicate that annual mean CO_2 efflux might decrease by 13% if hot-spot data are excluded. This means that the annual CO_2 efflux could decrease to $1,537 \text{ g C m}^{-2} \text{ year}^{-1}$ if hot-spots are excluded and the nocturnal decrease is taken into account. This value is close to the range obtained for other tropical forests.

Conclusion

This study presents the spatial and temporal characteristics of soil CO_2 efflux in relation to temperature and moisture for an aseasonal intact tropical rainforest in Southeast Asia. High spatial heterogeneity and sporadic CO_2 emission were observed. Soil CO_2 efflux significantly decreased during the unpredictable brief dry period, suggesting that soil CO_2 efflux might change seriously in the severe drought period of El Niño-Southern Oscillation (ENSO), which normally occur every 4–5 years and may last for a few to 10 months. Soil temperature might be also important for the decrease in soil respiration. These information suggest that there might be an annual variation in soil C balance in this forest. In this study, long-term variation in soil CO_2 efflux mainly correlated with SMC in the deep layer, whereas local variation of CO_2 efflux had a correlation with soil temperature in the surface layer, both spatially and diurnally. This result indicates soil CO_2 efflux in central South-east Asian tropical rainforests is extremely complex and requires further study to understand the process of CO_2 efflux and attain more reliable prediction of future soil C balance.

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