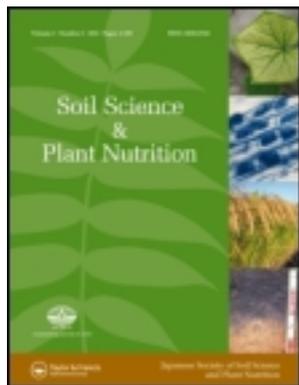


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ORIGINAL ARTICLE

Topographic variation in heterotrophic and autotrophic soil respiration in a tropical seasonal forest in Thailand

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Abstract

Soil respiration is a carbon flux that is indispensable for determining carbon balance despite variations over time and space in forest ecosystems. In Kanchanaburi, western Thailand, we measured the soil respiration rates at different slope positions—ridge (plot R), upper slope (plot U), and lower slope (plot L)—on a hill in a seasonal tropical forest [mixed deciduous forest (MDF)] to determine the seasonal and spatial variations in soil respiration on the slope. The heterotrophic (organic layer and soil) and autotrophic (root) respiration was differentiated by trenching. Soil respiration rates showed clear seasonal patterns: high and low rates in rainy and dry seasons respectively, at all plots, and tended to decrease up the slope. Soil respiration rates responded significantly to soil water content in the 0–30 cm layer, but the response patterns differed between the lower slope (plot L) and the upper slope (plots R and U): a linear model could be applied to the lower slope but exponential quadratic models to the upper slope. The annual carbon dioxide (CO₂) efflux from the forest floor was also associated with the slope position and ranged from 1908 gC m⁻² year⁻¹ in plot L to 1199 gC m⁻² year⁻¹ in plot R. With ascending position from plot L to R, the contribution of autotrophic respiration increased from 19.4 to 36.6% of total soil respiration, while that of the organic layer decreased from 26.2 to 9.4%. Mineral soil contributed to 46.3 to 54.4% of the total soil respiration. Soil water content was the key factor in controlling the soil respiration rate and the contribution of the respiration sources. However, the variable responses of soil respiration to soil water content create a complex distribution of soil respiration at the watershed scale.

Key words: carbon cycling, mixed deciduous forest, root respiration, soil CO₂ efflux, time-space variation.

INTRODUCTION

Carbon dynamics in a forest ecosystem are of great concern in relation to the influence of global warming and the function of forest ecosystems in mitigating atmospheric carbon dioxide (CO₂). In terrestrial ecosystems, soil is the largest carbon reservoir so their fluctuation may considerably affect the atmospheric

CO₂ concentration (Lal 2004; Knorr *et al.* 2005). With this in mind, soil respiration is a crucial parameter for evaluating the carbon balance in forest ecosystems (Raich and Schlesinger 1992; Raich and Tufekciogul 2000; Yang *et al.* 2007).

Previous reviews of soil respiration in global forest ecosystems did not distinguish dry and moist forests in the tropical biomes (Raich and Schlesinger 1992; Raich and Tufekciogul 2000; Subke *et al.* 2006). In monsoonal Asia, seasonal dry forests, where continuous drought periods occur, are widely distributed from the Indochina peninsula to India (Bullock *et al.* 1995). Following the climate pattern, soil respiration in a forest ecosystem

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shows seasonal fluctuation, whereby high and low soil respiration is recorded in the rainy and dry seasons respectively (Tulaphitak *et al.* 1985; Cuevas 1995; Hashimoto *et al.* 2004; Adachi *et al.* 2009). In contrast to the soil respiration in moist temperate forests, where the soil temperature mostly determines the soil respiration rate (Ishizuka *et al.* 2006; Shinjo *et al.* 2006), soil moisture is the most influential factor in controlling the soil respiration rate in tropical seasonal forests (Hashimoto 2005; Takahashi *et al.* 2009).

To scale up carbon balance from the stand level to the watershed level, spatial variation in soil respiration in the watershed must be examined. Because topography regulates soil water movement and drainage, lower slopes tended to be moist and upper slopes drier, which created a biogeochemical gradient on the slope (Swanson *et al.* 1988; Hirobe *et al.* 1999; Tsui *et al.* 2004). Likewise, soil respiration varies according to the topographical position on the hill slope. For instance, Nakane *et al.* (1984) reported that the lower slope had higher soil respiration rates than the mid-slope in a Japanese red pine forest. Shimada *et al.* (1998) also reported that the annual carbon efflux from the forest floor was $13.4 \text{ MgC ha}^{-1} \text{ year}^{-1}$ on the lower slope and $9.9 \text{ MgC ha}^{-1} \text{ year}^{-1}$ on the upper slope in a Japanese coniferous plantation. However, no correlation (Fang *et al.* 2009), and the opposite trend, namely lower soil respiration rates on the lower slope and at the valley bottom than the upper slope (Chambers *et al.* 2004; Tsutsumi *et al.* 1985; Epron *et al.* 2006; Mitani *et al.* 2006; Kosugi *et al.* 2007) have been reported in several forest ecosystems. Although many reports have suggested that soil respiration varies with slope position, no general principle concerning the relationship between slope position and soil respiration has yet been established.

Soil respiration comprises heterotrophic respiration by soil biota and autotrophic respiration by living plant roots hence separating these respiration sources is important to understand the carbon balance in an ecosystem (Hamilton *et al.* 2002; Bond-Lamberty *et al.* 2004; Cisneros-Dozal *et al.* 2006; Sakata *et al.* 2007; Yang *et al.* 2007). Although there are methodological difficulties in separating respiration sources (Hanson *et al.* 2000; Subke *et al.* 2006), one practical method to estimate root respiration is to dig a trench around the respiration monitoring chamber in order to exclude root respiration from the soil (Katagiri 1988; Lee *et al.* 2003; Sulzman *et al.* 2005; Vogel *et al.* 2005; Wang *et al.* 2006; Schaefer *et al.* 2009). The root trenching method in particular is often used in the forest ecosystem because of its high applicability to remote areas despite criticisms that disturbance by trenching affects root decomposition, soil moisture, and the soil microbial community (Hanson *et al.* 2000; Kuzyakov and Larionova 2005).

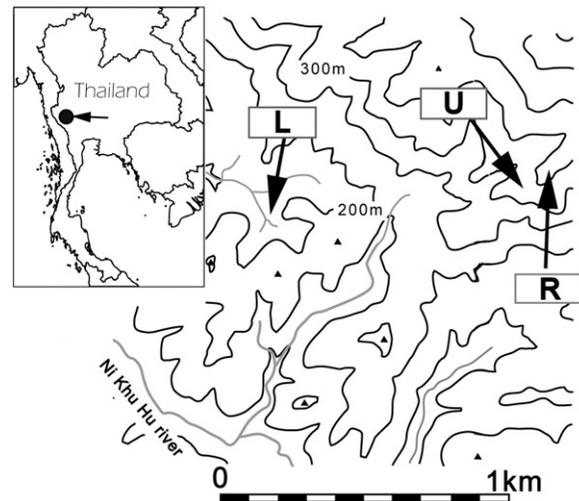


Figure 1 Map of the study site in Thailand. Plots R, U, and L denote the ridge, upper, and lower slopes, respectively.

Review articles have been written on the separation of autotrophic and heterotrophic respiration in forest ecosystems worldwide (Hanson *et al.* 2000; Bond-Lamberty *et al.* 2004; Subke *et al.* 2006), but few studies have yet been conducted on tropical forests, especially in a tropical monsoon climate (Schaefer *et al.* 2009; Takahashi *et al.* 2009; Yi *et al.* 2007). In addition, variations in heterotrophic and autotrophic respiration in different topographies have never been reported.

The purpose of this study is to (1) understand the spatial variation in soil respiration rates on a slope, and (2) estimate the contribution of CO_2 sources, i.e. organic layer, roots, and soil, in terms of the total soil respiration. We measured the soil respiration rates at three different positions on a hill, and analyzed the spatial variation in the soil respiration rates in a watershed of a tropical seasonal forest in western Thailand. Carbon dioxide sources were separated by removing the organic layer and roots by trenching. The annual carbon efflux from the forest floor over two years was also estimated.

MATERIALS AND METHODS

Study sites

The study was conducted in the Mae Klong Watershed Research Station ($14^{\circ}35'N$, $98^{\circ}52'E$), Lintin, Thong Pha Phum, Kanchanaburi province, western Thailand (Fig. 1). The average air temperature was about 25°C , ranging from 9.3 to 42.2°C , and the annual precipitation was 1650 mm , mostly falling during the rainy season from April to October (Suksawang 1995). Tributary streams dry up in the dry season. The monthly rainfall and temperature during the study period from 1997 to 1999

have been reported elsewhere (Takahashi *et al.* 2009). Rainfall sometimes fluctuates because of the El Niño Southern Oscillation (Nounmusig *et al.* 2006): the annual rainfall at the station was 1927 mm in 1997, 1243 mm in 1998, and 1733 mm in 1999 respectively. The forest in the watershed was mainly covered by mixed deciduous forest (MDF) (Rundel and Boonpragob 1995). Detailed descriptions of the vegetation and eco-physiological characteristics were given by Marod *et al.* (1999, 2002) and Ishida *et al.* (2006). The dominant tree species in the study area were *Shorea siamensis*, *Vitex peduncularis*, *Dillenia parviflora* var. *Keruii*, and *Xylia xylocarpa* var. *Keruii*. The tree density and basal area, DBH > 5 cm, of the forest were 171 trees ha⁻¹ and 17.3 m² ha⁻¹ respectively. Four bamboo species were distributed mosaically under the tree canopy (Takahashi *et al.* 2007). Although the forest is called a natural forest, there may have been selective felling of particular trees by local people. The dry weight of the annual litterfall on the upper part of the study slope (plots R and U, see later) was 5.91 Mg ha⁻¹ in 1997, 5.88 Mg ha⁻¹ in 1998, and 3.75 Mg ha⁻¹ in 1999, and leaf litter accounted for 55% of the total litterfall on average (Marod, unpublished data, 2000). The soil at the study sites was classified as Alfisols (Soil Survey Staff 2006) derived from sedimentary rock, gneiss, and limestone (Suksawang 1995). The chemical and physical characteristics of the soil at the pits close to the plots for soil respiration measurement are shown in Table 1. In the Mae Klong Watershed Research Station, the net ecosystem CO₂ and water exchange of the forest have been monitored by a flux tower (Huete *et al.* 2008; Fisher *et al.* 2009).

The watershed was mountainous, with an incline of about 40° in some places. To evaluate variation in the soil respiration rate according to slope positions in the watershed, three positions were selected: ridge (R), upper slope (U), and lower slope (L) (Fig. 1). The altitudes of the study plots ranged from 150 to 350 m above sea level (a.s.l.). The tree species composition and soil properties at the study plots varied slightly but were classified as the same, MDF and Alfisols, respectively.

Measurement of soil respiration

The soil respiration rate was measured by a static closed chamber (Takahashi *et al.* 2009), with a steel chamber 30 cm in diameter and 30 cm in height. The bottom rim of the chamber was inserted about 3 cm into the surface soil. Its top cover was sealed and about 0.5 L of the air in the headspace was collected at a 20-minute interval to determine the CO₂ concentration by an infrared gas analyzer (IRGA) (ZFP5, Fuji Electronics Co. Ltd, Japan). Measurements were performed mostly from 9 a.m. to 2 p.m. We confirmed the diurnal variation of soil

respiration was insignificant, similar to the other sites in Thailand (Adachi *et al.* 2009; Hanpattanakit *et al.* 2009). Soil respiration rates were calculated from the rate of increase of CO₂ concentration using a linear model with temperature correction as follows: $Sr = \rho \times V/A \times \Delta C / \Delta T \times 273 / (273 + T) \times 12/44$, where Sr is the CO₂ flux (in gC m⁻² h⁻¹), ρ is the CO₂ density (1.96 × 10³ g m⁻³), V is the chamber volume (in m³), A is the cross-sectional area (in m²), $\Delta C / \Delta T$ is the CO₂ concentration increase rate (in m³ m⁻³ h⁻¹) during time ΔT (in h⁻¹) and T is the temperature (in degrees centigrade) inside the chamber (Hu *et al.* 2004).

In 1997, the soil respiration rate in plot U was measured monthly to identify seasonal variation in the soil respiration in the study forest. Subsequently, in 1998 and 1999, the soil respiration of the different slope positions, i.e. plots R, U, and L, was compared by bimonthly measurement.

When the soil respiration rate was measured, the surface soil (0–5 cm) and organic layer samples around the chambers were collected to determine the moisture content. The sample was dried at 105°C in an oven and the water content was expressed on a fresh weight basis. The air and soil temperature at a depth of 10 cm were also measured at the plots. The volume metric soil moisture in the 0–15 and 15–30 cm layers were monitored every one to three days by TDR sensors (Moisture Point TM Model MP-917, Environmental Sensors Inc., Victoria, BC, Canada). The TDR measurement was performed from 7 a.m. to 10 a.m. by manual inspection.

Estimating the annual carbon efflux from the forest floor

Using the relationship between the soil respiration rate and soil water content, empirical models (Wen *et al.* 2006) were examined to estimate the former at each study plot. To estimate the annual carbon efflux from the surface of the forest floor, the cumulative amount of carbon was calculated by multiplying the soil respiration rate obtained by using the empirical model by the interval of days of soil moisture monitoring during that year. Variation in the annual soil carbon efflux in 1997 and 1998 was calculated from the soil moisture data over two years in the same manner, although the soil respiration rates in plots R and L were not measured in 1997. There were no annual estimates in 1999 due to TDR sensor troubles at certain periods of the year.

Separation of carbon dioxide sources

The CO₂ sources in soil respiration were separated by trenching as described previously (Takahashi *et al.* 2009). In short, four sets of three chambers were

Table 1 Chemical and physical properties of the representative soil profiles at the Mae Klong Watershed Research Station

Plot	Horizon	Depth (cm)	pH _{H₂O}	pH _{HCl}	pH _{KCl}	Carbon [†] (g kg ⁻¹)	Nitrogen [‡] (g kg ⁻¹)	Carbon/nitrogen ratio		Exchangeable										
								Carbon	nitrogen	Calcium (cmol kg ⁻¹)	Magnesium (cmol kg ⁻¹)	Potassium (cmol kg ⁻¹)	Sodium (cmol kg ⁻¹)	CEC [§] (cmol kg ⁻¹)	BS [¶] (%)	P ^{††} (mg kg ⁻¹)	BD ^{‡‡} (Mg m ⁻³)	HC ^{§§} (mm h ⁻¹)	Sand (g kg ⁻¹)	Silt (g kg ⁻¹)
R	A	6	5.7	5.3	4.7	30.7	2.13	14.4	10.9	3.00	1.30	0.00	16.2	94	0.9	1.15	73	536	368	96
	EB	20	5.4	4.7	16.1	1.05	15.3	3.33	3.33	1.21	0.55	0.00	10.6	48	n.d.	1.23	n.d.	n.d.	n.d.	n.d.
	Bt	42	5.4	4.7	11.4	0.71	15.9	1.44	1.44	0.69	0.26	0.04	9.3	26	1.7	1.21	223	575	209	216
	BCrt	53	5.6	4.5	7.32	0.52	14.1	1.29	0.44	0.22	0.09	8.4	24	0.4	1.15	220	432	136	432	432
	Crt1	98	5.6	4.3	5.67	0.44	13.0	1.87	0.56	0.25	0.00	8.4	32	0.3	1.41	n.d.	467	161	372	320
	Crt2	160+													0.4	1.67		557	123	320
U	A	13	6.4	5.5	23.0	1.38	16.7	17.9	17.9	1.39	0.46	0.00	15.5	127	14.6	1.05	160	495	374	132
	E	32	5.8	5.2	11.7	0.81	14.5	5.92	5.92	1.35	0.47	0.00	8.9	87	1.6	1.32	109	653	231	116
	Bt1	48	6.7	5.0	8.74	0.67	13.0	3.90	3.90	1.43	0.69	0.00	7.5	80	1.2	1.24	96	448	224	328
	Bt2	72	6.7	5.0	6.50	0.60	10.8	3.07	3.07	1.35	0.74	0.00	10.0	52	0.4	1.30	n.d.	323	165	512
	Bt3	130	7.2	4.8	3.66	0.35	10.5	2.72	2.72	0.78	0.63	0.01	9.0	46	0.5	1.34	n.d.	333	295	372
	BCrt1	160+	6.9	4.9												1.57	n.d.	450	254	296
L	AE	11	6.4	5.5	26.9	1.87	14.4	8.75	8.75	2.82	0.52	0.00	14.1	86	1.6	0.99	160	483	417	100
	Bt1	37	5.8	5.2	10.2	0.90	11.4	1.95	1.95	1.41	0.14	0.00	7.8	45	1.9	1.35	5	434	286	280
	Bt2	86	6.7	5.0	7.21	0.62	11.6	1.33	1.33	0.94	0.16	0.00	6.9	35	0.3	1.42	3	426	262	312
	Bt3	110	7.8	5.0	5.54	0.50	11.1	2.01	2.01	0.80	0.22	0.06	8.2	38	0.1	1.38	n.d.	413	263	324
	Bt4	135	7.2	4.8	4.93	0.47	10.5	2.80	2.80	1.10	0.27	0.00	7.3	57	0.1	1.55	n.d.	408	292	300
	BCrt	172+	6.9	4.9	4.99	0.52	9.6	4.10	4.10	1.46	0.22	0.00	7.5	78	0.1	1.64	n.d.	395	277	328

†Soil/solution = 1:2.5.

‡Dry combustion by nitrogen/carbon analyzer.

§Cation exchange capacity (CEC) and base cations were extracted using ammonium acetate at pH 7.

¶Base saturation.

††Available phosphorus (Bray II).

‡‡Bulk density.

§§Hydraulic conductivity.

“n.d.” not determined.

installed at each site. The first chamber (chamber A) was for measuring the total soil respiration. The second chamber (chamber B) was for measuring soil respiration without CO₂ respiration from the organic layer, and was prepared by removing the organic layer from the chamber. The third chamber (chamber C) was for measuring mineral soil only, and was prepared by removing the organic layer and cutting the roots with a 30 cm-deep trench around the chamber, which was treated for two months before measurement commenced. The difference in soil respiration between chambers A and B indicated CO₂ respiration from the organic layer. The difference between chambers B and C indicated CO₂ respiration from the roots at a depth of 30 cm.

The annual contribution of roots, organic layer, and soil to total soil respiration was estimated in the same way as for the calculation of the annual carbon efflux, i.e. using empirical models derived from the relationships between soil respiration rates in chambers B and C, soil water content in a 0–30 cm layer, and data from monitoring soil water content. Root respiration from soil layers deeper than 30 cm was corrected by the proportion of root biomass in the 0–30 cm layer to that in the deeper rooting zone. In this study we assumed that the rooting zone was 1.2 m deep and that root respiration was related to the fine root biomass (<3 mm).

Carbon stocks in the soil and organic layer and root biomass

The carbon stock in the soil was determined by the bulk density of the fine soil (<2 mm) measured by soil cylinder core (400 mL, 100 cm² × 4 cm) and the carbon content in the fine soil, which was collected from soil profiles of the pits located close to the plots for soil respiration monitoring (Table 1). The organic layer was collected using a 0.5 m × 0.5 m frame with four replications in March, July, September, and December in 1998, and weighed after oven-drying at 70°C. The carbon content was analyzed by dry combustion using an NC analyzer (NC-800, Sumitomo Chemical Co., Japan).

Root biomass (<2 cm in diameter) was measured at 30 cm intervals up to a final depth of 1.2 m via a 15 cm × 15 cm soil column. The sampling was performed in triplicate in November 1998, with dead roots eliminated by visible inspection. Roots of diameter finer than 3 mm were classified as fine roots. All roots, including trees, bamboo, and herbs, were washed to remove the soil, and weighted after oven-drying at 70°C.

Statistics

Differences in soil respiration and related parameters among plots were tested by repeated measures of analysis

Table 2 Carbon stock (in kgC m⁻²) in the organic layer (O-layer), soil at a depth of 0 to 0.3 m, and soil at a depth of 0 to 1.2 m

Plot	O-layer [†]	Soil		A/B
		(0–0.3 m) [‡] A	(0–1.2 m) [‡] B	
R	0.274 (0.192)	6.83	12.6	0.54
U	0.301 (0.209)	5.75	11.2	0.51
L	0.220 (0.095)	5.55	11.5	0.48

[†]O-layer values are mean (standard deviation) determined in March, July, September and December 1998.

[‡]Soil carbon stocks were calculated from Table 1.

Plots R, U, and L denote the ridge, upper, and lower slopes, respectively.

of variance (ANOVA). Regression analysis was also performed to analyze the soil respiration control factors. Models of linear and quadratic functions were selected to estimate the soil respiration rate from the soil water content. All the statistics were generated by STATISTICA (Stat Japan, Co., Ltd.).

RESULTS

Carbon stocks and root biomass along with slope position

The carbon stock in the organic layer, which mainly comprised fresh litter (O_i layer), was relatively larger on the upper slope (plots R and U) than the lower slope (plot L) (Table 2). For the surface soil 0–0.3 m deep, carbon stock increased up the slope. About half the carbon stock was concentrated in the surface soil layer (A/B in Table 2).

The total root biomass (<2 cm in diameter) increased up the slope from plots L to R (Table 3), and plot R had 3.2 times more root biomass than plot L. Fine roots (<3 mm) were mainly distributed in the surface soil 0–0.3 m deep, and the biomass in plot R was 1.8 times larger than in L.

Soil respiration rate, soil temperature, and water content

The soil respiration rates in all the plots showed a seasonal pattern: high and low in the rainy and dry seasons respectively (Fig. 2). The plot L tended to have higher soil respiration rates (CO₂-C g m⁻² d⁻¹) than plots U and R in both the dry and rainy seasons: 5.49 in the dry season and 7.35 during the rainy season in plot L, compared to 2.98 in the dry season and 6.35 during the rainy season in plot R of the average field measurements (Table 4). The dry season significantly reduced the soil respiration rate in plot R, when compared to plot L. The soil respiration rates in plot R decreased to 86 and 54% of that in plot L for the rainy and dry seasons.

Table 3 Total root biomass (<2 cm) and fine-root biomass (<3 mm) in soil up to 1.2 m deep and fine-root biomass 30 cm deep at the study plots

Plot	Total roots (0–1.2 m)	Fine roots (0–1.2 m)	Fine roots (0–0.3 m)
	kg m ⁻²		
R	3.41 (1.26)	0.44 (0.06)	0.32 (0.04)
U	2.83 (1.92)	0.40 (0.04)	0.23 (0.01)
L	1.05 (0.69)	0.25 (0.04)	0.18 (0.02)

The mean (in kg m⁻²) and standard error are shown in parentheses (*n* = 3). Plots R, U, and L denote the ridge, upper, and lower slopes, respectively.

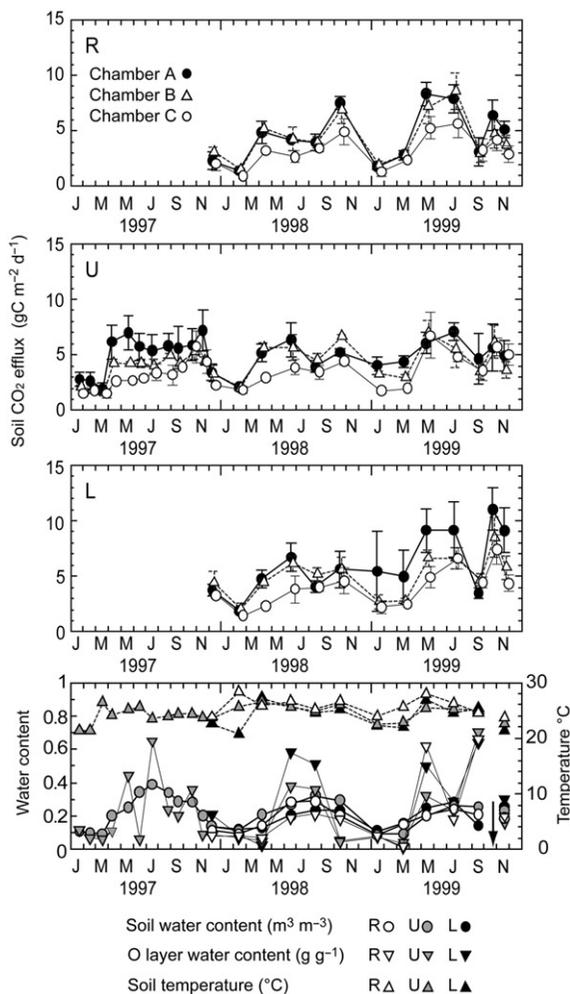


Figure 2 Seasonal changes in the soil carbon dioxide (CO₂) efflux at the ridge (R), upper slope (U), and lower (L) slope positions, soil water content, organic layer water content, and soil temperature at a depth of 10 cm. Symbols in the uppermost figure (R), i.e. soil respiration of chamber A (dot, total soil respiration), chamber B (open triangle, without organic layer respiration), and chamber C (circle, without root and organic layer respiration) can be applied to slope positions U and L. The vertical bar denotes standard error (*n* = 4). In the lowest figure, no data were available in October 1999 (the arrow mark).

The soil temperature and moisture regimes also differed depending on the slope position. The average soil temperature increased, but the soil water content decreased up the slope. In the dry season, the soil was severely dry in plot R, whereas during the rainy season, the soil temperature and water content did not differ significantly among the plots. For the organic layer, the water content was high, with significant fluctuation during the rainy season, and low in the dry season (Fig. 2 and Table 4).

The soil water content showed a clear seasonal pattern for every plot. During the rainy season, monitoring by a TDR sensor showed that the volumetric soil water content in the 0–30 cm layer was usually higher in the upper rather than lower slope (Fig. 3), although the surface soil layer (0–5 cm) in the upper slope was drier than that in the lower slope. During the dry season, the water content in the surface soil layer was low, especially in plot R, but no clear difference among the plots was found in the 0–30 cm layer.

Factors controlling soil respiration

To examine the factors for determining soil respiration, the relationship between total soil respiration and soil temperature at 10 cm depth, air temperature, water content in the organic layer, water content in the surface soil layer (0–5 cm), and the volumetric water content in the 0–30 cm soil layer, which was calculated by averaging the content in the 0–15 and 15–30 cm layers, were analyzed (Table 5). The factor most strongly correlated to the total soil respiration was water content in the 0–30 cm soil layer. In plot R, water content in the surface soil (0–5 cm) was also significantly related to the soil respiration rate. The soil temperature showed a positive correlation to soil respiration, although there was slight annual variation. Air temperature was negatively but not significantly correlated with soil respiration. Consequently, soil and air temperature had no significant correlations with the soil respiration rate.

An empirical model with a high coefficient of determination was selected to estimate the soil respiration rate by soil water content for each plot (Fig. 4). The simple linear function $Sr = a \times WC + c$ was selected for plot L, and the exponential quadratic function $Sr = \exp(a \times WC^2 + b \times WC + c)$ was selected for plots R and U, where WC was the volumetric water content in the 0–30 cm layer, and *a*, *b*, and *c* were the constants at each site. This means that the soil respiration rate increased almost linearly with the soil water content in plot L. In plots R and U, soil respiration increased with soil water content to peak: at 0.261 and 0.205 for plots U and R respectively, then decreased with increasing soil water content. High soil water content depressed the soil

Table 4 Comparison of average air temperature, soil temperature, water content in the organic layer (O-layer) and soil, and soil respiration rate during the dry and rainy seasons for each plot

Season†	Plot	Air temperature (°C)	Soil temperature‡ (°C)	Water content			
				O layer (g g ⁻¹)	Soil (0–5 cm)§ (g g ⁻¹)	Soil (0–30 cm)¶ (m ³ m ⁻³)	Soil respiration (gC m ⁻² day ⁻¹)
Rainy	R	27.5 (2.4)	25.8 (1.4)	0.302 (0.236)	0.204 (0.070)	0.225 (0.052)	6.35 (2.20)
	U	27.7 (2.5)	24.9 (1.0)	0.297 (0.207)	0.218 (0.061)	0.280 (0.056)	6.25 (0.89)
	L	27.6 (2.8)	25.3 (1.4)	0.371 (0.251)	0.250 (0.065)	0.211 (0.056)	7.35 (2.99)
Dry	R	28.6 (3.6)	25.0 (2.0)	0.093 (0.065)	0.054 (0.050)	0.127 (0.020)	2.98 (1.60)
	U	27.7 (4.8)	23.3 (1.8)	0.086 (0.036)	0.097 (0.062)	0.131 (0.052)	4.07 (1.81)
	L	25.4 (1.9)	21.7 (0.8)	0.138 (0.072)	0.134 (0.072)	0.157 (0.059)	5.49 (2.90)

†Dry season, November–March; rainy season, April–October. Data from December 1997 to November 1999 was used. Soil respiration and environmental parameters were measured once a month in 1997 and once every two months in 1998 and 1999.

‡Temperature at a depth of 10 cm.

§Fresh weight basis water content in the surface soil layer 0–5 cm deep.

¶Volumetric water content in the soil layer 0–30 cm deep.

The standard deviation is shown in parentheses. Plots R, U, and L denote the ridge, upper, and lower slopes, respectively.

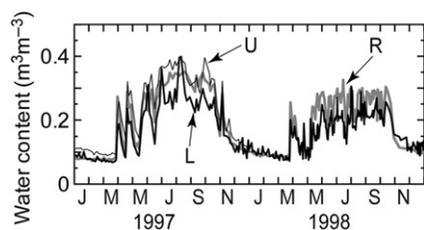


Figure 3 Changes in soil water content (in m³ m⁻³) in the 0–30 cm layer at the ridge (R), upper slope (U), and lower slope (L) positions. Plot U was monitored only in 1997 due to TDR sensor trouble.

respiration rate on the upper slope. Compared with plot L, the response of the soil respiration rate to the soil water content was sharp before the rate peaked.

Separation of carbon dioxide sources

The total soil respiration (chamber A) was usually the highest, followed by the soil respiration from the chamber without litter (chamber B), and the soil respiration from the chamber without litter and the roots respiration (chamber C), although these trends were sometimes disturbed in every plot (Fig. 2). Using empirical models (Fig. 4) and data from monitoring the soil water content (Fig. 3), the percentage contributions of fine roots, organic layer, and soil respiration to the total soil respiration were calculated on an annual basis (Table 6). The contribution of autotrophic (roots) respiration ranged from 19.4 to 36.6% of the total soil respiration and was higher in plots R and U than in plot L. For heterotrophic respiration, the proportion of the organic layer decreased up the slope from 26.6% (plot L)

to 9.4% (plot R). Mineral soil contributed 46.4 to 54.4% of the total soil respiration. Using these proportions, annual respiration from roots, organic layer and soil was calculated from total soil respiration in 1997 (Table 6).

Estimation of carbon dioxide efflux from the forest floor

The carbon efflux from the forest floor varied with the sites and years, ranging from 1199 to 1908 gC m⁻² year⁻¹ in the watershed (Table 7). The annual precipitation in 1998 was 35% lower than in 1997, and consequently, soil water content was low in 1998. Applying the model of each site, the annual carbon efflux was reduced to 90% in plot L but increased to 119% in plot R in 1998. As a result, annual carbon efflux in plot R was 63% that of plot L in 1997 and 83% in 1998. Although the lower slope usually had a higher soil respiration rate than the upper slope, the distribution pattern of soil carbon efflux in the watershed varied in 1997 and 1998.

DISCUSSION

Spatial variation in soil respiration rate on the slope

The total soil respiration rates decreased up the slope in the study watershed (Table 4), a trend which is similar to the results obtained by Nakane *et al.* (1984) and Shimada (1998) in temperate forests in Japan. As we reviewed in the introduction, however, opposite results, whereby lower slopes had a lower soil respiration rate than upper slopes were reported in several forest

Table 5 Correlation coefficient between total soil respiration and water content in soil layer 0–30 cm deep, water content in soil layer 0–5 cm deep, water content in organic layer, soil temperature at depth of 10 cm, and air temperature

Plot	Water content in soil 0–30 cm deep ($\text{m}^3 \text{m}^{-3}$)	Water content in soil 0–5 cm deep (g g^{-1})	Water content in organic layer (g g^{-1})	Soil temperature at depth of 10 cm ($^{\circ}\text{C}$)	Air temperature ($^{\circ}\text{C}$)
R	0.673*	0.647*	0.376	0.370	-0.285
U	0.621***	0.521	0.319	0.244	-0.307
L	0.777***	0.556	0.217	0.254	-0.105

Plots R, U, and L denote the ridge, upper, and lower slopes, respectively.

*** $p < 0.001$. * $p < 0.05$.

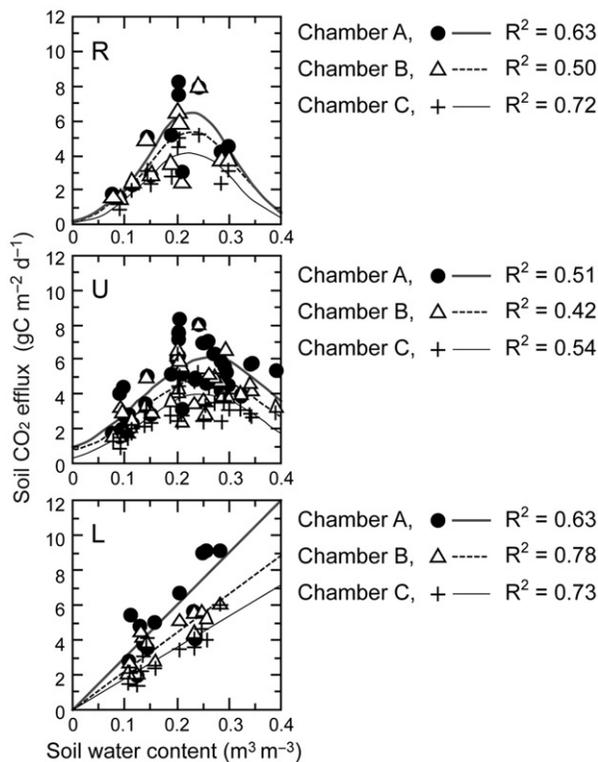


Figure 4 The relationships between soil carbon dioxide (CO_2) effluxes and water contents of soil layer (0–30 cm) at ridge (R), upper (U) and lower (L) slope positions. Soil respiration of chamber A (dot, total soil respiration), chamber B (open triangle, without root respiration) and chamber C (cross, without root and organic layer respiration) are denoted in the figures. Empirical equations; $y = \exp(ax^2 + bx + c)$ for plots R and L and $y = ax + b$ for plot L, are applied to each dataset of the chambers and R-squared values are also shown.

ecosystems (e.g. Chambers *et al.* 2004; Kosugi *et al.* 2007). The discrepancy of these reports may result from the different characteristics of the study sites, such as vegetation-soil association, soil microbes, the physical and chemical properties of the soil, and soil water legumes on the slope.

Table 6 Contribution (%) of autotrophic (roots) and heterotrophic (organic layer and soil organic matter decomposition) respiration to total soil respiration and annual respiration from roots, organic layer and soil in 1997

Plot	Roots	Organic layer	Soil
<i>Contribution (%)</i>			
R	36.6	9.4	54.0
U	34.6	19.1	46.3
L	19.4	26.2	54.4
<i>Annual respiration (gC m⁻² year⁻¹)</i>			
R	439	113	647
U	564	311	754
L	370	500	1038

Plots R, U, and L denote the ridge, upper, and lower slopes, respectively.

Table 7 Annual soil carbon dioxide (CO_2) effluxes at the ridge (R), upper slope (U) and lower slope (L) positions in 1997 and 1998 (in $\text{gC m}^{-2} \text{year}^{-1}$)

Plot	Year	
	1997	1998
<i>Soil CO₂ efflux (gC m⁻² year⁻¹)</i>		
R	1199	1421
U	1629	n.d.†
L	1908	1715

†Soil respiration was not calculated due to soil-moisture sensor problems.

One aspect we should consider is the distribution of soil-vegetation associations on the slope. Some reports compared the soil respiration rates of sites with different soil-vegetation associations that existed on a hill slope (Chambers *et al.* 2004; Epron *et al.* 2006) but others compared sites within the range of the same soil-vegetation association (Nakane *et al.* 1984). In this study we focused on the variation in soil respiration within a soil-vegetation association, i.e. Alfisols-MDF and considered that the main process and response of soil respiration would be relatively similar among the sites. As the principal factor, we assumed that the soil moisture

gradient in the watershed would determine the soil respiration rate.

The results showed that the lower slope (plot L) usually showed higher soil respiration rates than the upper slope (plots U and R) were within our expectation. However, it was unexpected to see for the soil water gradient that the soil water content in the 0–30 cm layer was higher in the upper slope than in the lower slope during the rainy season (Fig. 3) because rainwater usually runs off from the upper to the lower slope. Despite the surface soil being drier in the upper than the lower slope, which might be related to the concentration of fine roots in the surface soil, the subsurface soil layer was actually relatively moist during the rainy season. We have no data on the soil porosity of the monitoring plots, and the available data on the soil physical properties (Table 1) do not explain the reason for the trend in water content. However, the responses of soil respiration to soil water condition, as expressed by the exponential quadratic functions, seem to be reasonable for the upper slope because under a soil water condition of near-saturation, soil respiration is often depressed by the increase in the water-filled pore space (Doff sotta *et al.* 2004; Kang *et al.* 2003) or by the decline in microbial activity due to the oxygen deficit (McGroddy and Silver 2004; Skopp *et al.* 1990). Similar results were found in the other areas of Thailand; depression of soil respiration occurred under high soil moisture content over 0.21 (Adachi *et al.* 2009). Meir *et al.* (2008) suggested that an accurate relationship between soil respiration and soil moisture is an important key to specify when constructing a spatially consistent model of soil respiration.

Beside the physiological responses of the soil microbe to soil moisture, the quality of the organic matter would differ among the sites. A lower contribution of heterotrophic respiration in the upper slope, indicating the slow decomposition of organic matter, might result in the accumulation of labile organic matter at the site, which is suggested by the fact that soil organic matter on the upper slope has a relatively high carbon/nitrogen (C:N) ratio (Table 1). In addition, root exudates from the dense fine-roots on the upper slope could have been a source of labile organic matter (Chapin *et al.* 2009), which might have resulted in a sharp increase in soil respiration rates under moderate soil water conditions on the upper slope (Fig. 4).

In contrast, soil respiration on the lower slope showed no limits in terms of high water content although we did not observe the soil respiration rate when the soil water content exceeded 0.3. This type of linear response is the same as the observation for teak plantations (Takahashi *et al.* 2009) that were located close to plot L in the watershed. Because plot L was well-drained, probably due to its stand position (over 2 m high) from

the bed of the brook and water uptake by roots, soil gas exchange would be smooth, even during the rainy season. Therefore, we concluded that the soil water gradient formed on the slope basically controlled the spatial variation in soil respiration rates in the watershed. In addition, the quality of the organic matter, physical soil properties, and the physiological responses of the soil microbes should be examined, which would create a complex spatial distribution of soil respiration rates in the watershed.

Variation of carbon dioxide sources in different slope positions

The reviewed data from forest biomes worldwide indicated that autotrophic respiration occupied about 50% of the total soil respiration (Hanson *et al.* 2000; Bond-Lamberty *et al.* 2004; Subke *et al.* 2006). Subke *et al.* (2006) found that the contribution of autotrophic respiration increased with increasing total soil respiration on a global scale, which suggests that autotrophic respiration is related to the biomass production of forests. However, Asian seasonal tropical and subtropical forests showed relatively lower autotrophic respiration, although the separation methodology for autotrophic respiration differed among researchers (Table 8). Autotrophic respiration ranged from 14.6 to 50.5% of the total soil respiration and averaged 31.7% (standard deviation, 10.8). Although unconfirmed, this might be responsible for the swift decomposition of litter and soil organic matter under a moist and warm environment during the rainy season and low autotrophic respiration during the dry season. Schaefer *et al.* (2009) also demonstrated that autotrophic respiration occurred in a small proportion of a monsoon forest in China by their sophisticated manipulation experiment for separating root respiration. However, we may need to wait before drawing a conclusion because root trenching may have side effects such as root decomposition and changes in soil microbial community (Díaz-Pinés *et al.* 2010).

Regarding the variation of the slope position, root respiration may be correlated to root biomass. The root biomass regression was used to estimate root respiration in some studies (e.g. Beheraa *et al.* 1990; Rodeghiero and Cescatti 2006; Wang *et al.* 2008). High root density would result in a high contribution of root respiration to the upper slope (Table 3). Many studies have reported that dry conditions tended to enhance the growth of fine roots in the surface soil (e.g. Noguchi *et al.* 2007), which would result from a preferable allocation of photosynthesis assimilates to belowground parts in drier soil on the upper slope (Tateno *et al.* 2004). In tropical seasonal forests in Mexico, root systems were densely distributed

Table 8 Comparison of autotrophic and heterotrophic respiration in total soil respiration among Asian monsoon tropical and subtropical seasonal forests

Forests type	Period, Slope position	Autotrophic respiration %	Heterotrophic respiration %	Location	Reference
Mixed deciduous forest	Annual	50.5	49.5	Orissa, India	Behera <i>et al.</i> 1990
Evergreen <i>Castanopsis</i> natural forest	Annual	47.8	52.2	Samming, Fujian, China	Yang <i>et al.</i> 2007
<i>Castanopsis</i> plantation	Annual	42.1	57.9	Samming, Fujian, China	Yang <i>et al.</i> 2007
Chinese fir	Annual	40.3	59.7	Samming, Fujian, China	Yang <i>et al.</i> 2007
Alder-cypress mixed plantation	Annual	31.8–37.2	68.2–62.8	Yanting, Sichuan, China	Wang <i>et al.</i> 2006
Evergreen broadleaved forest	Rainy season	35.4	64.4	Dinghushan, Guangdong, China	Yi <i>et al.</i> 2007
Evergreen broadleaved forest	Dry season	22.1	77.9	Dinghushan, Guangdong, China	Yi <i>et al.</i> 2007
Pine and broadleaf mixed forest	Rainy season	29.1	70.9	Dinghushan, Guangdong, China	Yi <i>et al.</i> 2007
Pine and broadleaf mixed forest	Dry season	20.0	80.0	Dinghushan, Guangdong, China	Yi <i>et al.</i> 2007
Pine forest	Rainy season	26.1	73.9	Dinghushan, Guangdong, China	Yi <i>et al.</i> 2007
Pine forest	Dry season	18.1	81.9	Dinghushan, Guangdong, China	Yi <i>et al.</i> 2007
Evergreen broad-leaved forest	Annual	<33.3	>66.7	Ailao, Yunnan, China	Schaefer <i>et al.</i> 2009
Teak plantation	Annual, Lower slope	14.6	85.4	Kanchanaburi, Thailand	Takahashi <i>et al.</i> 2009
Mixed deciduous forest	Annual, Ridge	36.6	64.4	Kanchanaburi, Thailand	This study
Mixed deciduous forest	Annual, Upper slope	34.6	65.4	Kanchanaburi, Thailand	This study
Mixed deciduous forest	Annual, Lower slope	19.4	80.6	Kanchanaburi, Thailand	This study

in the top 20 cm soil layer (Castellanos *et al.* 1991). Thus, the large contribution of autotrophic respiration would be reasonable in dry soil conditions on the upper slope position.

As for heterotrophic respiration, soil respiration contributed in relatively stable proportions, comprising 46.3–54.4% of total soil respiration, meaning respiration from litter was a key factor in variation of heterotrophic respiration. The contribution of the organic layer respiration decreased up the slope. Although the amounts of organic layer were relatively large on the upper slope (Table 2), they were still smaller than the annual litterfall input: 3.75 to 5.91 Mg ha⁻¹. Somrithipol (1997) reported that the decomposition of leaf-litter was quick in this watershed: 85% of bamboo leaves and 95% of *Shorea siamensis* leaves had disappeared within a year. Despite the lack of comparisons of litterfall among the plots, however, significant litterfall may occur in plot L due to the greater biomass production on the lower slope. These results indicate that the litterfall may be an indicator of the heterotrophic respiration rate from the organic layer and its contribution to total soil respiration.

Seasonal variation in soil respiration

The overall seasonal pattern of soil respiration rates; high and low rates during the rainy and dry seasons respectively, was the same as other observations in Thailand (Tulaphitak *et al.* 1985; Hashimoto *et al.* 2004; Adachi *et al.* 2009; Takahashi *et al.* 2009). The moist soil condition enhanced the physiological activities of soil microbes and the root respiration to increase the soil respiration rate. Regarding temperature, the small year-round fluctuation in soil temperature resulted in no clear statistical correlation with the soil respiration rate. Conversely, an increase in temperature sometime depressed the soil respiration rate. Adachi *et al.* (2009) also reported that high temperatures in the dry season led even to a midday depression of the soil respiration rate in a forest of Thailand. Thus, in seasonal tropical forests, soil water content would be the most influential factor for seasonal and temporal fluctuations of the soil respiration, but high temperature may sometimes also have an effect as a stress factor for the respiration.

The organic layer is also a source of heterotrophic respiration and its water content would certainly be a significant factor for decomposing litter. However, no close relationship between the soil respiration rate and the moisture in the organic layer was detected in our observation. This is probably because of the lower contribution of the organic layer to total soil respiration in plots R and U (Table 6) and significant fluctuations in

its water content even during the rainy season (Table 4). Chambers *et al.* (2004) also pointed out that the organic layer and deadwood were very sensitive to moisture stress, thereby affecting CO₂ efflux from the forest floor. The development of a monitoring system for water content in the organic layer may improve the precision of soil respiration rate estimates, especially during the rainy season.

Annual soil respiration

Variation in annual carbon efflux was considerable in the watershed, from 1199 to 1908 gC m⁻² year⁻¹ in 1997 (Table 7), although the range is comparable to the review data by Raich and Tufekciogul (2000). Similar to the soil respiration rate, the efflux decreased up the slope. However, the differences between plots L and R were minor in 1998 when rainfall declined because moderate soil water content during the rainy season resulted in a high soil respiration rate on the upper slope while efflux on the lower slope decreased. This suggests that scaling up the carbon balance from a stand scale to a watershed scale could not be achieved from soil water distribution data in the watershed alone. It is noted that annual variation in rainfall did not linearly determine the annual soil carbon efflux.

Carbon stock and soil respiration

There was no apparent relationship between the total carbon stock in soil and soil respiration rates ($r=0.34$, $p=0.66$). As we discussed, the labile fraction of soil carbon may be responsible for short-term heterotrophic soil respiration (Gu *et al.* 2004; Knorr *et al.* 2005). The reasons for the high soil carbon stock on the ridge would be the slow decomposition of soil organic matter and concentration of fine roots (Santantonio and Hermann 1985; Tsutsumi *et al.* 1985). The sheet erosion of surface soil should also be a factor in reducing the accumulation of soil carbon stock on steep slopes. Therefore, carbon stock is not likely to be a key parameter to estimate the soil respiration rate in the short run.

CONCLUSION

Seasonal and spatial variations in soil respiration in the watershed under a tropical seasonal forest in Thailand were significantly dictated by changes in the soil moisture regime. Seasonal variation, whereby the soil respiration rate was high and low during the rainy and dry seasons respectively was observed. For spatial variation, the soil

respiration rate was usually higher on the lower slope (plot L) than on the upper slope (plots R and U). However, the response patterns of soil respiration to soil water content differed between the lower and upper slopes. Annual CO₂ efflux from the forest floor ranged from 1199 gC m⁻² year⁻¹ in plot R to 1908 gC m⁻² year⁻¹ in plot L. The contribution of autotrophic respiration to the total soil respiration increased and the contribution of organic layer respiration decreased up the slope. We concluded that the soil respiration rate and the contribution of CO₂ sources was influenced by the soil water content formed on the sloping topography. The varying responses of the soil respiration rate to soil water content at different slope positions create complex spatial variation in the soil respiration rate at a watershed scale.

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