






Spatial and seasonal variation in soil respiration along a slope in a rubber plantation and a natural forest in Xishuangbanna, Southwest China

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Abstract: Soil respiration is a key component of the global carbon cycle, and even small changes in soil respiration rates could result in significant changes in atmospheric CO₂ levels. The conversion of tropical forests to rubber plantations in SE Asia is increasingly common, and there is a need to understand the impacts of this land-use change on soil respiration in order to revise CO₂ budget calculations. This study focused on the spatial variability of soil respiration along a slope in a natural tropical rainforest and a terraced rubber plantation in Xishuangbanna, Southwest (SW) China. In each land-use type, we inserted 105 collars for soil respiration measurements. Research was conducted over one year in Xishuangbanna during May, June, July and October 2015 (wet season) and January and March 2016 (dry season). The mean annual soil respiration rate was 30% higher in natural forest than in rubber plantation and mean fluxes in the wet and dry season were 15.1 and 9.5 Mg C ha⁻¹ yr⁻¹ in natural forest and 11.7 and 5.7 Mg C ha⁻¹ yr⁻¹ in rubber plantation. Using a linear mixed

effects model to assess the effect of changes in soil temperature and moisture on soil respiration, we found that soil temperature was the main driver of variation in soil respiration, explaining 48% of its seasonal variation in rubber plantation and 30% in natural forest. After including soil moisture, the model explained 70% of the variation in soil respiration in natural forest and 76% in rubber plantation. In the natural forest slope position had a significant effect on soil respiration, and soil temperature and soil moisture gradients only partly explained this correlation. In contrast, soil respiration in rubber plantation was not affected by slope position, which may be due to the terrace structure that resulted in more homogeneous environmental conditions along the slope. Further research is needed to determine whether or not these findings hold true at a landscape level.

Keywords: Soil respiration; Tropical rain forest; Rubber plantation; Land-use change; Carbon cycle; Transect

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Introduction

Carbon dioxide emissions from the soil, i.e., soil respiration, account for about 25% of global CO₂ exchange capacity and are 10 times higher than CO₂ emissions from fossil fuel combustion (Li et al. 2007; Raich and Potter 1995). The increasing concentration of CO₂ in the Earth's atmosphere is the primary driver of global climate change (Jenkinson et al. 1991) and small changes in the magnitude of soil respiration are capable of causing large changes in atmospheric carbon dioxide levels. As soil respiration is the main output pathway of soil carbon, a full understanding of the determinants of soil respiration in different land use types is critical for accurately modelling the global carbon cycle and carbon budgets.

Soil respiration includes root respiration, microbial respiration and soil-fauna respiration (Rochette et al. 1991). These processes are governed by various factors including soil temperature and soil moisture (Davidson et al. 2000; Franzluebbers 1999; Yuste et al. 2007). Surface topography can lead to variations in soil drainage that can indirectly influence soil respiration through changes in soil moisture and soil temperature (Fang et al. 2008; Hanson et al. 1993; Kang et al. 2003). Furthermore, nutrient availability changes along slopes, typically with nutrient accumulation at the lower end of slopes due to the downward translocation of soil particles with runoff water (Berryman et al. 2015; Takyu et al. 2003). Studies show that these soil physical and chemical gradients may significantly affect soil respiration even along short slopes of less than 100 m change in elevation (Epron et al. 2006; Kosugi et al. 2007; Luan et al. 2012; Saiz et al. 2006; Takahashi et al. 2011; Tsui et al. 2004; Wood and Silver 2012). However, so far, no overall relationship between soil respiration and slope position has been found (Wood and Silver 2012). Furthermore, there are only a few studies on soil respiration along slopes in tropical ecosystems (Brito et al. 2009; Epron et al. 2006; Fang et al. 2009), where spatial heterogeneity has been shown to be high (Ohashi et al. 2008; Schwendenmann et al. 2003; Song et al. 2013).

Xishuangbanna is located in the southwest of China and is recognized as an important biodiversity hotspot. The typical topography in this

region is mountainous and hilly. Mountain areas account for 95% of the total area of the state (Li et al. 2016), with slopes between 5 and 35 degrees accounting for 86% of the total area. In recent years Xishuangbanna has experienced rapid land use change. In particular, there has been a large expansion in the cultivation of natural rubber. Over the period 2000-2010, the area covered by rubber plantations increased by 70% to 1.4×10^5 ha, and between 2010 and 2014 increased again by 12% to 0.4×10^5 ha (Liao et al. 2014). Rubber plantations have become the region's most widespread monoculture plantations and 90% are the result of forest conversion (Ziegler et al. 2009). This land cover change will affect the regional soil, water and carbon flux, and ultimately have an impact on soil CO₂ emissions in this region. In Xishuangbanna, unlike traditional rubber-growing regions in SE Asia, most rubber plantations are on slopes of more than 15 degrees incline (Ahrends et al. 2015). The slopes are terraced when establishing rubber plantation, which reduces surface runoff and soil and nutrient loss caused by erosion - one of the main negative environmental impacts of monocultures in mountainous areas (e.g., Liu et al. 2017; Wu et al. 2001). Since terracing results in a more homogenous pattern of soil moisture and soil nutrient distribution along the slope (e.g., de Blécourt et al. 2014; Goldberg et al. 2017), the soil respiration should be less affected by slope position as compared to forests with natural slopes. So far, only very few studies have compared soil respiration in natural tropical forests and rubber plantations (Fang et al. 2010; Fang and Sha 2006; Lang et al. 2017; Lu et al. 2009; Zhang et al. 2015). And, none of these studies have studied the effect of topography (i.e., terraced land) on soil respiration in rubber plantations. In order to obtain reliable estimates when upscaling site measurements on a landscape, and regional level, we must improve our understanding of the topography effect on soil respiration (Adachi et al. 2005; Yim et al. 2003).

In this study, we investigated the spatial variability of soil respiration along a slope in two neighboring sites in Xishuangbanna: a tropical rain forest and a mature rubber plantation. Our goal was to evaluate the role of topography on the spatial variation of soil respiration in each site and to identify differences in the spatial patterns of soil

respiration along the slope of a natural tropical forest and a terraced site in close proximity that has been converted from a tropical forest to a rubber plantation.

1 Materials and Methods

1.1 Site description

The study region was situated in Mandian, Nabanhe watershed Nature Reserve of Xishuangbanna (22°04'–22°17'N, 100°32'–100°44'E), Yunnan Province, China. The reserve is a watershed surrounded by hills and mountains, covering a total area of 26,600 ha and at an elevation of 539 m to 2304 m. Mean annual temperature varies from 18 to 22°C. Annual precipitation varies between 1200 mm to 1700 mm (Yang et al. 2016). However, 81%–95% of the rainfall occurs in the rainy season. Climatic data were obtained from a local weather station in Mandian (Figure 1). The main forest types in the reserve are evergreen broad-leaved forest and tropical monsoon forest (Yang et al. 2016).

The two study sites were located close to Mandian village; one site was located in a rubber plantation (rubber plantation), and the other site was in a seasonal rain forest, referred to henceforth as natural forest (Sheng et al. 2010). Both sites were <1 km apart and between 200 m and 500 m away from tributaries to the Mandian River. The two sites were located at similar elevations: natural

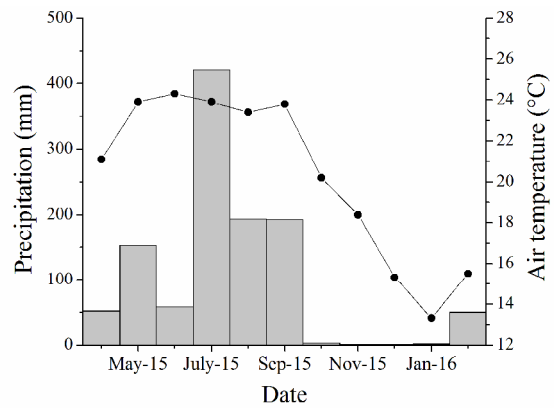


Figure 1 Mean monthly precipitation (mm, bars) and air temperature (°C, line) in Xishuangbanna.

forest at 650 to 790 m asl. (22°07' N, 100°40' E) and rubber plantation at 650 to 760 m asl. (22°07' N, 100°40' E). Slopes ranged between 19° and 31° in rubber plantation and between 19° and 38° in natural forest. The slopes were measured using a theodolite (NTS-312L, South survey company, China; Figure 2).

The rubber trees were planted 18 years ago in rows on terraces. Management practices in rubber plantations include terrace establishment, fertilization, pest control, removal of understory vegetation and rubber tapping. The terrace benches in the rubber plantations were constructed using a hoe. The tree spacing is 2 to 3 m in a row, and 5 to 6 m between rows. According to the local farmers, rubber plantations were fertilized with 45% compound fertilizer (N-P-K=15-1-15) at a rate of 1.5 kg per tree in July. In order to control powdery

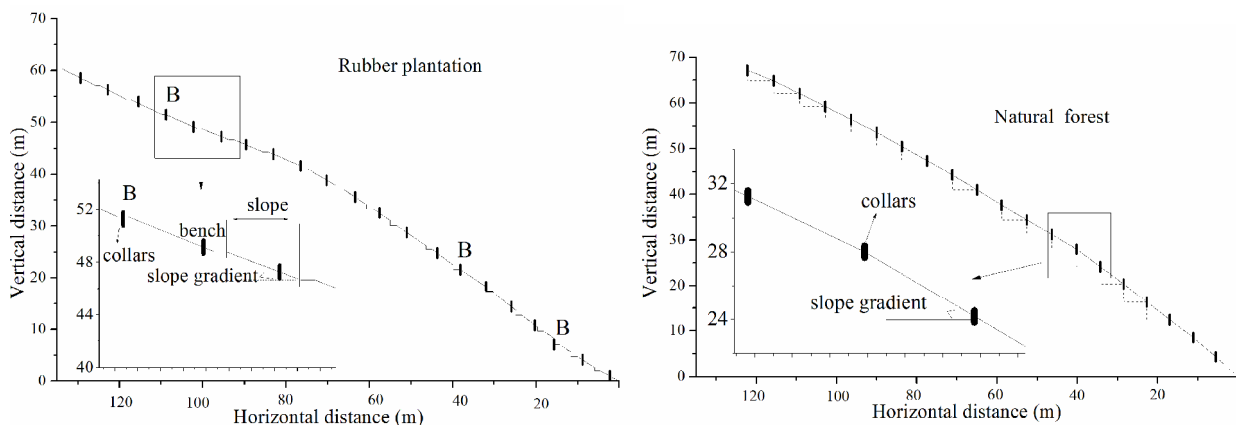


Figure 2 Schematic overview of the transect profiles in rubber plantation and natural forest. The bold vertical lines represent the rows (in total 21), where collars were installed with 5 replicates per row. The X-axis represents the horizontal distances from the 1st row. The Y-axis represents the vertical distance from the first monitoring row. “B” in the rubber plantation indicates rows of collars that were installed along the bench. All others were installed on slope positions.

mildew disease, 10 kg ha⁻¹ of 99% sulphur powder was applied once during January to March. Herbicides (30% glyphosate) were applied at a rate of 6 kg ha⁻¹ twice a year in July and December and there was no groundcover throughout the year. Rubber trees are tapped after they are 6-7 years, and farmers tap from April to October, according to the onset and ending of the rainy season. Rubber latex is harvested every second day. At the lower end of the rubber plantation, between the second and fourth row of rubber trees, tea (*Camellia sinensis* L. O. Ktzein) has been intercropped for 10 years. Only 1 out of 21 rows of soil respiration measurement was in this tea intercropping zone (Figure 2, row 3). In the rubber plantations, mean tree height was 20 m.

The natural rainforest had tall emergent trees of up to 40 m height with epiphytes, lichens and a rich herbaceous layer. Forests in this region can have over 100 tree species per hectare and dominant trees families include Burseraceae, Annonaceae and Euphobiaceae (Cao and Zhang 1997). Natural forest had not been disturbed by any recent human activities.

1.2 Soil respiration measurements

Two topographical transects were established in both sites. We started 10 m away from the forest or plantation edge in order to avoid edge effects. The length of each transect was 140 m. Vertical distance was 67 m in natural forest, and 58 m in the rubber plantation (Figure 2). Twenty-one rows were established at 7 m intervals along the slope. In each row, 5 collars were installed around 2 m apart from each other as replicates. Each collar was at least 1 m away from trees in order to reduce the influence of the roots on the results. Altogether, 105 collars were installed in both sites along the slope (Figure 2). In the bench position the slope gradient was 0°. PVC collars of 20 cm in diameter and 20 cm in height were inserted 5 cm deep into the soil (Wu et al. 2016; Goldberg et al. 2017) in March 2015. Soil respiration measurements were performed in May, June, July and October 2015 during the rainy season, and in January, and March 2016 in the dry season. In order to reduce the influence of diurnal variation, measurements were taken at random intervals along the slope. Measurements were carried out on two consecutive

days with no rainfall between 9:00 a.m. and 5:00 p.m. For each measurement, the collars were manually closed with a plastic lid and connected to a portable infra-red gas analyser (LI-8100, LI-COR, Lincoln, Nebraska, USA). Air was circulated in this closed system by a pump at a constant flow rate of 0.5 L min⁻¹ and the CO₂ concentration inside the chamber was logged every 10 s for a period of 5 min. CO₂ fluxes were calculated from linear regressions of increasing CO₂ concentrations.

1.3 Soil physical and chemical parameters

A sensor attached to the LI-8100 system measured soil moisture and soil temperature at a depth of 10 cm. In addition, data loggers (Hobo U30) were installed in three different slope positions (lower, middle and upper slope) for daily monitoring of soil temperature. Soil temperature sensors (S-TMB-M002) were permanently installed at 10 cm depth. Data were logged in 30 min intervals and averaged daily. Due to problems with the soil temperature sensor attached to the LICOR, we used the soil temperature data from the loggers installed at the three slope positions. According to data derived from the first four months from the LICOR soil temperature sensor, spatial variation in soil temperature was much smaller (CV (coefficient of variation) 1%-6%) than seasonal variation (CV 24%-27%). The use of soil temperature data from the three plot locations should therefore have little effect on the results.

Soil sampling was carried out in the three plots along the slopes. At each plot, 10 samples were taken with an auger (2.5 cm diameter) from 0-10 cm once in the wet season (September 2015) and once in the dry season (March 2016) and for each date bulked into one sample for analysis. The bulked soil was air-dried at room temperature prior to physical and chemical analysis. Soil samples were sent to Biogeochemical laboratory, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. All physical and chemical analysis stated below followed the protocols from the National Forest Service of China (1999). Soil particle size was examined by the pipette method which fractionated into clay (<0.002 mm), silt (0.002-0.05 mm) and sand (0.05-0.2 mm) according to the USDA classification system. Soil pH was measured

potentiometrically at a soil: water ratio of 1:2.5 in H₂O. Organic matter (OM) was quantified by oxidation with a potassium dichromate solution in sulfuric acid (H₂SO₄-K₂Cr₂O₇). Organic carbon was calculated using the formula $OM = OC \times 1.724$. Total nitrogen (TN) was measured using a CN Analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Germany). Total phosphorus was digested with perchloric acid and hydrofluoric acid (HClO₄-HF) solution and determined using an inductively coupled plasma atomic emission spectrometer (iCAP6300, Thermo Fisher Scientific, U.S.A). Cation exchange capacity (CEC) was exchanged with 1 M ammonium acetate (CH₃COONH₄) (pH=7.0) and tested by auto Kjeldahi unit (K370, BUCHI Labortechnik AG, Schweiz).

1.4 Statistics

All data analyses were conducted using the open source statistical software R (R software version 2.13.0, R Core Team 2012) at a significance level of 0.05 unless otherwise stated. In order to estimate annual soil respiration, time weighted soil respiration rates were created by multiplying soil CO₂ emission rates of two consecutive gas flux rates with the corresponding time period. The same is true for annual soil moisture. "Hot spots" of soil respiration were defined as soil respiration values higher than the sum of the upper quartiles and 1.5 times the interquartile range (Song et al. 2013; Vankessel et al. 1993). The non-parametric Mann-Whitney U test without any data transformation was used to identify seasonal and spatial variations of soil respiration and soil moisture.

Linear mixed effects models (LME) using the nlme (Linear and Nonlinear Mixed Effects Models) package were used to determine the contributions of the fixed factors soil temperature, soil moisture, slope gradient and vertical distance on soil

respiration. Soil respiration rates were log transformed in order to achieve normality and homogeneity of variance. The five collars at each rows were treated as replicates, the positions of single collars were set as random factor allowing estimation of individual intercepts, with common parameters for fixed factors. A standardized coefficient was used to assess the relative importance of each environmental factor (soil temperature, soil moisture, slope gradient, vertical distance) on soil respiration. The best-fit model was selected on the basis of AIC (Akaike Information Criterion) and higher determinant coefficient. Furthermore, we simulated 3D surfaces with back transformation of the LME model with maximum and minimum intercepts (Lang et al. 2017). Pearson's correlation analyses and linear regression models between soil respiration and soil temperature, soil moisture, slope gradient, vertical distance and two-way interactions of the environmental parameters were further examined. All graphs were created using OriginPro – 9.0.

2 Results

2.1 Soil chemical and physical parameters

The rubber plantation soil had higher pH than the natural forest (Table 1). Total P was lower in rubber plantation compared to natural forest. SOC and TN were similar between the two study sites. Regarding the soil texture, rubber plantation soil was silty clay and natural forest soil was clay loam. The clay content of the rubber plantation was higher and the sand content lower as compared to the natural forest (Table 1).

2.2 Seasonal characteristics

Mean soil respiration for all collars ($n=105$)

Table 1 Mean ($n=6$, \pm SE) soil characteristics in rubber plantation and natural forest: organic carbon (OC), total nitrogen (TN), total phosphorus (TP), cation exchange capacity (CEC), Sand content (0.5-2 mm, %), Silt content (0.002-0.5 mm, %), and clay content (<0.002 mm, %). Different letters represent significant differences between the two land-use types. (Mann-Whitney U test; $p<0.05$)

	pH	OC (g kg ⁻¹)	TN (g kg ⁻¹)	TP (g kg ⁻¹)	CEC (cmol ⁺ kg ⁻¹)	Sand (%)	Silt (%)	Clay (%)
Rubber plantation	4.7 \pm 0.1 ^b	28.9 \pm 2.1	2.3 \pm 0.1	0.5 \pm 0.1 ^b	13.89 \pm 1.4	12.8 \pm 0.9 ^b	45.2 \pm 1.5	42.0 \pm 1.7 ^a
Natural forest	6.2 \pm 0.2 ^a	28.5 \pm 1.4	2.6 \pm 0.2	0.8 \pm 0.0 ^a	15.14 \pm 0.8	29.6 \pm 4.5 ^a	40.7 \pm 3.4	29.7 \pm 1.4 ^b

significantly decreased from July to January. Over that time period, mean soil respiration in natural forest fell from 4.5 ± 0.2 to $2.3 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$, and in rubber plantation from 3.6 ± 0.1 to $1.4 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 3, γ). Soil respiration in the wet season was significantly higher than in the dry season in both sites (Table 2). Soil respiration in rubber plantation was lower than in natural forest throughout the study: 23% lower in the wet season, and 40% lower in the dry season (Table 2).

Soil temperature did not differ substantially between natural forest and rubber plantation, and ranged between 14°C and 25°C in both land-use types. From the warm-wet to the cool-dry season, soil temperature decreased by 48% and 42% in rubber plantation and natural forest, respectively. Seasonal variation in soil respiration followed the same pattern as soil temperature (Figure 3, α and γ) and was positively correlated with soil temperature (rubber plantation: $r^2 = 0.48$ natural forest: $r^2 = 0.30$) (Figure 4).

Soil moisture was higher in rubber plantation ($0.32 \text{ m}^3 \text{ m}^{-3}$) compared to natural forest ($0.26 \text{ m}^3 \text{ m}^{-3}$) (Table 2). The soil moisture in natural forest increased with the onset of the wet season in June. However, soil moisture was 21% lower in July compared to June. Our measurements in July occurred after one week with less than 100 mm rainfall. Unlike natural forest, soil moisture in rubber plantation did not show any clear seasonal variation and was also lowest in July (Figure 3). Soil moisture was positively correlated with soil respiration across the monitoring period in natural forest but negatively correlated with soil respiration in the rubber plantation, although both relationships were weak (natural forest $r = 0.13$; rubber plantation $r = -0.32$) (Table 3).

2.3 Spatial distribution

During the monitoring period, mean soil respiration rates ranged between 1.41 and $8.35 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the natural forest, and between 0.74 and $6.85 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the rubber plantation along the 140 m experimental transects (Figure 5). Topography had a significant effect on annual soil respiration in the transects of both natural forest and rubber plantation (natural forest: $W = 145.87$, $df = 20$, $n = 615$, $p < 0.001$, rubber plantation: $W = 85.61$, $df = 20$, $n = 628$, $p < 0.001$). Increases in

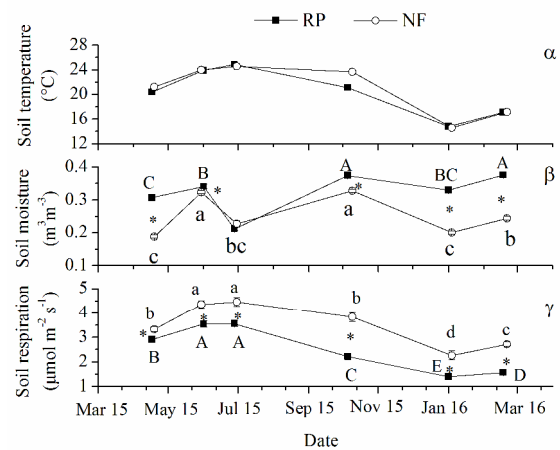


Figure 3 Average daily soil temperature (\pm SE, 0-10 cm, $n=3$, α), mean soil moisture (\pm SE, 0-10 cm, $n=105$, β) and mean soil respiration (\pm SE, $n=105$, γ) in rubber plantation (RP) and natural forest (NF) on each sample occasion. The different letters represent significant differences within the month (capital for the RP, lowercase for the NF, parametric Mann-Whitney U test; $p < 0.05$) “*” represent the significant differences between the two land use types (non-parametric Mann-Whitney U test; $p < 0.05$). There were no significant differences in ST between months or land-use types.

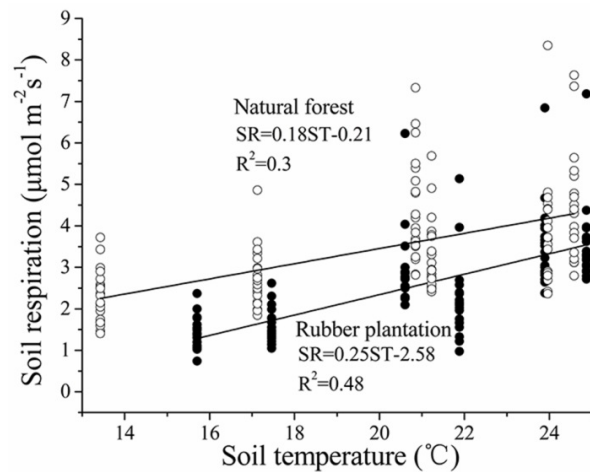


Figure 4 Regression of mean soil respiration (SR) in single rows and mean soil temperatures (ST) along the slope in the rubber plantation and natural forest.

vertical distance explained 10%-32% of the decrease in soil moisture, and 12%-28% of the decrease in soil respiration. However, changes in soil moisture alone could not explain variation in soil respiration along the transect (Table 3). In the rubber plantation, slope gradient significantly affected soil respiration throughout the year. However, this was solely driven by the bench position (0° slope), which had significantly higher soil respiration rates (dry season: $1.77 \pm 0.19 \mu\text{mol}$

Table 2 Mean soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$, wet season: $n=420$; dry season: $n=210$), mean soil moisture at 10 cm depth ($\text{m}^3 \text{m}^{-3}$, wet season: $n=420$; dry season: $n=210$), and mean soil temperature at 10 cm depth ($^{\circ}\text{C}$, $n=3$) in the rubber plantation and the natural forest. The different letters represent significant differences between the different seasons and between the land-use types. (non-parametric Mann-Whitney U test; $p<0.05$) Annual SR, SM, and ST represent time weighted means.

	Rubber plantation			Natural rainforest		
	Wet season	Dry season	Annual	Wet season	Dry season	Annual
Mean soil respiration	3.1 ± 0.07^b	1.5 ± 0.04^d	2.48 ± 0.06	4.0 ± 0.08^a	2.5 ± 0.07^c	3.56 ± 0.07
Mean soil moisture at 10 cm depth	0.34 ± 0.08^b	0.35 ± 0.004^a	0.32 ± 0.003	0.28 ± 0.004^c	0.22 ± 0.004^d	0.26 ± 0.003
Mean soil temperature at 10 cm depth	22.6 ± 1.1^a	15.9 ± 1.2^b	20.4 ± 1.6	23.4 ± 0.7^a	15.8 ± 1.3^b	20.9 ± 1.7

Table 3 Correlation coefficients for soil respiration (SR) and soil moisture (SM), vertical distance (VD) and slope gradient (SG), and the relationships between the SM and VD, and SM and SG. Bold numbers represent statistically significant correlations.

	Rubber plantation					Natural forest				
	SR×SM	SR×VD	SR×SG	SM×VD	SM×SG	SR×SM	SR×VD	SR×SG	SM×VD	SM×SG
May 3	-0.05	-0.22	-0.16	-0.1	-0.03	-0.38	-0.07	-0.01	0.32	-0.29
Jun 15	-0.21	-0.22	-0.13	0.36	-0.2	-0.22	-0.35	0.26	-0.37	0.4
Jul 12	-0.18	-0.13	-0.23	-0.06	-0.23	0.05	-0.36	0.28	0.06	-0.05
Oct 19	-0.06	0.06	-0.22	-0.59	-0.01	-0.12	-0.42	0.36	-0.37	0.36
Jan 15	0.03	0.03	-0.13	-0.28	-0.15	0.07	-0.53	0.53	-0.32	0.34
Mar 3	0.04	-0.03	-0.2	-0.18	-0.35	0.03	-0.43	0.42	-0.57	0.64
Wet season	-0.26	-0.12	-0.17	-0.03	-0.08	0.006	-0.3	0.23	-0.05	0.06
Dry season	0.09	-0.001	-0.16	-0.21	-0.22	0.13	-0.47	0.47	-0.42	0.47
Annual	-0.32	-0.08	-0.13	-0.07	-0.11	0.13	-0.3	0.25	-0.13	0.16

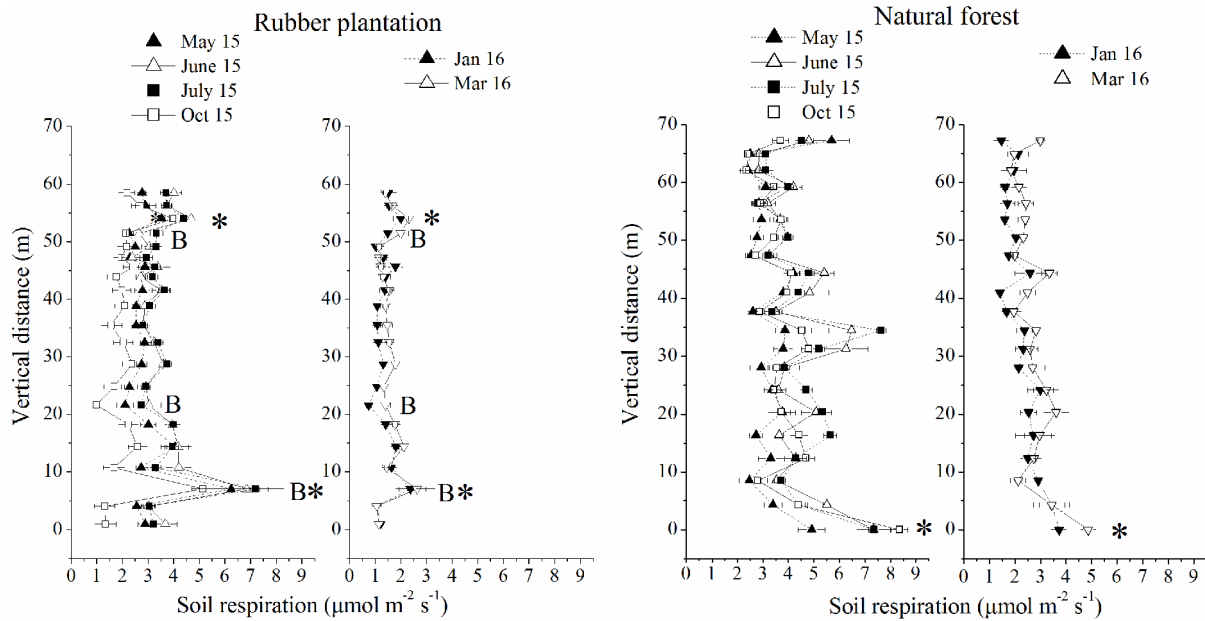


Figure 5 Mean soil respiration along the topographical transect (mean±SE) in rubber plantation and natural forest throughout the study. “B” represents collars positions on the bench in the rubber plantation, others were on the slope. “*” represents “upper outliers”, i.e. soil respiration values in these positions were higher than the sum of the upper quartiles and 1.5 times the interquartile range.

$\text{m}^{-2} \text{s}^{-1}$, wet season: $3.76\pm 0.36 \mu\text{mol m}^{-2} \text{s}^{-1}$) than that for slope positions (dry season: $1.38\pm 0.05 \mu\text{mol m}^{-2} \text{s}^{-1}$, wet season: $2.87\pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) in both seasons. This significant difference in turn was driven by higher soil respiration in one of the

three bench positions. This bench position, which was the one located in the tea-rubber intercropping zone, was identified as “hot spot” of soil respiration (Figure 5). When we excluded the bench positions from the model, slope gradient did

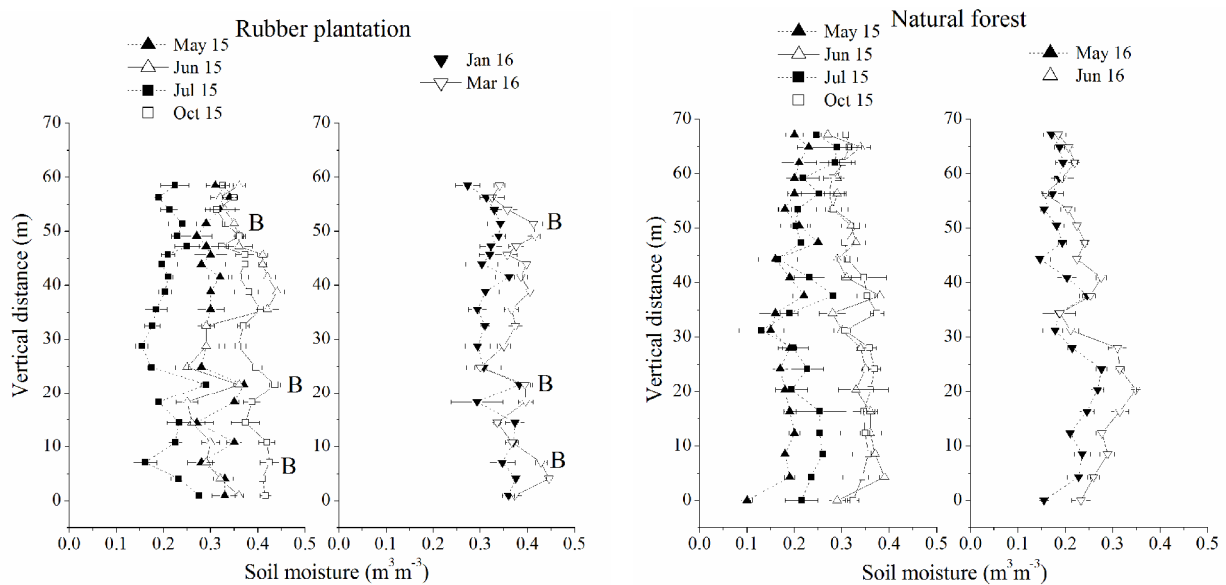


Figure 6 Mean soil moisture along the topographical transect (mean±SE) in rubber plantation and natural forest throughout the study. “B” represents collars positions on the bench in the rubber plantation, others were on the slope.

not have a significant impact on soil respiration. In the dry season, the soil moisture at bench positions was significantly higher ($0.38 \pm 0.01 \text{ m}^3 \text{ m}^{-3}$; **Figure 6**) compared to slope positions ($0.35 \pm 0.004 \text{ m}^3 \text{ m}^{-3}$, $p < 0.001$). Soil temperature did not significantly differ between the three monitored slope positions at the bottom, middle and upper part both in natural forest and rubber plantation throughout the study. The biggest difference between slope positions during a single measurement campaign was 0.6°C . Regarding soil respiration, in both natural forest and rubber plantation one to two rows were identified as hot spots (**Leon et al. 2014**).

An LME model that included soil temperature, soil moisture and a quadratic soil moisture term explained 70% of the variation in soil respiration in natural forest and 76% of the variation in soil respiration in rubber plantation (**Figure 7, Table 4**). In rubber plantation, soil temperature (standard coefficient 0.61) was a more powerful determinant of soil respiration than soil moisture (standard coefficient 0.36 for single soil moisture, -0.42 for quadratic soil moisture). In natural forest, soil temperature (standard coefficient 0.55) was also more important than soil moisture (standard coefficient 0.37 for single soil moisture, -0.35 for quadratic soil moisture) for soil respiration. From the equation in **Table 4**, with a parabolic relationship between soil moisture and soil respiration, we calculated the optimum soil

moisture for soil respiration (also referred to as “tipping point”). In natural forest, this optimum occurred at soil moisture of $0.28 \text{ m}^3 \text{ m}^{-3}$, and in rubber plantation at $0.38 \text{ m}^3 \text{ m}^{-3}$.

Table 4 Parameters of linear mixed effect (LME) model respect to soil respiration ($\log(\text{SR}) = a + b\text{ST} + c\text{SM} + d\text{SM}^2$). *** represents significant level at $p \leq 0.001$, ** at $p \leq 0.01$.

Parameters	Rubber plantation	Natural rainforest
Intercept (a)	$-1.26 \pm 0.16^{***}$	$-0.46 \pm 0.13^{***}$
ST-Soil temperature (b)	$0.088 \pm 0.004^{***}$	$0.065 \pm 0.003^{***}$
SM-Soil moisture(c)	$2.3 \pm 0.83^{**}$	$2.02 \pm 0.75^{**}$
SM ² -Quadratic moisture (d)	$-4.36 \pm 1.37^{**}$	$-3.75 \pm 1.46^{**}$
n	625	614
df	517	506
R ²	0.76	0.70

3 Discussion

3.1 Annual and seasonal soil respiration

The annual average soil respiration over the period of observation was $9.4 \pm 1.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in rubber plantation and $13.5 \pm 1.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in natural forest. For both sites, our results were higher than those reported in other studies conducted in Xishuangbanna: $7.7 - 8.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in rubber plantation, $6.8 - 10.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in natural

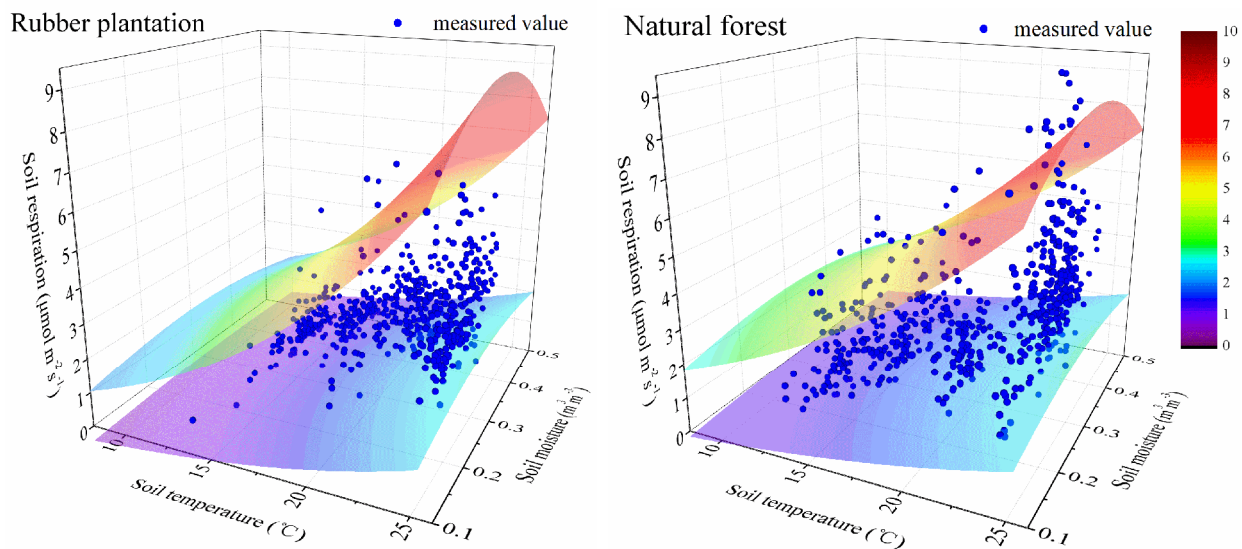


Figure 7 Single soil respiration measurements (points) with corresponding soil temperature and soil moisture, and simulated 3D surfaces (back transformation of linear mixed effect model) with maximum and minimum intercept in rubber plantation and natural forest.

forest (Fang and Sha 2006; Lang et al. 2017; Lu et al. 2009), but lower than for studies in other south east Asian tropical regions: 11.2 - 19.0 Mg C ha⁻¹ yr⁻¹ in rubber plantation (Mande et al. 2014; Satakhun et al. 2013; Wang et al. 2013), 15.8 - 25.6 Mg C ha⁻¹ yr⁻¹ in natural forest (Hashimoto et al. 2004; Katayama et al. 2009; Takahashi et al. 2011). Our study had a high level of spatial resolution (with 105 chambers per site), but comparisons of annual rates were not as robust as we would have liked, because they were based on relatively few measurement dates (6 measurement dates throughout the one-year study period). However, measurements over a single year displayed the same seasonal soil respiration pattern as existing studies on both land-use types. In our study, the highest soil respiration rates year-round were observed in June (3.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in rubber plantation and 4.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in natural forest), and these were higher than the highest wet season fluxes reported in previous studies of 2.3-2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in rubber plantation and 2.5-3.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in natural forest (Fang and Sha 2006; Lu et al. 2009) in Xishuangbanna. However, the highest values observed in our study were lower than the average seasonal rates of soil respiration reported for southeast Asian natural forest (5.6-7.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season and 2.9-6.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season) (Hashimoto et al. 2004; Katayama et al. 2009; Takahashi et al. 2011) and rubber plantation

(4.6-9.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season and 1.6-2.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season (Mande et al. 2014; Satakhun et al. 2013; Wang et al. 2013).

Our observation of seasonal variation in soil respiration was consistent with the results of previous studies in the tropics with distinct seasons that is characterized by higher soil respiration in the wet season compared to the dry season for both natural forest (Adachi et al. 2009; Fang and Sha 2006; Hashimoto et al. 2004; Takahashi et al. 2011) and rubber plantation (Fang and Sha 2006; Satakhun et al. 2013). In our study, we identified soil temperature as a more powerful determinant of soil respiration than soil moisture. Changes in soil temperature alone explained only 48% of seasonal variation in soil respiration in rubber plantation, and 30% of seasonal variation in soil respiration in natural forest. Changes in soil moisture explained less than 10% of the seasonal variation of soil respiration in both rubber plantation and natural forest. And in a dry period during the wet season, soil moisture was significantly lower in both sites in July than in June (by 30% and 38% in natural forest and rubber plantation, respectively), but soil respiration was not significantly different. Likewise, Ohashi et al. (2015) found that a short-term drought treatment in a seasonal tropical forest produced a drop in soil moisture of between 33% and 62%, but this did not result in any change in soil respiration. In the wet

season, abundant rainfall and rising temperatures bring increased plant photosynthesis and soil microbial activity, leading to higher rates of root and microbial respiration (Kuzakov and Cheng 2001; Zhou et al. 2008). In dry season, instantaneous rain events could result in rapidly stimulated soil respiration (Birch 1958). Dong et al. (2012) found that 2 hours after simulated rainfall, soil respiration reached 7 and 11 times greater than that of the control.

The LME model we used combined soil temperature and a quadratic soil moisture term after (Lang et al. 2017) and explained 76% of the soil respiration variation in rubber plantation and 70% in natural forest. According to this model, the optimum soil moisture for soil respiration that is also referred to as tipping point, as it was a parabolic function, was $0.28 \text{ m}^3 \text{ m}^{-3}$ in natural forest and $0.38 \text{ m}^3 \text{ m}^{-3}$ in rubber plantation. Therefore, the optimum soil moisture value in natural forest was reached in the wet season, whereas the optimum soil moisture for rubber plantation, even though much higher than that for natural forest, was close to the soil moisture values observed during the dry season. This explains why across the year soil respiration was positively related with soil moisture in natural forest, but negatively related with soil moisture in rubber plantation. The difference in soil moisture can be partly explained by different soil texture, with the soil in the rubber plantation having higher clay content and the soil in the natural forest having higher sand content. Soil moisture is linearly correlated with soil clay content due to the different pore system and drainage capacity (Balogh et al. 2011). Our findings are in line with those of (Wood et al. 2013), who found that sandy soils had a lower optimum level of soil moisture compared with that of higher clay content soils in tropical forests.

In this study, mean annual soil respiration was 30% lower in rubber plantation compared to natural forest. The higher level of soil respiration in natural forest can be explained by the complex community structure of the various layers in natural forest, which results in higher levels of plant root autotrophic respiration (Werner et al. 2006) and increases both the abundance and diversity of soil microbial communities, which in turn leads to increased soil respiration.

3.2 Spatial variation of soil respiration along the slope

Slope gradient significantly affected soil respiration in natural forest, which could be explained by the effect of slope gradient on soil moisture by 8%-14%. In the natural forest, the slope decreased with increasing vertical distance and likewise soil moisture and soil respiration decreased from the bottom position of our transect upwards. Accordingly, different studies in tropical forests have reported higher levels of soil moisture on lower compared to upper slopes (Epron et al. 2006; Tsui et al. 2004). However, in other studies the reverse was true with highest soil moisture on upslope positions (Takahashi et al. 2011; Wood and Silver 2012). Martin and Bolstad (2009) showed in a northern hardwood forest that elevation (vertical distance) regulated drivers of soil respiration such as soil water and soil carbon at large scales (4 km^2). Creed et al. (2012) reported that soil respiration rates on steep hillsides of 35° incline were higher than on moderately steep slopes of 25° , and that soil respiration rates were lowest on gently sloping hillsides of 15° . In the latter study the primary driver of soil respiration rates was identified to be dissolved organic carbon, which was in turn determined by differences in topography. This indicates that the effects of slope position, and associated soil physical and chemical parameters, on soil respiration need to be further analyzed in order to increase our understanding of spatial variations in soil respiration in complex terrain. Our soil sampling protocol did not allow for robust statistical analysis of variation in soil chemical parameters along the slope. However, Monkai (unpublished data), in a separate study in the same study area, did not find significant differences in soil chemical parameters along a 100 m elevation gradient in three rubber plantations and three natural rainforests close to our study sites.

In the rubber plantation, we only found a weak negative relationship between slope gradient and soil respiration and this was solely driven by significantly higher soil respiration in the bench positions (0° slope), compared to the slope positions that account for >90% of the rubber plantation area. The terraces are created during the establishment of rubber plantations in order to reduce runoff and consequent losses of water and

nutrients (de Blécourt et al. 2014; Lang et al. 2017). This management practice together with the characteristics of a monoculture tree plantation, where understory is removed leads to a much higher homogeneity of physico-chemical soil parameters compared to the natural forest.

The higher soil respiration measured at the bench position compared to the slope in our study could be due to: 1) cumulated above-ground litter (which is the primary input of fresh carbon into the soil, with higher decomposition rates likely resulting in increased microbial respiration (Epron et al. 2004; Satakhun et al. 2013), 2) little surface soil runoff from the bench leading to higher substrate quantity for soil respiration compared to the slope (Almagro and Martínez-Mena 2014), 3) higher fine root biomass from rubber trees (Adachi et al. 2006). However, only one out of three bench positions was identified as a hotspot for soil respiration. This bench position was in the area of tea intercropping, which is common for our study region. In this area fine root biomass as well as microbial activity is likely to be enhanced compared to the plantation area without intercropping. Likewise, Ishizuka et al. (2005) observed that the highest soil respiration was found around dense weeds and Leon et al. (2014) identified higher root biomass and leaf area index as reasons for the existence of hot spots in a water-limited ecosystem.

In both rubber plantation and natural forest, two and one out of the 21 rows, respectively, were identified as soil respiration hotspots (Leon et al. 2014). When excluding the soil respiration hotspots from our study, mean soil respiration rates were reduced by about 9% in rubber plantation and by 4% in natural forest across the year. This emphasizes the need of high resolution studies in different land-use systems on soil respiration in order to improve regional, and ultimately, global CO₂ budgets. Furthermore, soil

respiration in the natural seasonal rainforest in our study depended on the slope position due to changing soil physical parameters along the slope. This highlights that estimating soil respiration from this site with a few collars only, as the commonly used practice, would result in over- or underestimating ecosystem soil respiration, depending on the position of the collars, if the full range of the slope is not covered. In contrast, soil respiration in the rubber plantation was not affected by slope position (when excluding the bench position with intercropping) due to homogenous soil physical parameters along the slope. We conclude that in terraced monoculture rubber plantations the risk of over- or underestimating soil respiration due to fewer sampling points is small compared to the natural forest. However, sampling of the hotspot bench positions with the tea intercropping was necessary for an accurate picture of patterns of variation in soil respiration. More studies will be needed to establish if our findings hold true at landscape level.

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