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Spatial and temporal variation in soil respiration in a seasonally dry tropical forest, Thailand

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Abstract: Spatial and seasonal variation in soil respiration rates were investigated in a tropical dry forest in Thailand. The spatial variation was examined at 50 points within a 2-ha plot in the forest floor during the dry and wet seasons. The seasonal and diurnal variations in soil respiration were measured at 16 and 5 points, respectively. The mean soil respiration rate during the wet season was 1041 ± 542 mg CO_2 m^{-2} h^{-1} (mean ± SD), which is about twice that during the dry season. Soil respiration rate was negatively correlated with soil water content during the wet season. A polynomial equation using seasonal data describes soil respiration and water content: soil respiration rate increased with soil water content, but started to drop when soil water content exceeded 21%. The diurnal variation in soil respiration rate during the wet season was positively correlated with soil temperature, whereas during the wet season it was not correlated with soil temperature. The diurnal variation in soil respiration rate during the dry season showed a midday depression. The estimation of soil carbon flux with polynomial equations should incorporate different functions for the wet and dry seasons in tropical dry forests.

Key Words: seasonal dry tropical forest, soil respiration, soil temperature, soil water content

INTRODUCTION

Soil is a major carbon (C) reserve in terrestrial ecosystems. Tropical forest vegetation and soil contain large amounts of C, equivalent to 37% of global terrestrial C pools (Dixon *et al.* 1994). The CO_2 efflux from soil (soil respiration) is an important component of the C balance in terrestrial ecosystems. Soil respiration rate exhibits large variations in time and space even within a forest ecosystem. Soil respiration is a result of the integration of autotrophic (root) and heterotrophic (soil organic matter and litter) respiration processes. These biotic factors are mainly dependent on the biomass and activity of plants and soil microbes. Furthermore, abiotic factors, such as gas diffusion capability in soil, also affect soil respiration rate. Soil respiration rate is thus affected by soil temperature, soil water content and soil physical traits. Understanding the variation in soil respiration rates and its determining factors is important for reducing errors in evaluation and scaling up of soil carbon flux. For that reason, soil respiration rates in many of the world's ecosystems have been measured (Raich & Schlesinger 1992, Raich & Tufekcioglu 2000). Inventories have been made to explain the relation between soil respiration rate and environmental factors in soil. In temperate regions, soil temperature is the most important determinant of temporal variation in soil respiration rate (Xu & Qi 2001). Therefore, the carbon efflux from soil in temperate regions can be estimated using an empirical function and soil temperature data. For tropical regions, some reports have also described the relation between soil respiration rates and environmental factors (Davidson *et al.* 2000, Hashimoto 2005, Kiese & Butterbach-Bahl 2002, Schwendenmann & Veldkamp 2006, Sotta *et al.* 2004). Soil respiration rate is influenced by soil temperature and water content in tropical regions (Sotta *et al.* 2006) in addition to CO_2 concentration in soil and gas diffusivity (Hashimoto & Komatsu 2006,

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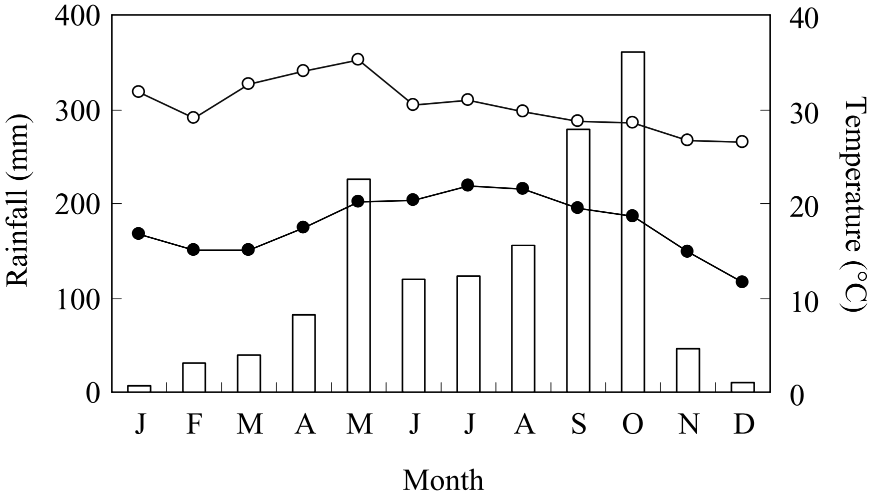

Figure 1. Climatic data at the Huai Kha Khaeng wildlife sanctuary, in a seasonally dry tropical forest, Thailand (original data are from Bunyavejchewin *et al.* 2004). Bars indicate total monthly rainfall (1992–1995); open and closed circles represent maximum and minimum diurnal air temperatures (1992–1994). Broken lines represent the monthly mean soil temperature at 5 cm (June 2003–September 2005).

Schwendenmann *et al.* 2003), tree basal area (Sotta *et al.* 2004), fine-root biomass (Adachi *et al.* 2006, Silver *et al.* 2005) and microbial communities (Cleveland *et al.* 2007). However, soil temperatures in tropical regions do not strongly influence the soil respiration rate. Sotta *et al.* (2004) pointed out that short-term variation in soil respiration rate depends on soil temperature, but the soil water contents might be a limiting factor of long-term variation in soil respiration rates in central Amazonian tropical forests.

Thailand has a distinct dry season of 4–6 mo. The cessation of rainfall strongly affects the physiological function of canopy trees (Ishida *et al.* 2006). Therefore, the soil water content can be more important than the soil temperature as the main determinant of seasonality in soil respiration rates. Nevertheless, few reports in the relevant literature describe soil respiration rates and the environment for South-East Asia's seasonal dry tropical forests. Continuous measurements were especially difficult. For instance, the site used for the present study accommodated no electrical equipment. Some studies have undertaken long-term measurement of soil respiration rate and CO_2 production in soil in Amazonian rain forests. For instance, Sotta *et al.* (2007) reported a reduction of soil respiration rates caused by water stress in a forest with a severe dry season. We hypothesize that soil respiration rate in South-East Asia's seasonal dry tropical forests also responds mainly to soil water content. However, the magnitude of soil drying differs from that in an Amazonian rain forest. In this study, we quantify spatial and temporal variation in soil respiration rates and examine the effects of soil water content on soil respiration rate variation in a seasonal dry tropical forest in Thailand.

MATERIALS AND METHODS

Study plot

The experimental plot is located in Huai Kha Khaeng Wildlife Sanctuary (HKK) of the UNESCO World Heritage Plot in western Thailand (15°20′N, 99°27′E). The altitude of the experimental plot was 549–638 m asl. The mean annual air temperature was 23.5 °C (1992–1994; Bunyavejchewin *et al.* 1998). The mean annual precipitation was 1242 mm (1992–1995; Figure 1). The air and soil temperatures (at depths of 1 cm and 5 cm) were measured every hour using a data logger during May 2003–September 2005 (StowAway TidbiT; Onset Computer Corp., MA, USA); the soil water contents were measured every 8 h using a data logger (THLog-1; Dynamax Inc., TX, USA). The dry season normally lasts from November through April, during which time the monthly precipitation is less than 100 mm. The vegetation is dry evergreen forest dominated by Dipterocarpaceae trees. The forest has never been logged. Soil textures are sandy loam in the surface horizon and sandy-clay loam in subsurface horizons (Bunyavejchewin *et al.* 2004). We measured the topsoil (0–5 cm) pH as 6.7 ± 0.5 (mean ± SD, n = 10); topsoil C and N concentrations (mean ± SD, n = 10) were, respectively, 2.95% ± 0.61% and 0.26% ± 0.05%. Bulk density was 1.02 Mg m^{-3} (0–5 cm), 1.18 Mg m^{-3} (5–10 cm) and 1.49 Mg m^{-3} (10–23 cm), CEC was 19.2 m-equiv per 100 g (0–5 cm), 16.0 m-equiv per 100 g (5–10 cm) and 8.9 m-equiv per 100 g (10–23 cm) (Lauprasert 1988).

Experiment I – Spatial variation in soil respiration rates in the 2-ha plot

Soil respiration rates were measured at 50 points respectively over 2 d during dry and wet seasons. The soil respiration rates were measured at 50 lattice positions within a 100 m × 200-m plot (2-ha plot) at 20-m intervals in the two seasons in 2005: February (middle of the dry season) and September (late wet season). Measurements of the soil respiration rates at 50 points were conducted at 09h00–12h00 local time for 2 d during each season. Measurements were made almost entirely at identical points in February and September using a portable soil respiration rate measuring system (LI–6400; Li-Cor Inc., Lincoln, NB, USA) equipped with a closed soil chamber (soil area is 71.6 cm^2; 6000–09; Li-Cor Inc., NB, USA). This system used a dynamic closed-chamber technique to measure the CO_2 efflux (Butnor *et al.* 2005, Liang *et al.* 2004). The IRGA was calibrated in the field using a CO_2 scrubber (soda lime) as the zero-standard. Soil respiration rate was measured automatically three times at the same point, the mean value of them was used as a value of one point. The soil chamber was put directly on the soil to measure soil respiration rate.

Experiment II – Seasonal and diurnal variation in soil respiration rate in the small plot

We set up a small quadrat (8 m × 8 m; small plot) adjacent to the 2-ha plot to elucidate detailed diurnal changes of soil respiration rates. Seasonal variation in soil respiration rate was measured at 16 points in a grid pattern within the small plot in May and September 2003, March 2004, and February and September 2005. The diurnal variation in soil respiration rates was measured periodically at five points during 06h00–18h00 for 2 d in February and September in 2005.

We followed a closed-chamber method described by Bekku *et al.* (1995) only when we measured the diurnal variation in soil respiration rates during the wet season to avoid halting the continuous measurements of soil respiration rates even during rain. We carefully set five chambers (soil area is 346.2 cm^2 and 14 cm height) into the soil to 4-cm depth; we left the chamber in the field for more than 1 d before gas sampling. Gas samples were collected using 5-ml glass vacuum bottles at 2-min intervals for 6 min. The gas samples were brought back to Japan and analysed using a gas chromatograph (GC-9AM; Shimadzu Corp., Japan). Soil respiration rate was calculated from linear change in CO_2 concentration; the coefficient of determination (r^2) of the regression was over 0.90.

Table 1. Descriptive statistics (mean ± SD) for soil respiration and soil environmental factors in a 2-ha plot. * differs significantly from the dry season at $P < 0.0001$.

	Wet season ($n = 50$)	Dry season ($n = 50$)
Soil respiration (mg CO_2 m^{-2} h^{-1})	1041 ± 542*	402 ± 206
Soil water content (%)	31.8 ± 5.0*	3.5 ± 1.8
Soil temperature (1 cm depth)	23.8 ± 0.6*	22.1 ± 1.3
Soil temperature (5 cm depth)	23.6 ± 0.4*	21.8 ± 0.9

In addition to measurements of soil respiration rates, soil temperatures at depths of 1 cm and 5 cm and soil water contents at 5-cm depth were measured for all measurement points. The soil temperatures were measured using a thermometer (TM-150; Custom, Tokyo, Japan); the soil water contents were measured using a time-domain reflectometry sensor (TDR, TRIME-FM; IMKO Micromodultechnik GmbH, Ettlingen, Germany). Additional microclimatological data (air temperature, soil temperature and soil water content) were measured beside the small plot during May 2003–September 2005. The air and soil temperatures (at depths of 1 cm and 5 cm) were measured hourly using a data logger (StowAway TidbiT; Onset Computer Corp., MA, USA); the soil water contents were measured every 8 h using a data logger (THLog-1; Dynamax Inc., TX, USA). The annual C efflux from soil was estimated using these observation data.

Statistical analyses

All statistical analyses were conducted using software (StatView 5.0; SAS Institute Inc., NC, USA). Student's *t*-test was used to determine the differences in average soil respiration rates and environmental factors between the dry and wet season in the 2-ha plot (Table 1). Repeated-measures ANOVA and the post hoc test (Scheffé's test) were used to compare the seasonal differences in soil respiration rates and environmental factors. Pearson's product-moment correlation coefficient was used to clarify relations between soil respiration rates and environmental factors (soil temperature and soil water content).

Patterns of spatial variation in soil respiration rates and environmental factors during the wet and dry season were analysed using geostatistical analyses. We calculated the semivariance, $\gamma(h)$ using software (GS+, version 7; Gamma Design Software LLC, USA) as follows,

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(xi) - z(xi + h)]^2,$$

where $N\ (h)$ is the number of pairs of points separated by distance h, $z\ (x_i)$ and $z\ (x_i + h)$ respectively

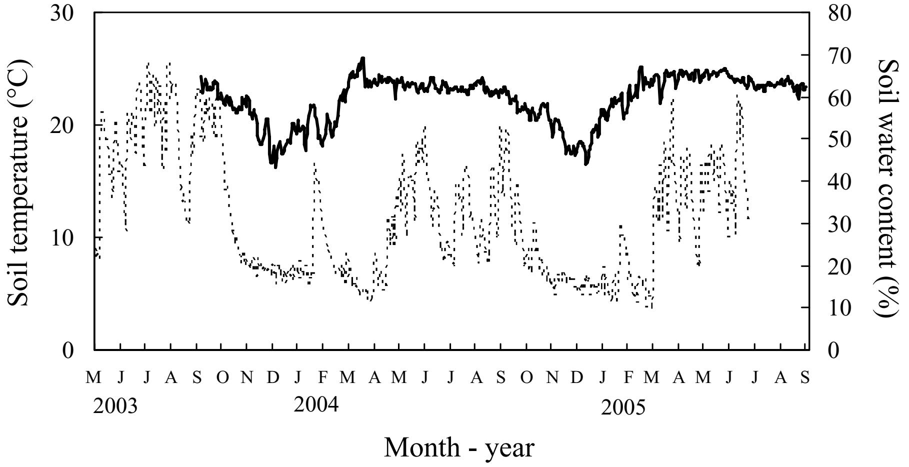

Figure 2. Seasonal variation in soil temperature (solid line) at 5-cm depth, and soil water contents (broken line) in the small plot in a seasonally dry tropical forest, Thailand. Soil temperature and soil water content were measured by data loggers.

signify the measured values at point x_i and $x_i + h$. Semivariograms for all variables of 2-ha plot data were fitted to spherical, linear or Gaussian models using a least-squares technique.

RESULTS

Experiment I

Figure 2 portrays the seasonal variation in soil temperature at 5-cm depth, and soil water contents at the study site. The mean soil temperature was 22.2 °C ± 2.2 °C (mean ± SD), and mean soil water content was 30.5% ± 14.4%. The data logger showed variation of 15.2 °C to 26.5 °C of the soil temperature at 5-cm depth; soil water contents varied from 9.2% to 68.9%. The mean soil respiration rate, soil temperature and soil water content in the wet season differed significantly from those in the dry season in the 2-ha plot (Table 1; Student's t-test, $t = -37.8$ to -7.79, $P < 0.0001$). The mean soil respiration rates in the wet season were approximately twice as large as those in the dry season. The coefficients of variation (CVs) were very high: 52.1% during the wet season and 51.1% during the dry season. Spatial variation in soil temperature during the dry season (CV = 4.2%) in the 2-ha plot was higher than in the wet season (CV = 1.8%). The differences of mean soil temperatures between wet and dry seasons were less than 2 °C. Soil respiration rates showed no significant correlation with soil temperature through either season (Figure 3a). The soil water contents in the 2-ha plot were less than 10% in the dry season, but were 20–50% in the wet season (Figure 3b). The CVs of soil water contents in the dry season (51.8%) were higher than in the wet season (15.6%). Soil respiration rates in the wet season were significantly and negatively correlated with soil water contents (Figure 3b; closed circles, $r = -0.415$, $P = 0.0028$), but no such relation was found for the dry season (Figure 3b; open circles, $r = -0.065$, $P = 0.665$).

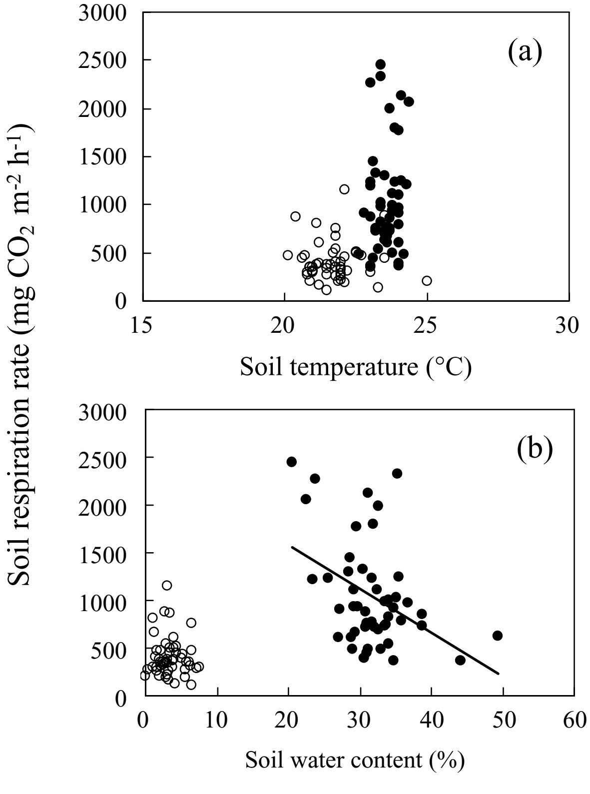

Figure 3. Relationship between soil respiration rates and soil temperature at 5-cm depth (a), soil water contents for the wet and dry seasons in the 2-ha plot (b) in a seasonally dry tropical forest, Thailand. Closed and open circles represent data for the wet and dry seasons, respectively. The line in (b) indicates a linear regression ($r = -0.415$, $P = 0.0028$) as determined by the single regression between soil respiration and soil water content in the wet season.

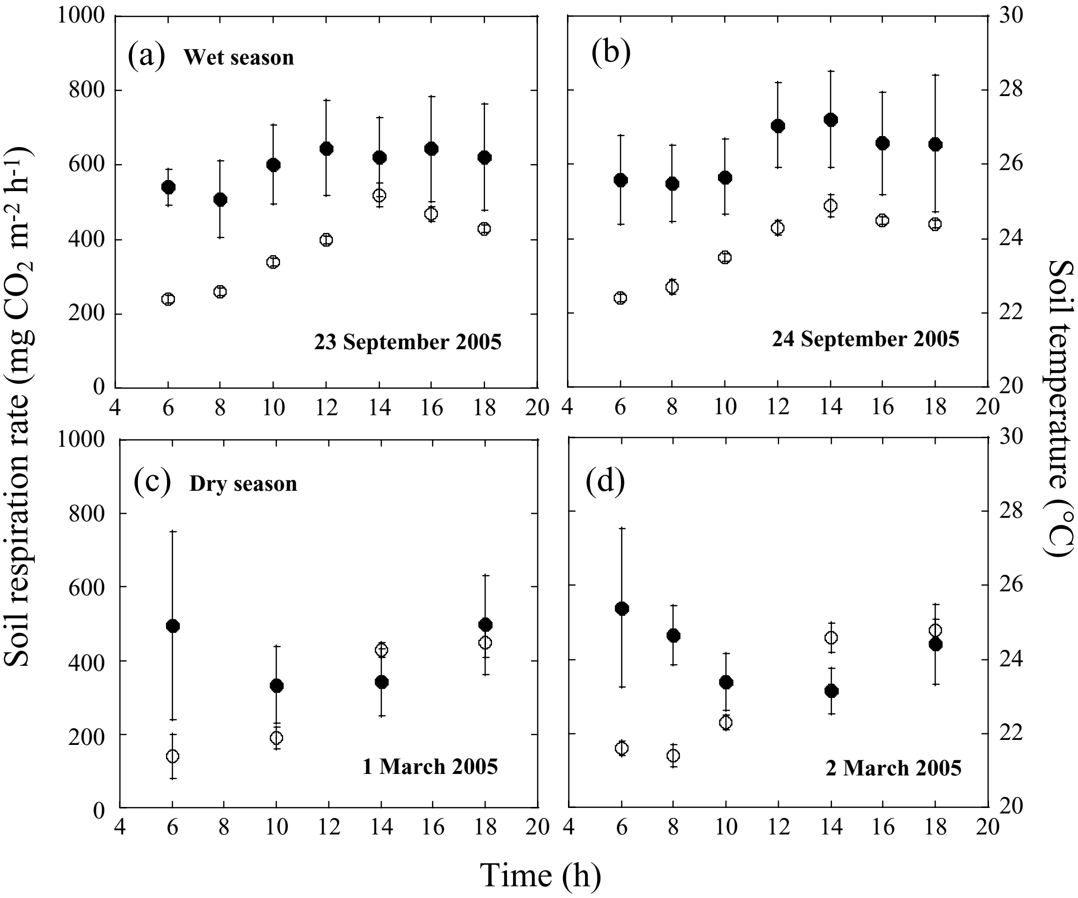

Figure 4. Diurnal variation in soil respiration rates and soil temperatures (1-cm depth) at the small plot during 2 d in the wet season (a, b), and in the dry season (c, d) in a seasonally dry tropical forest, Thailand. Soil respiration and soil temperatures are represented as closed and open circles, respectively. The error bar shows 1 SD (n = 5).

Required sample sizes for estimating soil respiration rates were not calculated for this study plot because the soil respiration rates were not normally distributed. Table 3 shows fitted semivariogram parameters for soil respiration rates, environmental factors, and elevation in the 2-ha plot in the wet and dry seasons. Many factors (except for soil temperature during the wet season and elevation) showed no spatial autocorrelation, especially soil respiration rates. The spatial autocorrelation for soil temperatures at 1-cm depth ranged from 43.8 m in the dry season to 451 m in the wet season. Additionally, effects of topographical positions on soil respiration rate were not consistent (data not shown).

Experiment II

Figure 4 depicts the diurnal variation in soil respiration rates and soil temperature in the small plot. The diurnal soil respiration rates in the dry season were lower than in the wet season. The mean soil respiration rates varied from 508–712 mg CO_2 m^{-2} h^{-1} in the wet season and 314–540 mg CO_2 m^{-2} h^{-1} in the dry season. Diurnal variation in soil respiration rates and soil temperature increased at midday from 22.4 °C to 25.2 °C in the wet season, from 21.4 °C to 24.8 °C in the dry season. The soil respiration rate in wet season was positively correlated with soil temperatures at 1 cm ($r = 0.418$, $P = 0.0003$) and 5 cm deep ($r = 0.408$, $P = 0.0004$). In contrast, the soil temperatures increased at around midday, but the soil respiration rates decreased during the dry season (Figure 4b). The maximum ratio of midday depression in soil respiration rate between morning and noon was about 42% (second day, 6h00 and 14h00).

The obtained soil respiration rates in the small plot varied seasonally from 390 ± 249 mg CO_2 m^{-2} h^{-1} to 1327 ± 352 mg CO_2 m^{-2} h^{-1} (mean ± SD) (Table 2). Means of soil respiration rates in February 2005 were significantly lower than in the wet season (Scheffé's test, $P < 0.05$). Soil temperatures at 5-cm depth in the dry seasons were significantly lower than in wet seasons. Using all of the seasonal data for the small plots,

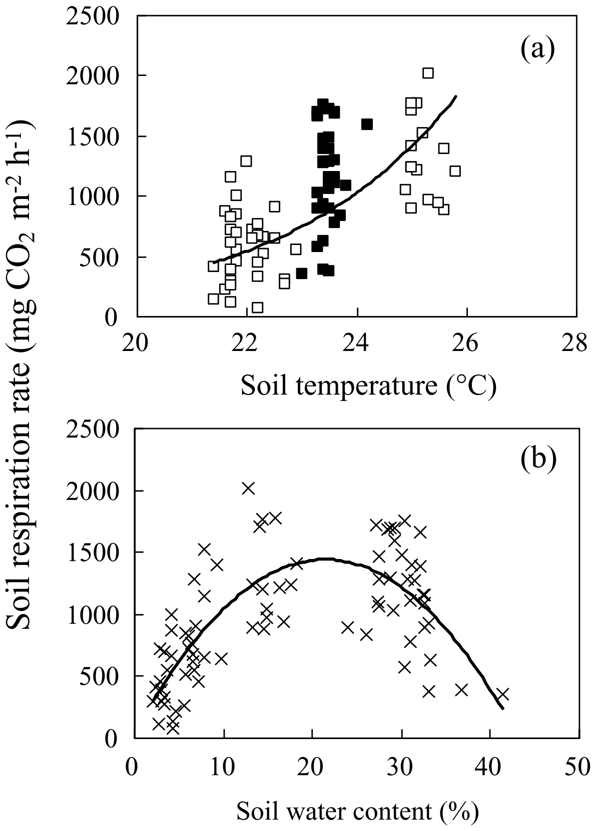

Figure 5. The relationship between the soil respiration rate and soil temperature at 5-cm depth (a) and soil water content (b) from seasonal variation in the small plot in a seasonally dry tropical forest, Thailand. Open and closed squares in (a) represent data obtained under the condition of low (below 21%) and high (above 21%) soil water content, respectively. The lines on the graph were regression equations at each relationship. Soil respiration = 0.498 exp(0.318 × soil temperature), $R^2 = 0.346$, P = 0.0001 (a) and Soil respiration = −3.05(soil water content)^2 + 131(soil water content) + 43.6, $R^2 = 0.531$, P = 0.0001 (b).

soil respiration rate can be expressed as an exponential function of the soil temperature (Figure 5a).

$$y = 0.498\exp(0.318x) \quad R^2 = 0.346 \quad \mathrm{P} = 0.0001 \tag{1}$$

The relation between the soil respiration rate and soil water content can be expressed as a polynomial expression (Figure 5b).

$$y = -3.05x^2 + 131x + 43.6 \quad R^2 = 0.531 \quad \mathrm{P} = 0.0001 \tag{2}$$

Seasonal variation in soil respiration rates decreased in conditions where soil water contents were greater than 21%.

DISCUSSION

Soil water contents at the study site, as shown in Figure 2, ranged from less than 10% to more than 30%. Those values were higher than those reported for an Amazonian forest between November 2001 and November 2003 (Sotta *et al.* 2007). Soil wetting and drying affected the activity of plants and microbes: most species of trees at the present study site flushed new leaves during the dry season (Williams *et al.* 2008). Microbial activity of the soil generally increases with wetting of dry soils, and soil drought reduces mineralization of the soil (Borken & Matzner 2009). Soil respiration rates within a 2-ha area showed a negative correlation with soil water content in the wet season (Figure 3b). Reasons for this negative correlation were that the shortage of oxygen and disturbance of gas diffusion within soils reduced soil respiration rates when the values of soil water contents become greater than a critical point (Linn & Doran 1984, Olesen *et al.* 2001, Skopp *et al.* 1990). Li *et al.* (2006) reported that heterotrophic respiration was strongly correlated with the soil water content in a tropical forest, suggesting that the low soil water contents reduced biotic activity, especially that of microbes within the soil.

The patterns of diurnal variation in soil respiration rates during the wet and dry seasons differed (Figure 4). The soil respiration rates in the wet season reached a peak value between 12h00 and 14h00. Soil temperature increased by about 3 °C at midday during both seasons; the diurnal soil respiration rates were well correlated with soil temperatures measured at both 1 cm and 5 cm in the wet season. In contrast, soil respiration rates in the dry season were lower in the daytime. They increased in the morning and evening, suggesting a midday depression in soil respiration rates during the

Table 2. Seasonal variation in soil respiration and soil environmental factors (mean ± SD) in the small plot (n = 16). Means followed by different letters within a row are significantly different (Scheffé's test, $P < 0.05$).

Date	Season	Soil respiration (mg CO_2 m^{-2} h^{-1})	Soil water content (%)	Soil temperature (5 cm depth, °C)
May 2003	Wet	1327 ± 352ac	14.3 ± 2.72a	25.2 ± 0.28a
September 2003	Wet	1130 ± 408ac	29.8 ± 2.81b	23.4 ± 0.09b
March 2004	Dry	760 ± 221ab	6.45 ± 1.35c	22.1 ± 0.36c
February 2005	Dry	390 ± 249bc	3.44 ± 0.94d	21.9 ± 0.39c
September 2005	Wet	1186 ± 430ac	31.3 ± 3.69b	23.5 ± 0.26b

Table 3. Fitted semivariogram model parameters for soil respiration and environmental factors in wet and dry season, and elevation at each measuring point. NA means not applicable.

Factor	Season	Model	R^2	Nugget (C0)	Sill (C0 + C)	Range (m)	Proportion C/(C0 + C)
Soil respiration rate	Wet	Linear	NA	284150	284150	184	NA
	Dry	Linear	NA	42169	42169	184	NA
Soil temperature	Wet	Gaussian	0.709	0.082	2.16	451	0.962
(1-cm depth)	Dry	Spherical	0.022	0.001	1.41	44	0.999
Soil temperature	Wet	Gaussian	0.682	0.075	2.03	712	0.963
(5-cm depth)	Dry	Linear	0.371	0.74	0.74	184	NA
Soil water content	Wet	Linear	0.012	24.7	24.7	184	NA
	Dry	Linear	0.047	3.3	3.3	184	NA
Elevation		Gaussian	0.996	2.3	75.6	230	0.970

dry season. Such a midday depression was also reported for a savanna in California (Baldocchi *et al.* 2006, Tang *et al.* 2005) and for a Norway spruce forest in northern Sweden (Ekblad *et al.* 2005, Högberg *et al.* 2001). Data from those studies show a time lag between the soil respiration and photosynthesis rates. The data suggest that respiration of root systems constitutes about 24–70% of soil respiration rates in tropical deciduous forests (Subke *et al.* 2006). Recently, the diurnal change of the contents of C dissolved in xylem sap (CO_2, H_2CO_3 and HCO_3^-) with sap flow rates has been reported in many woody plants in the temperate region (Maier & Clinton 2006, Teskey & McGuire 2002). Stem respiration rates were 25–50% lower than what would be expected based solely on temperatures on warm sunny days (Lavigne 1987). The partially respired C in roots carried upward by the transpiration stream can therefore engender underestimation of the actual respiration by root systems. Renewed interest has surrounded clarification of the origin of the midday depression of soil respiration rates. There is a new necessity for evaluation of the midday depression of soil respiration rates.

Seasonal data for soil respiration rates in this study have been taken only five times over 3 y. Therefore, the variation was not explainable in detail based on these data. Some reports described seasonal variation in soil respiration rate in Amazonian (Schwendenmann & Veldkamp 2006, Sotta *et al.* 2007) and South-East Asia's forests (Hashimoto *et al.* 2007, Ohashi *et al.* 2007). At this study site, the mean soil respiration rate during the wet season (September 2003 and 2005) was 1158 mg CO_2 m^{-2} h^{-1}, this rate was higher than that reported for an Amazonian forest site (519 and 597 mg CO_2 m^{-2} h^{-1}, Schwendenmann & Veldkamp 2006; 665 mg CO_2 m^{-2} h^{-1}, Sotta *et al.* 2007). Hashimoto *et al.* (2007) also reported a high soil respiration rate of more than 1000 mg CO_2 m^{-2} h^{-1} during the wet season in a natural evergreen forest in Thailand. Litton & Giardina (2008) wrote that the mean annual temperature explained 57% of the global variation in below-ground carbon flux. However, the mean air temperature recorded at the present study site and that reported by Hashimoto *et al.* (2007) were, respectively, 23.5 °C and 20.0 °C; these data were lower than those reported for other forests (26.0 °C from Ohashi *et al.* 2007; 25.0 °C from Schwendenmann & Veldkamp 2006). Moreover, the soil C and N concentrations found in the present study were lower than those reported for an Amazonian rain forest. This result suggests that evaluation of soil respiration rate includes a large error in tropical regions, especially in South-East Asia. More investigation of soil respiration rate data is needed.

The relation between soil respiration rates and soil water contents can be expressed as a polynomial formula (Figure 5). Sotta *et al.* (2006, 2007) reported that soil respiration rate and soil water content can be described using a parabolic function under the different soil textures in an Amazonian rain forest. Chambers *et al.* (2004) reported that the relation between soil respiration rates and soil water contents is curvilinear: the wet-season C efflux is twice as high as the dry-season C efflux in an Amazonian tropical forest. Kosugi *et al.* (2007) and Hashimoto *et al.* (2007) reported that temporal variation in soil respiration rate is positively correlated with the soil water content in South-East Asian tropical forests. The relations between soil respiration rates and soil water contents were not consistent. One reason might be the difference of bulk density at each site, but no clear tendency is apparent. Aspects of the biotic activity and physical parameters should be investigated further to elucidate the relations between soil respiration rates and soil water contents.

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