

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet



Litter and microclimate controls on soil heterotrophic respiration after converting seasonal rainforests to rubber plantations in tropical China

Min Zhang^{a,b,*}, Wenting Feng^c, Jianhui Chen^b, Xiaoming Zou^{d,*}

^a Zhejiang Key Laboratory of Recycling and Eco-treatment of Waste Biomass, Zhejiang University of Science and Technology, Hangzhou, 310023, China

^b Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Jinghong, 650223, China

^c Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, 830011, China

^d Department of Environmental Sciences, University of Puerto Rico, P. O. Box 70377, San Juan PR 00936-8377, USA

ARTICLE INFO

Keywords: CO_2 emission land use changes Q_{10} soil moisture translocation experiment

ABSTRACT

Land-use changes can alter carbon cycling. Soil carbon loss resulting from the conversion of natural forests to rubber plantations (RP) may occur due to changes in litter inputs or in biotic and abiotic environmental conditions. In this study, we conducted a reciprocal soil and litter translocation mesocosm experiment for 15 months in a seasonal rainforest (SR) and RP to elucidate the effect of litter, soil and site conditions on heterotrophic respiration and its temperature sensitivity after land-use conversion. We found that rate of soil heterotrophic respiration (R_h) was higher at RP site than at SR site or for SR litter than RP litter with significant interactions between forest site and litter type, and did not differ between SR and RP soils. The Q_{10} values of R_h did not differ between forest sites, soils, or litter types but were substantially lower when litter was absent and substantially higher when RP soil was incubated in SR site and vice versa. Removal of surface litters led to a reduction of R_h by 27-45%. Soil labile organic C pool and microbial biomass were not influenced by litter type and soil but differed between forest sites with higher moisture at RP site than SR site. Our results suggested that changes in physical environmental conditions, rather than changes in litter input or soil biochemical properties, attributed to the elevated soil heterotrophic respiration in RP, resulting in soil carbon loss following the tropical land-use changes.

1. Introduction

Deforestation is known as the second largest source of the elevated atmospheric carbon dioxide. Carbon loss through deforestation and degradation of tropical forests was estimated at 0.8 Pg to 1.0 Pg C yr^{-1} in the last decades (Bacciniet al., 2012; Harris et al., 2012). Southeast Asia is one of the global deforestation hot spots where almost 250,000 hectares of natural forest was converted to rubber plantation (RP) between 2005 and 2010 (Ahrends et al., 2015). Rubber and other economic crops have been the major land-use changes in this region. The area of RP in Southeast Asia reached 10.4 million ha by 2017, accounting for 89% of world total RP area (FAOSTAT, 2019). Since the first rubber establishment in the 1950s, the area of RPs has increased up to 24.2% of land cover by 2014 in Xishuangbanna, Southwest of China (Chen et al., 2016).

It is recognized that soil carbon sequestration ability in RPs is much

lower than that of natural forests (Jiang et al., 2017; Yang et al., 2016). This reduction in soil organic C may result from either reduced litter input or accelerated decomposition due to changed litter quality, microclimate, or soil activity. Litter production was reported to be lower in RP than in seasonal rain forest (SR) (Zhang and Zou, 2009; Zhang et al., 2013; Kotowska et al., 2016). Litter quality is lower in RP than in SR as indicated by a higher C/N ratio and aromatic carbon fractions (Zhang and Zou, 2009; Zhang et al., 2013). However, thinner floor layer in RP than SR (Zhang and Zou, 2009; Lan et al., 2020) suggests a cause of either reduced litter inputs or accelerated litter decomposition due to improved soil physical environment and soil activity, rather than litter decomposability in RP.

Soil is responsible for 60–90% of the carbon dioxide (CO₂) released into the atmosphere in terrestrial ecosystems (Goulden et al., 1996). Soil CO₂ efflux is the outcome of the metabolic processes of plant roots (autotrophic respiration, R_a) and microbial communities (heterotrophic

* Corresponding authors *E-mail addresses:* zhangmin524@163.com (M. Zhang), xzou2011@gmail.com (X. Zou).

https://doi.org/10.1016/j.agrformet.2021.108623

Received 2 September 2020; Received in revised form 18 August 2021; Accepted 22 August 2021 Available online 17 September 2021 0168-1923/© 2021 Elsevier B.V. All rights reserved. respiration, R_h). The R_a refers to CO₂ efflux derived from roots and the associated symbiotic organisms, R_h refers to microbial respiration of litter and root exudates as well as the transformed soil organic carbon (Sulaman et al., 2005; Kuzyakov, 2005). Because R_h could account for up to 70% of the total soil respiration (R_s) in forest stands (Sulaman et al., 2005; Fernández-Alonso et al., 2018), it is therefore important to determine how R_h responds to land-use changes from native forests to monoculture agroforestry systems (Barba et al., 2016; Fernández-Alonso et al., 2018).

The conversion of native forest to monoculture RP may result in changes in plant litter input, soil biochemical properties such as microbial biomass and soil labile organic carbon, or in environmental conditions that include microclimate and soil water content (Liu et al., 2011; Meijide et al., 2018; Song et al., 2017; Lan et al., 2020), and consequently alter soil respiration and soil carbon stock. Temperature is the essential factor controlling soil metabolic activities; thus, the kinetics been of CO₂ efflux had modeled by various temperature-dependent functions. Many hypotheses were postulated to link the response of R_h to soil temperature (Tuomi et al., 2008; Tremblay et al., 2018; Salazar et al., 2019). However, the temporal variability of *R*_b observed in field experiments captures not only its dependence on soil temperature, but also reflects the influence on decomposition caused by seasonal changes in substrate quality and quantity, soil moisture and soil community (Gonzalez et al., 2001; Hou et al., 2005; Fernández-Alonso et al., 2018; Huang et al., 2020), as well as their interactions (Wall et al., 2008). Strong variations in seasonality of modeled soil R_h was commonly observed, suggesting an apparent limitation to soil metabolic activity beyond that could be explained by temperature. Furthermore, homeostasis of native soil microbial community would suggest R_h dependency on soil organisms, which were also greatly constrained by soil water and temperature (Fernández-Alonso et al., 2018).

We conducted this study to elucidate the influence of aboveground litter input, forest soils and its organisms, and forest microclimate and water content on soil Rh and its temperature sensitivity following conversion of natural forest to RPs. A 15-month reciprocal soil and litter translocation mesocosm experiment were performed in Xishuangbanna of SW China. In the root-exclusion treatment it was assumed that R_a was completely suppressed and hence solely $R_{\rm h}$ occurred that the CO₂ efflux derived from the microbial decomposition of soil organic matter and litter. We collected in-situ data on soil R_h, litterfall, soil labile organic carbon, soil microbial biomass, and soil temperature and moisture from these mesocosms in SR and RP. We hypothesized that reduction of TOC in RPs was resulted from (1) reduced production of above-ground rubber litter, or (2) accelerated soil heterotrophic respiration and altered temperature sensitivity of TOC due to improved physical environmental conditions such as temperature and moisture or soil biochemical properties such as microbial biomass and soil labile organic carbon.

2. Materials and methods

2.1. Site description

Study sites were located in the Xishuangbanna Tropical Botanical Garden (XTBG, 21°54′N, 101°46′E), near the monitoring plots of the Chinese Ecological Research Network supported by the Chinese Academy of Sciences. The annual mean temperature in the region is 21.8°C and the annual mean precipitation is 1493 mm (Cao et al., 2006). This region is strongly influenced by the tropical monsoons that bring warm and humid air from the northeastern Indian Ocean during the months of May through October. Eighty-four percent of the annual precipitation occurs during this monsoon season. Heavy nocturnal fogs form frequently during the cool-dry season from November to next April (Lang et al., 2017).

This study was conducted in a native SR and a 25-year-old RP adjacent to the SR. The soil was a lateritic Oxisol developed from

arenaceous shale sediments (Zhang et al., 2013). The dominant tree species of SR are *Pometia tomentosa, Terminalia myriocarpa, Gironniera subaequalis*, and *Garuga floribunda*. SR has an average canopy height of approximately 40 m and canopy closure of 90% (Cao and Zhang, 1996; Ren, et al., 1999; Zhu, et al., 2006). Rubber plantations were established on terraces, with wide-narrow row distance and tree spacing of 3.1and 2.5 m. It has an average canopy height of approximately 20 m, density of 370 specie per ha and canopy closure of 65% (Ren, et al., 1999; Zhu, et al., 2006). The area was selectively logged in the 1960's and was cleared for slash-and-burn agriculture before rubber planting. The plantation was fertilized with a composite fertilizer (N, P, and K) at a rate of approximately 60 kg N ha⁻¹ yr⁻¹. Fertilizers were point-applied in March and August at a dose of about 0.15 kg N per tree hole per year. Latex of the rubber trees was harvested starting at age 8-years old from March to November with a mean yield of 2.6 Mg dry latex ha⁻¹ yr⁻¹.

The reciprocal translocation experiment

Five 4×4 m plots were established at 20-50 m spacing in both the RP and SR. Six soil mesocosms of $50 \times 50 \times 10$ cm (depth) were buried randomly in each plot in August. Soils used in the mesocosms were collected from the 0-10 cm layer in SR and RP and passed through a 1cm mesh to remove plant roots, rocks and large soil animals. Two layers of 53 µm nylon mesh were placed underneath the soil to separate it from the local soil. Litters were collected (square baskets with side length of 50 cm were placed 30cm above each soil mesocosm with litter removal) and put in the corresponding soil mesocosms every 10 days. There were six treatments in each plot: 1) Soil derived from SR, without litter cover $(S_{SR} + NL)$, 2) Soil derived from RP, without litter cover $(S_{RP} + NL)$, 3) Soil origination from SR, with aboveground litter of SR ($S_{SR} + L_{SR}$), 4) Soil derived from RP, with above round litter of SR ($S_{RP} + L_{SR}$), 5) Soil derived from SR, with above ground litter of RP (S $_{\rm SR}$ + $L_{\rm RP}$), 6) Soil derived from RP, with above round litter of RP ($S_{RP} + L_{RP}$). After 15 months of field incubation, soils in these six treatments and the nearby control soil that was not disturbed were sampled to a depth of 5 cm for chemical analyses. Three soil cores (5 cm diameter) from each mesocosm were bulked into one composite sample. Samples were then passed through a 2 mm sieve and plant materials were removed by hand. A subset of the sieved soil samples was air-dried and grounded for the analyses of soil C and N content. Five conical baskets of 50 cm in diameter were randomly placed adjacent to each plot and plant litter was collected 2-3 times per month from each basket. Litters were oven dried at 60 °C to obtain dry weight.

2.2. Soil heterotrophic respiration (R_h)

Since plant roots were excluded from the mesocosms and litter was removed when measuring soil CO₂ efflux, we attribute the respiration measured within the collars mostly to microbial decomposition of soil organic matter in the non-rhizosphere. Soil respiration was measured using an infrared gas analyzer (IRGA, LI-COR 820, LI-COR, Lincoln, NE, USA) in November and February, April, and August of the next year. A PVC soil chamber (inner diameter 20.3 cm) was installed on soil surface and the total volume of the chamber was 5700 cm³. The chamber was pressed slightly into the soil to keep gas tight. An integrated pump circulated the headspace air from the chamber to the analyzer in which CO₂ concentration was recorded. Soil respirations of all plots were measured within 4 hours from 8:00 to 12:00 am. Soil temperature (C) was measured using a thermometer (TM-150, Custom, Tokyo, Japan), and soil moisture (v/w) was measured with a time domain reflectometry sensor (TDR; TRIME-FM, IMKO, Ettlingen, Germany), both at 5 cm depth.

2.3. Laboratory processing

Soil microbial biomass carbon (MBC) was determined by the difference in soil CO₂-C evolved from the control and fumigated samples following the procedures of Jenkinson and Powlson (1976). We used a sequential fumigation-incubation (SFI) procedure (Zou et al., 2005) to estimate soil labile organic carbon (LOC). The fumigated samples for microbial biomass carbon (MBC) were subject to five additional fumigation-incubation cycles. Total CO_2 evolved from the fumigated soils during six incubation cycles (10 days for each cycle) was used to estimate LOC. Total organic C and N in soils were determined using an Elementar Vario Max CN combustion analyzer (Hanau, Germany).

2.4. Statistical analysis

An exponential growth equation combined with a Gaussian function for soil moisture were used to calculate the temperature (T) sensitivity (Q_{10}) in relation with soil moisture (M).

$$R_h = a e^{bT - 0.5 \left(\frac{M - M_0}{c}\right)^2}$$
(1)

$$Q_{10} = e^{10b}$$
 (2)

where a, b, c and M_0 are fitted parameters. Soil respirations were Gaussian correlated with soil moisture under different litter and environment treatment.

All data presented here are means (\pm SD) of five plot replicates and statistical analyses were performed with Stat View 8.0 (SAS Institute, Cary, NC, USA). The mixed-model ANOVA was used to examine the effects of litter, soil and forest site (independent variables) on Q_{10} , and three-way repeated measures ANOVA for soil $R_{\rm h}$, total organic carbon (TOC), total nitrogen (TN), MBC and LOC contents (dependent variables). Pearson correlations analyses were conducted to show relationships between two variables. The Nonlinear regression and coefficient of determination were used to identify the relationship between respiration and soil temperature and moisture. All data were tested for homogeneity variance (Levene's test, p > 0.05). Fisher's least significant difference (LSD) was used for estimation of differences between treatments. All significance level was set at alpha = 0.05

3. Results

3.1. Controls on heterotrophic respiration

Soil respiration rates varied greatly, ranging from 1.8 μ mol m⁻² s⁻¹ to 14.3 μ mol m⁻² s⁻¹ at the SR site and from 3.6 to 28.1 μ mol m⁻² s⁻¹ at the RP site. Soil respiration rate without litters was on average about 68% of that with litters. Annual R_h was apparently greater in RP than SR sites, and in treatment with litter than without litter inputs, suggesting that physical environment and the presence of litter had significant influences on annual R_h (Fig. 1). The average R_h of soils incubated at the RP site were 90% greater than that at the SR site in dry season and 30% greater in rainy seasons, regardless of litter inputs and soil origins (Table 1). Annual R_h was not affected by soil origin (SR versus RP) or litter type. There was a significant interaction between litter type and forest site, but there were no interactions among forest site, litter type, and soil origin, or between forest site and soil origin, or between litter type and soil origin (Fig. 1).

3.2. R_h Sensitivity to soil temperature and moisture

Temperature sensitivity of R_h (Q_{10}) was lower in litter removal treatments than those with litter (Fig. 2, Table 2). Soil origin, litter type or forest site did not significantly affect Q_{10} values of soil R_h . There was a significant interaction between soil origin and forest site where soil Q_{10} values appeared to be higher in foreign site than that in native sites. All other interactions were not significant.



Fig. 1. Means (\pm SD) of annual soil respiration rates (R_h) as affected by forest site, litter input, soil origin, and their interactions by the repeated measure ANOVA.

Note: Black bars represent Soil $_{SR}$ (Soil derived from SR); Grey bars represent Soil $_{RP}$ (Soil derived from RP); Site $_{SR}$ indicates incubation in SR; Site $_{RP}$ indicates incubation in RP; NL means no litter; L_{SR} means litter from SR; L_{RP} means litter from RP.

Table 1

Means (\pm SD) of soil R_h in a rubber plantation (site_{RP}) and a seasonal forest (site_{SR}) during rainy and dry seasons.

Treatments	Dry	Rainy	
site _{sr} site _{rp}	$\begin{array}{l} 2.94 \pm 0.14a \\ 5.61 \pm 0.30b \end{array}$	6.74 ± 0.54 a 8.88 ± 0.94 ab	



Fig. 2. Means (\pm SD) of the Q_{I0} of R_h as affected by forest site, litter input and soil origin by the mixed functions of ANOVA.

Note: Black bars represent Soil_{SR} (Soil derived from the SR); Grey bars represent Soil_{RP} (Soil derived from RP); Site_{SR} indicates incubation in SR; Site_{RP} indicates incubation in RP; NL means no litter; L_{SR} means litter from SR; L_{RP} means litter from RP; Q_{10} value was calculated using Eq. (2): $Q_{10} = e^{10b}$.

3.3. Soil environment and carbon pools

Soil temperature at the depth of 5 cm was 0.45 °C higher in the rainy season (May through November) in the RP site than in SR site (Table 3).

Table 2

Parameters of fitted equations with soil respiration rate (Eq. (1): $R_h = bT - 0.5 \left(\frac{M - M_0}{r}\right)^2$

ue							
Site	Parameter name	Treatments					
		NL Soil _{SR}	Soil _{RP}	Litter _{sR} Soil _{sR}	Soil _{RP}	Litter _{RP} Soil _{SR}	Soil _{RP}
SR	Intercept a	1.36	0.98	0.63	0.18	0.65	0.07
	Soil temperature (T) b	0.06	0.08	0.14	0.18	0.09	0.20
	Soil moisture (M) M ₀	31.21	29.16	31.53	30.49	26.73	23.49
	Soil moisture (M) c	13.43	9.40	6.95	8.01	22.22	13.91
	R^2	0.40	0.74	0.65	0.72	0.30	0.67
RP	Intercept a	0.45	2.18	0.19	1.32	0.19	0.73
	Soil temperature (T) b	0.13	0.07	0.18	0.09	0.18	0.16
	Soil moisture (M) <i>M</i> ₀	29.94	28.62	28.92	30.77	30.73	32.20
	Soil moisture (M) c	10.55	9.57	11.11	12.49	10.94	6.92
	R^2	0.59	0.44	0.63	0.45	0.65	0.51

Soil moisture was also 3.3% greater in the RP site than in the SR site for both the dry and wet seasons or for the entire year (Table 3). Furthermore, soil moisture was greater with SR litter than RP litter in the rainy season, and in the SR soil than the RP soil for both dry and rainy seasons.

Table 3 Average temperature and moisture in soil mesocosms in rainy and dry seasons

Litter input increased soil moisture compared with treatment without litter input. There was higher annual litterfall mass in SR (8.4 ± 0.9 t ha⁻¹ a⁻¹) than RP (7.6 ± 0.4 kg ha⁻¹ a⁻¹) with apparent more canopy opening in the latter. Canopy opening was further enhanced in January and February in RP (Fig. 3) when rubber trees senescence their leaves, which would lead to higher soil temperature in RP than SR sites during the dry season.

Soils derived from SR (Soil_{SR}) still had higher C and N contents and microbial biomass than those from RP (Soil_{RP}) under the same treatments (Fig. 4). TOC, LOC and MBC ranged from 17.09 to 28.97 g kg⁻¹, 0.83 to 2.20 g kg⁻¹, and 0.34 to 0.70 g kg⁻¹ in SR soil; and from 14.96 to 20.65 g kg⁻¹, 0.57 to 1.37 g kg⁻¹, and 0.26 to 0.63 g kg⁻¹ in RP soil, respectively. Soils without litter cover had lower TOC contents than those with litter. There was no significant difference in soil TOC content between treatments of L_{SR} and L_{RP}. Soil respiration rate was positively correlated with soil temperature and moisture, rather than soil C pools in dry seasons (Table 4). No correlations were found between Q_{10} and soil carbon pools.

4. Discussion

Reduction in TOC following conversion from SR to RP may have resulted from one or more of these factors: improved physical environment for decomposition, improved quality of organic C for decomposition, reduced litter input, and increased biotic activity in decomposition. In this study, soil R_h in RP site was overall higher than that in SR site, whereas aboveground litter input and soil origin had no significant

	Temperature (°C)			Moisture (v/w)	Moisture (v/w)		
Treatments	Dry	Rainy	Annual	Dry	Rainy	Annual	
site _{sR}	$21.52{\pm}0.20$	$25.43 {\pm} 0.04$	$23.58 {\pm} 0.16$	$21.49 {\pm} 0.58$	42.38±0.48	$27.02{\pm}0.98$	
site _{RP}	$21.12{\pm}0.20$	$25.88 {\pm} 0.04$	$23.40 {\pm} 0.16$	$24.63 {\pm} 0.58$	47.6±0.48	$30.37 {\pm} 0.98$	
	<i>p</i> =0.1651	p < 0.001	<i>p</i> >0.05	p = 0.001	p < 0.001	p = 0.016	
NL	$21.17{\pm}0.24$	$25.70 {\pm} 0.05$	$23.39 {\pm} 0.19$	$22.17 {\pm} 0.70$	$43.16 {\pm} 0.60$	$27.42{\pm}1.19$	
litter _{SR}	$21.36 {\pm} 0.24$	$25.62{\pm}0.05$	$23.51 {\pm} 0.19$	$23.51 {\pm} 0.70$	45.64±0.60	$29.05{\pm}1.19$	
litter _{RP}	$21.43 {\pm} 0.24$	$25.65 {\pm} 0.05$	$23.57 {\pm} 0.19$	$24.12{\pm}0.70$	44.24±0.60	$29.63{\pm}1.19$	
	<i>p</i> >0.05	<i>p</i> >0.05	<i>p</i> >0.05	<i>p</i> =0.1401	p = 0.0016	<i>p</i> =0.4020	
Soil _{SR}	$21.37 {\pm} 0.20$	$25.63 {\pm} 0.04$	$23.52{\pm}0.16$	$24.33 {\pm} 0.58$	45.74±0.48	$29.68{\pm}0.98$	
Soil _{RP}	$21.26 {\pm} 0.20$	$25.68 {\pm} 0.04$	$23.46 {\pm} 0.16$	$22.21 {\pm} 0.58$	$44.23 {\pm} 0.48$	$27.71 {\pm} 0.98$	
	<i>p</i> >0.05	<i>p</i> >0.05	<i>p</i> >0.05	p = 0.0103	p = 0.0324	<i>p</i> =0.1571	



Fig. 3. Seasonal litterfall rate in the seasonal rain forest (SR) and rubber plantation (RP).



Fig. 4. Effects of site, litter type and soil source on means (SD) of (A) soil total organic carbon (TOC), (B) nitrogen (TN), (C) microbial biomass carbon (MBC) and (D). labile organic carbon (LOC).

Notes: Results of three-way ANOVA are showed in the figures, with absence of interactions among the three factors. * and ** Indicate significant difference between RP and SR soils for each litter treatment and incubation site at 0.01 and <math>p < 0.01, respectively.

Table 4 Correlation coefficient (r) between soil respiration and soil environment conditions and properties

Season	Temperature	Moisture	TOC	TN	C/N	LOC	MBC
Rainy	ns	-0.29*	ns	-0.31*	0.26*	Ns	-0.27*
Dry	0.38**	0.52**	ns	ns	ns	Ns	ns

Note: TOC indicates soil total organic carbon; TN for soil total nitrogen; LOC for labile organic carbon; MBC for soil microbial biomass carbon; C/N is the ratio of TOC to TN; and ns indicates no significant difference.

* and ** Indicate significant difference between treatments at 0.01 and <math>p < 0.01, respectively.

influences on R_h . Higher C/N ratio (Zhang et al., 2013) of RP litter (42.5±1.0) than SR (27.6 ± 4.1) and lower RP litter production did not appear to influence soil R_h . Furthermore, there were no differences in soil MBC, and LOC between treatments of RP and SR litter or incubation sites. Our data suggested that physical environment became the main control for the increased soil R_h following conversion from SR to RP, rather than changes in aboveground litter mass, litter decomposability and soil biochemical properties, and consequently reduced TOC in RP.

Compared with SR, higher soil temperature and moisture were usually found in RPs (Zhu et al., 2018; Lang et al., 2020). Soil moistures in various treatments at RP sites were higher than those at SR, but soil temperature was not significantly different between RP and SR sites except in the rainy season when RP soil was 0.45 °C warmer than the SR soil, likely due to the increased light level following the peak litterfall near the end of dry season. First, conversion of SR to RP resulted in less vegetation and reduced canopy cover. Canopy openness is recognized as a key driver of below-canopy microclimate following the conversion from SR to RP, which were found positively related to air temperature and soil temperature (Meijide et al., 2018). Second, conversion from SR to RP changed multi-layered canopy into single-layered canopy induced decreased canopy cover, increased throughfall water and reduced water transpiration, consequently increased soil water content (Zhu et al., 2018).

Either with or without litter present, both the RP and SR soils delivered at least 30% more CO_2 efflux when they were incubated at the RP site than at the SR site in the dry season. The elevated soil moisture and temperature were likely a key factor regulating soil respiration in RP. Hawakes et al., (2017) found the sensitivity of soil respiration to

moisture increased with increasing rainfall and litter mass, resulting in greater C loss in historically wetter soils than historically drier soils. In tropical regions, soil respiration is more sensitive to moisture than to temperature (Fernández-Alonso, et al., 2018), resulting in more rapid soil C loss in the tropical soils than in the temperate soils due to land-use changes. Lang et al. (2017) reported similar results that soil moisture was 40% higher in August in a RP than in a natural forest in Xish-uangbannan, SW China. In our study, R_h responded more sensitively to changes in soil moisture with an exponent power of 2 than to temperature with an exponent power of 1. Soil respiration became suppressed during the rainy season even with higher soil temperature in the RP than the SR site, likely due to over-saturation that might inhibit the decomposition and/or alter CO₂ pathways through dissolution into soil solution (Lang et al., 2017).

Theoretically, increase of R_h in RP can be caused by changes in soil biochemical properties. However, we found that soil microbial biomass, soil labile organic carbon, soil total organic carbon and soil total nitrogen were not affected by forest site or by litter type, but were affected only by the origin of soils with no interactions with other factors, suggesting that the elevated R_h in RP was not caused by changes of soil biochemical properties. However, invasion of soil animals occurs often after land-use changes. Exotic Pontoscolex corethrurus became a dominant earthworm in RPs of Xishuangbanna with an average population density of 182 \pm 29 ind m⁻² compared with only 89 ind.m⁻² in SR, dominated by native species (Yu, 2007). Our earlier study with 20-months field incubation showed that Pontoscolex corethrurus invasion induced a decrease of 6% total TOC and increased the turnover rate of soil labile organic carbon in the surface soil layer of RPs (Zhang et al., 2010). A global meta-analysis shows that earthworm density correlated linearly with litter mass loss and TOC decay (Huang et al., 2020). Earthworms can increase soil respiration primarily by increasing the proportion of bacteria or lowering fungi-to-bacteria ratio, because bacteria have a higher turnover rate and lower carbon assimilation efficiency than fungi. In contrast, P. corethrurus was reported to have no effect on soil respiration through stabilizing organic carbon to form large macro-aggregates (Wu et al., 2017). Because we rarely saw earthworms present in our soil mesocosms that were constructed with 53 µm nylon mesh to prevent the entry of earthworms, the difference in soil respiration between SR and RP sites were unlikely caused by earthworms in this study.

Changes in litter input following land-use conversion can also be an important factor altering soil $R_{\rm h}$. The presence of either SR or RP litter elevated soil $R_{\rm h}$ as expected. However, soil with RP litter decomposed faster (higher $R_{\rm h}$) in RP site than SR site, whereas soil with SR litter decomposed invariantly between the SR and RP sites (Fig. 1), suggesting a possible "home-court" advantage for RP litter decomposition in which plant litter decompose faster in its home site compared with "exotic" sites (Rodríguez-Calcerrada et al., 2019). This "home-court" advantage might be compensated by the accelerated decomposition in RP site for the SR litter. Regardless of reduced litter input, $R_{\rm h}$ is still greater in the RP site than in the SR site, suggesting combustion of existing organic carbon in the RP site. The improved microclimate conditions and a possible "home-court" advantage effect together might attribute to the elevated $R_{\rm h}$ in the RP sites.

We found that Q_{10} of R_h was negatively related to temperature and positively to moisture, consistent with previous results (Suseela et al., 2012). Furthermore, Q_{10} increased when soils were transplanted to a foreign forest site in this study. Bai et al. (2017) suggested a tightly coupled relationship between Q_{10} and microbial trophic guilds: the copiotrophic prokaryotes responded positively to high Q_{10} values, while the oligotrophs showed a negative response. Salazar et al. (2019) suggested that the response of R_h to temperature was stronger when soil contains more active microbes. Higher Q_{10} in foreign forest site may be caused by the dominance of copiotrophic strategists. In this study we showed that Q_{10} increased when nutrient-rich plant litter was added to soils, suggesting a dominance of copiotrophic strategists with litter addition treatment. Although Q_{10} of R_h was not affected after converting SR to RP, itwas increased when soils were placed in exotic sites with altered environmental conditions. This might also attribute to the reduction of TOC in RP immediately following the land-use conversion since there appeared to have an "exotic-court" advantage in Q_{10} of R_h .

The microbial community in rainforest is dominated by fungi that can decompose cellulose and lignin in litter (Schneider et al. 2012). Removal of forest litter might decrease the fungi to bacteria (F/B) ratio in the soil. Since most fungi have a higher C use efficiency than bacteria (Keiblinger et al. 2010), a shift in the F-B ratio is likely to affect soil CO₂ emissions. Previous studies found that aboveground litter does not influence microbial community composition of mineral soils in long term (Creamer et al., 2015; Leitner, et al., 2016). Removal of above-ground litter results in removal of young carbon that may result in alteration of microbial community. Lan (2020) found conversion from SR to RP resulted in shifts in soil bacterial composition (from the Proteobacteria to Chloroflexi), Archaeal composition (from Thaumarchaeota to Bathyarchaeota), and fungal composition (from Basidiomycota to Ascomycota). Compared with that in SR, the RP leaf litter is poorer in N and lignin. This would favor Ascomycota at the expense of Basidiomycota which contain many lignin decomposers and other specialists on recalcitrant substrates. The more sunlight would benefit chloroflexi in RP.

In conclusion, our study clearly suggested that the increase of soil R_h in RP was resulted from an elevated soil moisture condition. Both R_h and its temperature sensitivity were substantially lower when litter was absent. Although temperature sensitivity of R_h was not influenced by litter type, soil origin, and forest site, it was elevated when soils were incubated in foreign forest site, suggesting likely an "exotic-court" advantage effect. Converting SR to RP can lead to decrease in soil organic carbon stock through accelerating soil heterotrophic respiration and elevating its temperature sensitivity following tropical land-use changes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was financially supported by the Asia-Pacific Network for Global Change Research (ARCP2008-19NMY).

References

- Ahrends, A, Hollingsworth, PM, Ziegler, A., Fox, JM, Chen, H, Su, Y, Xu, J, 2015. Current trends of rubber plantation expansion may threaten biodiversity and livelihoods. Global Environmental Change 34, 48–58. https://doi.org/10.1016/j. gloenycha.2015.06.002.
- Baccini, A, Goetz, SJ, Walker, WS, Laporte, NT, Sun, M, Sulla-Menashe, D, Hackler, J, Beck, PSA, Dubayah, R, Friedl, MA, Samanta, S, Houghton, RA, 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nature Climate Change 2. 182–185. https://doi.org/10.1038/nclimate1354.
- Bai, Z, Xie, H, Kao-Kniffin, J, Chen, B, Shao, P, Liang, C, 2017. Shifts in microbial trophic strategy explain different temperature sensitivity of CO₂ flux under constant and diurnally varying temperature regimes. FEMS Microbiology Ecology 93, 5. https:// doi.org/10.1093/femsec/fix063.
- Barba, J., Curiel Yuste, J., Poyatos, R., Janssens, I.A., Lloret, F., 2016. Strong resilience of soil respiration components to drought-induced die-off resulting in forest secondary succession. Oecologia 182, 27–41. https://doi.org/10.1007/s00442-016-3567-8.
- Cao, M, Zhang, JH, 1996. Tree species composition of a seasonal rain forest in Xishuangbanna, Southwest China. Tropical Ecology 37, 183–192. http://ir.xtbg.org. cn/handle/353005/5797.
- Cao, M, Zou, X, Zhu, WH, 2006. Tropical forests of Xishuangbanna, China. Biotropica 38, 306–309. https://doi.org/10.1111/j.1744-7429.2006.00146.x.
- Chen, H, Yi, Z, Schmidt-Vogt, D, Ahrends, A, Beckschäfer, P, Kleinn, C, Ranjitkar, S, Xu, J, 2016. Pushing the limits: the pattern and dynamics of rubber monoculture expansion in Xishuangbanna, SW China. PLoS One 11, e0150062. https://doi.org/ 10.1371/journal.pone.0150062.
- Creamer, CA, De Menezes, AB, Krull, ES, Sanderman, J, Newton-Walters, R, Farrell, M, 2015. Microbial community structure mediates response of soil C decomposition to

M. Zhang et al.

litter addition and warming. Soil Biology & Biochemistry 80, 175–188. https://doi.org/10.1016/j.soilbio.2014.10.008.

FAOSTAT, 2019. Food and agriculture data. Crops. Retrieved from: www.fao. org/faostat/en/#data/QC.

- Fernández-Alonso, MJ, Eugenio, D-P, Ortiz, C, Rubio, A, 2018. Disentangling the effects of tree species and microclimate on heterotrophic and autotrophic soil respiration in a Mediterranean ecotone forest. Forest Ecology and Management 430, 533–544. https://doi.org/10.1016/j.foreco.2018.08.046.
- González, G, Seastedt, TR, 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82, 955–964. https://doi.org/10.2307/2679895.
- Goulden, ML, Munger, JW, Fan, SM, Daube, BC, Wofsy, SC, 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271, 1576–1578. https://doi.org/10.1126/science.271.5255.1576.
- Harris, NL, Brown, S, Hagen, SC, Saatchi, SS, Petrova, S, Salas, W, Hansen, MC, Potapov, PV, Lotsch, A, 2012. Baseline map of carbon emissions from deforestation in tropical regions. Science 336, 1573–1576. https://doi.org/10.1126/ science.1217962.
- Hawkes, CV, Waring, BG, Rocca, JD, Kivlin, SN, 2017. Historical climate controls soil respiration responses to current soil moisture. Proceedings of the National Academy of Sciences of the United States of America 114, 6322–6327. https://doi.org/ 10.1073/pnas.1620811114.
- Hou, P, Zou, X, Huang, CY, Chien, HJ, 2005. Plant litter decomposition influenced by soil animals and disturbance in a subtropical rainforest of Taiwan. Pedobiologia 449, 539–547. https://doi.org/10.1016/j.pedobi.2005.07.001.
- Huang, W, González, G, Zou, X, 2020. Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: A global metaanalysis. Applied Soil Ecology 150, 103473. https://doi.org/10.1016/j. apsoil.2019.103473.
- Jenkinson, DS, Powlson, DS, 1976. The effects of biocidal treatment on metabolism in soil-V: a method for measuring soil biomass. Soil Biology and Biochemistry 8, 209–2013. https://doi.org/10.1016/0038-0717 (76)90005-5.
- Jiang, XJ, Liu, W, Wu, J, Wang, P, Liu, C, Yuan, ZQ, 2017. Land degradation controlled and mitigated by rubber–based agroforestry systems through optimizing soil physical conditions and water supply mechanisms: a case study in Xishuangbanna, China. Land Degradation & development 28, 2277–2289. http://ir.xtbg.org.cn/ handle/353005/10671.
- Keiblinger, KM, Hall, EK, Wanek, W, Szukics, U, Hammerle, I, Ellersdorfer, G, Bock, S, Strauss, J, Sterflinger, K, Richter, A, Zechmeister-Boltensterm, S, 2010. The effect of resource quantity and resource stoichiometry on microbial carbon-use-efficiency. FEMS Microbiology Ecology 73, 430–440. https://doi.org/10.1111/j.1574-6941.2010.00912.x.
- Kotowska, MM, Leuschner, C, Triadiati, T, Hertel, D, 2016. Conversion of tropical lowland forest reduces nutrient return through litterfall, and alters nutrient use efficiency and seasonality of net primary production. Oecologia 180, 601–618. https://doi.org/10.1007/s00442-015-3481-5.
- Kuzyakov, Y, 2005. Sources of CO2 efflux from soil and review of partitioning methods. Soil Biology & Biochemistry 38, 425–448. https://doi.org/10.1016/j. soilbio.2005.08.020.
- Lan, G, Wu, Z, Yang, C, Sun, R, Chen, B, Zhang, X, 2020. Forest conversion alters the structure and functional processes of tropical forest soil microbial communities. Land Degradation & Development 1-15. https://doi.org/10.1002/ldr.3757.
- Lang, R, Blagodatsky, S, Xu, J, Cadisch, G, 2017. Seasonal differences in soil respiration and methane uptake in rubber plantation and rainforest. Agriculture, Ecosystems and Environment 240, 314–328. https://doi.org/10.1016/j.agee.2017.02.032.
- Lang, R, Goldberg, SD, Blagodatsky, S, Piepho, HP, Cadisch, G, 2020. Mechanism of methane uptake in profiles of tropical soils converted from forest to rubber plantations. Soil Biology and Biochemistry 145, 107796. https://doi.org/10.1016/j. soilbio.2020.107796.
- Leitner, S, Sae-Tun, O, Kranzinger, L, Zechmeister-Boltenstern, S, Zimmermann, M, 2016. Contribution of litter layer to soil greenhouse gas emissions in a temperate beech forest. Plant & Soil 403, 455–469. https://doi.org/10.1007/s11104-015-2771-3.
- Liu, W, Liu, W, Lu, H, Duan, W, Li, H, 2011. Runoff generation in small catchments under a native rain forest and a rubber plantation in Xishuangbanna, southwestern China. Water and Environment Journal 25, 138–147. http://ir.xtbg.org.cn/handle/353 005/688.
- Meijide, A, Badu, CS, Moyano, F, Tiralla, N, Gunawan, D, Knohl, A, 2018. Impact of forest conversion to oil palm and rubber plantations on microclimate and the role of the 2015 ENSO event. Agricultural and Forest Meteorology 252, 208–219. https:// doi.org/10.1016/j.agrformet.2018.01.013.

- Ren, YH, Cao, M, Tang, JW, 1999. A comparative study on litterfall dynamics in a seasonal rain forest and a rubber plantation in Xishuangbanna, SW China. Acta Phytoecolog ica Sinica 23, 418–425, 1999in Chinese abstract.
- Rodríguez-Calcerrada, J, Salomón, R, Barba, J, Gordaliza, GG, Gil, L, 2019. Regeneration in the understory of declining overstory trees contributes to soil respiration homeostasis along succession in a sub-mediterranean beech forest. Forests 10, 727. https://doi.org/10.1007/s10310-002-0022-y.
- Salazar, A, Lennon, JT, Dukes, JS, 2019. Microbial dormancy improves predictability of soil respiration at the seasonal time scale. Biogeochemistry 144, 103–116. https:// doi.org/10.1007/s10533-019-00574-5.
- Schneider, T, Keiblinger, KM, Schmid, E, Sterflinger-Gleixner, K, Riedel, K, 2012. Who is who in litter decomposition? Metaproteomics reveals major microbial players and their biogeochemical functions. The ISME Journal 6, 1749–1762. https://doi.org/ 10.1038/ismej.2012.11.
- Song, QH, Deng, Y, Zhang, Y, Deng, X, Lin, Y, Zhou, L, Fei, X, Sha, L, Liu, Y, Zhou, W, Gao, J, 2017. Comparison of infrared canopy temperature in a rubber plantation and tropical rain forest. International Journal of Biometeorology 61, 1885–1892. https://doi.org/10.1007/s00484-017-1375-4.
- Sulzman, EW, Brant, JB, Bowden, RD, Lajtha, K, 2005. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest. Biogeochemistry 73, 231–256. https://doi.org/ 10.1007/s10533-004-7314-6.
- Suseela, V, Conant, RT, Wallenstein, MD, Dukes, JS, 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old field climate change experiment. Global Chang Biology 18, 336–348. https://doi.org/ 10.1111/j.1365-2486.2011.02516.x.
- Tremblay, SL, D'orangeville, L, Lambert, M-C, Houle, D, 2018. Transplanting boreal soils to a warmer region increases soil heterotrophic respiration as well as its temperature sensitivity. Soil Biology and Biochemistry 116, 203–212. https://doi.org/10.1016/j. soilbio.2017.10.018.
- Tuomi, M, Vanhala, P, Karhu, K, Fritze, H, Liski, J, 2008. Heterotrophic soil respirationcomparison of different models describing its temperature dependence. Ecological Modelling 211, 182–190. https://doi.org/10.1016/j.ecolmodel.2007.09.003.
- Wall, DH, Bradford, MA, St. John, MG, Trofymow, JA, Behan-Pelletier, V, Bignell, DE, Dangerfield, JM, Parton, WJ, Rusek, J, Voigt, W, 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate dependent. Global Change Biology 14, 2661–2677. https://doi.org/10.1111/j.1365-2486.2008.01672.x.
- Wu, J, Li, H, Zhang, W, Li, F, Huang, J, Mo, Q, Xia, H, 2017. Contrasting impacts of two subtropical earthworm species on leaf litter carbon sequestration into soil aggregates. Journal of Soils and Sediments 17 (6), 1672–1681. https://doi.org/ 10.1007/s11368-017-1657-9.
- Yang, X, Blagodatsky, S, Lippe, M, Liu, F, Hammond, J, Xu, J, Cadisch, G, 2016. Land use change impact on time-averaged carbon balances: rubber expansion and reforestation in a biosphere reserve, South-West China. Forest Ecology and Management 372, 149–163. https://doi.org/10.1016/j.foreco.2016.04.009.
- Yu, GB, 2007. Effects of earthworm on soil microbial growth activity in tropical forests in Xishuangbanna, SW China. Master's thesis. Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan, pp. 5–6.
 Zhang, M, Schaefer, DA, Chan, OC, Zou, X, 2013. Decomposition differences of labile
- Zhang, M, Schaefer, DA, Chan, OC, Zou, X, 2013. Decomposition differences of labile carbon from litter to soil in a tropical rain forestrainforest and rubber plantation of Xishuangbanna. European Journal of Soil Biology 55, 55–61. https://doi.org/ 10.1016/j.ejsobi.2012.12.003.
- Zhang, M, Zou, X, Schaefer, D, 2010. Alteration of soil labile organic carbon by invasive earthworms (*Pontoscolex corethrurus*) in tropical rubber plantations. European Journal of Soil Biology 46, 74–79. https://doi.org/10.1016/j.ejsobi.2009.11.004.
- Zhu, H, Cao, M, Hu, H, 2006. Geological history flora, and vegetation of Xishuangbanna, Southern Yunnan, China. Biotropica 38, 310–317. https://doi.org/10.1111/j.1744-7429.2006.00147.x.
- Zhu, X, Liu, W, Jin, JX, Wang, P, Li, W, 2018. Effects of land-use changes on runoff and sediment yield: implications for soil conservation and forest management in Xishuangbanna. SW china. Land Degradation and Development 29, 1–13. https:// doi.org/10.1002/ldr.3068.
- Zou, X, Ruan, HH, Fu, Y, Yang, XD, Sha, L, 2005. Estimating soil labile organic carbon and potential turnover rates using a sequential fumigation incubation procedure. Soil Biological and Biochemistry 1923–1928. https://doi.org/10.1016/j. soilbio.2005.02.028.