

Characteristics of root decomposition based on *in situ* experiments in a tropical rainforest in Sarawak, Malaysia: impacts of root diameter and soil biota

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Abstract

Aims Tropical forests contribute significantly to the stability of global carbon (C) balance; however, little is known about root litter decomposition in tropical rainforests. In this study, we aimed to (1) characterise the effect of soil depth, root diameter and soil organisms on root litter decomposition and (2) estimate the contribution of root decomposition to soil carbon dioxide (CO₂) efflux in a tropical rainforest in Malaysian Borneo.

Methods We incubated soil chambers with fine and coarse root litterbags at varying soil depths. Soil chambers were covered with nets of different mesh sizes, and

CO₂ efflux was monitored from the top of each soil chamber during the incubation.

Results Our results showed that coarse roots decomposed faster than fine roots. There was no impact of soil depth, but soil animals and fungi had a significant impact on coarse root decomposition from 398 days after the start of the experiment. Soil CO₂ efflux increased linearly with C loss from root decomposition, indicating that 40% of the CO₂ efflux originates from root litter.

Conclusions The variation in root decomposition rates suggests the possible role of root litter in soil C storage and emission in a tropical rainforest.

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Introduction

Tropical forests store large amounts of carbon (C) and the annual C input in tropical forests is much higher than that in other forest ecosystems (Malhi et al. 1999). Tropical forests contain nearly 55% of all the C stored in the world's forested ecosystems (Pan et al. 2011), and CO₂ fluxes in these area are two- to fivefold faster than those in temperate or boreal forests (Luyssaert et al. 2007). Therefore, tropical forests contribute significantly to the stability of global carbon balance.

Belowground roots play an important role in forest carbon cycling. Up to 60% of the photosynthetic products of trees are allocated to belowground parts (Litton et al. 2007). Roots are dynamic and especially fine roots are short-lived, supplying considerable input to belowground litter (Finér et al. 2011). Freschet et al. (2013) estimated that nearly half of the forest litter is originally produced in belowground parts. This suggests that root litter decomposition strongly relates to soil C sequestration (Rasse et al. 2005) and could be one of the main processes driving heterotrophic carbon dioxide (CO₂) fluxes from forest soil (Silver et al. 2005; Cong et al. 2015). Several studies have been conducted in tropical forests to clarify the mechanisms of spatiotemporal variation in soil CO₂ efflux (e.g. Kosugi et al. 2007; Ohashi et al. 2008). However, the contribution of root litter decomposition to soil heterotrophic CO₂ efflux remains unexplored in tropics.

The root decomposition rate varies globally and locally, temporally and spatially, and within and between species depending on various factors. Meteorological factors such as temperature, rainfall and evaporative demand affect global patterns of root decomposition (Silver and Miya 2001). Soil conditions, such as soil temperature, moisture, carbon-to-nitrogen (C:N) ratio and pH, relate to local variation in root decomposition rate between (Solly et al. 2014; Guerrero-Ramírez et al. 2016) and within ecosystems (Arunachalam et al. 1996). In a tropical forest, soil conditions vary with depth, showing clear vertical variation in soil particle size, litter accumulation, organic carbon and nutrient concentrations (Baillie et al. 2006). Changes in soil condition with soil depth can cause variation in root decomposition rate within an ecosystem (Solly et al. 2015), but we know

little about the absolute changes in root decomposition rate relative to soil depth in tropical forests.

Root diameter could be another factor influencing root decomposition in tropical forests. Fine roots (diameter < 2 mm in many cases) decompose faster than small and coarse roots (diameter ≥ 2 mm in many cases) in several ecosystems (Silver and Miya 2001; Sariyildiz 2015). However, recent study has shown that there were no differences in low-latitude areas (Zhang and Wang 2015). Additionally, Sun et al. (2013) reported that lower-order roots decompose slower than higher-order roots because they are chemically more resistant to decomposition. These studies suggest that fine roots might be more chemically resistant to decomposition in a tropical forest, causing slow decomposition as coarse roots. However, few studies have determined the differences in root decomposition rate and chemical properties among varying root sizes in the tropics (Fujimaki et al. 2008).

Biological regulation of root litter decomposition remains almost unexplored in tropical forests. Although fungi and bacteria are the main decomposers globally, soil macrofauna, such as ants, termites and earthworms, have a significant effect on leaf litter decomposition in tropical forests (Gonzalez and Seastedt 2001; Yang and Chen 2009). Recently, Briones (2014) suggested that soil macrofauna could have a more significant effect on organic matter mineralisation than other soil biota under tropical climate conditions. The relative contribution of different microorganisms, fungi and bacteria, to root decomposition is also unknown. Evaluating the contribution of each group of soil organisms on root decomposition is necessary to understand soil C dynamics in tropical forests.

The first aim of this study is to characterise root litter decomposition in a tropical rainforest in Sarawak, Malaysian Borneo, based on soil depth, root diameter and soil organisms. We incubate soil chambers with root litterbags after equalising initial soil condition to minimise errors caused by high spatial forest soil heterogeneity on this island (Baillie et al. 2006). Soil chambers are covered with different size meshes to control the effects of soil animals, fungi and bacteria, as suggested by Heinemeyer et al. (2007). The second aim of this study is to estimate the contribution of root decomposition to soil CO₂ efflux. To this end, we monitor soil CO₂ effluxes from the top of incubation chambers where root litterbags with different decomposers are enclosed.

Material and methods

Study site

This study was conducted at Lambir Hills National Park in Sarawak, Malaysia (4° 12' N, 114° 02' E, 200 m a.s.l.). This park has an area of 6500 ha and is located 10,000 m from the sea. Between 2000 and 2009, the mean annual rainfall at the study site was 2600 mm. The mean annual temperature was 26 °C for the same period, with indistinctive seasonal variation (Kumagai et al. 2005). The major area of this park is covered by mixed dipterocarp forest containing various types of dipterocarp trees, such as *Dryobalanops aromatica* Gaertn. f. and *Shorea beccariana* Burck. The continuous canopy of this forest grows about 40 m tall with emergent trees exceeding 50 m. Soils were classified as ultisols with a high sand, low clay, and high porosity (62–72, 15–22 and 54–68%, respectively), and low pH (4–4.3) (Ishizuka et al. 1998). Total nitrogen and carbon contents were very variable in space and relatively high in the A horizon (0–5 cm), 17–115 g kg⁻¹ and 1.7–4.2 g kg⁻¹, respectively, but decreased to 0.1–11.0 g kg⁻¹ and 0.1–0.6 g kg⁻¹ in deeper horizons (Ishizuka et al. 1998).

Root litterbag and soil chamber

We established three 20 × 20-m plots, namely P1, P2 and P3, in the park. Each plot was 50–100 m apart from the other two plots. Root samples for the litterbags were collected in advance from each plot using a soil corer with 10-cm diameter and 30-cm length. In each plot, we randomly collected soil core from surface to 30-cm depth at 36 locations. The holes made by the core sampling were used for soil chamber incubation later.

All roots in each soil core were extracted manually using forceps and oven-dried at 50–60 °C for > 48 h (Ohashi et al. 2015). Root litterbags were made from a casting net of synthetic fabric with 6-mm mesh size. Two kinds of root litterbag with sizes of 5 × 5 cm and 20 × 20 cm were prepared for enclosing 5 g of fine roots with a diameter of < 2 mm (Finér et al. 2011) and 80 g of coarse roots with a diameter of 2–10 mm.

Root litterbags were placed in soil chambers 10 cm wide and 30 cm long, where soil was once taken out and filled back after all living roots, detritus and mycelium in the soil were removed by washing with water to equalise the initial soil condition. Soil chambers were

made of plastic net with 2-cm mesh size, and three chamber types were prepared. One of the three chamber types had no cover (SC_{NC}), and the other two were covered by polyamide nets with 50- μ m (SC₅₀) and 1- μ m (SC₁) mesh sizes to control the access of soil organisms (Supplementary Fig. S1). The SC_{NC} chamber allowed all living organisms, soil animals, roots and microbes, to access the root litter. The SC₅₀ chamber allowed fungal mycelium, bacteria and microfauna to access the chamber but excluded tree roots (Heinemeyer et al. 2007, Osawa and Aizawa 2012). The SC₁ allowed only bacteria to access the chamber (e.g. Heinemeyer et al. 2007; Moyano et al. 2008).

We placed two coarse root litterbags in the upper (0–15 cm) and lower (15–30 cm) parts of each chamber and one fine root litterbag in one of the three soil depths: top (0–10 cm), middle (10–20 cm) or bottom (20–30 cm) (total of three litterbags per chamber). Fine root litterbags were placed in each of the three depths for every chamber type, SC_{NC}, SC₅₀ and SC₁ chambers. This means 9 types of chambers with fine root litterbag in 3 different depths (top, middle, bottom) and 3 different net covers (SC_{NC}, SC₅₀, SC₁) were prepared. Note that all types had two coarse root litterbags.

We collected the 9 types of soil chambers from each plot in four different periods over 27 months, meaning 36 chambers (9 chamber types × 4 periods) were installed in each plot. The installation of 108 soil chambers in total (9 chamber types × 4 periods × 3 plots) was conducted in February 2013 (T0) and the chamber sampling was conducted at 134 days (T1), 226 days (T2), 398 days (T3) and 763 days (T4) after installation.

After the soil chambers were collected, root litterbags were removed. Litter samples were carefully isolated from surrounding soil and organic matter, and soil particles were removed gently taking care to avoid mass loss. Two of 216 coarse root and five of 108 fine root samples were not used for further analysis because of the failure of sample manipulation. The remaining roots were dried at 50–60 °C for > 48 h and then weighed (Ohashi et al. 2015).

Chemical analysis of root litter

To determine the initial quality of root samples, three fine and coarse root subsamples were collected from 0- to 30-cm depth at three locations outside of the plot or 18 subsamples in total. Root subsamples were ground and total C and N concentrations were determined using

an elemental analyser (FLASH 2000, Thermo Fisher Scientific, MA). Concentrations of aluminium (Al), calcium (Ca), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), silica (Si) and phosphorus (P) were analysed after wet-ashing in $\text{HNO}_3 + \text{HClO}_4$ using inductively coupled plasma emissions spectrometry (iCAP 6300-ICP-OES, Thermo Fisher Scientific).

Soil CO_2 efflux

CO_2 efflux from each soil chamber (F_s , $\text{gCO}_2 \text{ m}^{-2} \text{ h}^{-1}$) was measured once a month. A commercial respiration chamber (SRC-1, PP-system, Hitchin, UK) and infrared gas analyser (EGM-4, PP-systems) were used following the methods of Ohashi et al. (2008). We inserted PVC collars (height 3–4 cm, diameter 10 cm) at each measurement point at least 0.5 cm deep to mount the commercial respiration chamber. The collars were set up one day before the first soil CO_2 measurement and left in place throughout the experiment. The top of each collar was covered by a 15×15 -cm mesh sheet with 1.5-cm hole size to prevent leaf litter falling into the chamber. Each measurement was taken as the average value of 3–5 repeated measurements.

Data analysis and statistical analysis

The decomposition rate (k) was calculated using a simple negative exponential decay model proposed by Olson (1963): $M_t = M_0 \exp(-kt)$, where M_t is the percentage of dry mass (DM) remaining at time t , and M_0 is the initial percentage of DM, 100.

Concentrations of each chemical in initial root samples were compared between fine and coarse roots using paired T tests where fine and coarse root data collected from the same location were used as a pair.

We conducted linear mixed model analysis to compare the percentage of DM remaining in 0–30-cm soil chamber between fine and coarse roots at each sampling time. DM percentage was modelled as a function of the fixed factors, root diameter (coarse, fine), sampling time (T1, T2, T3, T4) and their combination. Sampling plot (P1, P2, P3) was included as a random factor. We also used linear mixed model analysis to determine the impact of soil depth and soil chamber type on remaining root DM for fine and coarse root litter, respectively. Root litter DM was the dependent variable and sampling time (T1, T2, T3, T4), depth (upper and lower for coarse roots; top, middle and bottom for fine roots), mesh size

of covering net (SC_{NC} , SC_{50} , SC_1) and their combinations were fixed factors. Sampling plot (P1, P2, P3) was again included as a random factor. In both analyses, Bonferroni post hoc tests were used to compare means when statistically significant differences were found.

To understand the contribution of root decomposition to total CO_2 emission, linear correlation analysis was used to determine the relationship between carbon loss from decomposition and carbon efflux from the soil surface for each soil chamber type. Carbon loss from the soil chamber through decomposition (gC) was estimated from the total amount of root litter loss. Carbon content in the litter was assumed to be half of root litter DM (Fujimaki et al. 2008). Total carbon efflux from the soil surface (gC) was estimated by scaling up soil CO_2 efflux, F_s ($\text{gCO}_2 \text{ m}^{-2} \text{ h}^{-1}$), in each measurement period. Since our previous studies found no clear temporal patterns in soil CO_2 efflux (Ohashi et al. 2007, 2008), we assumed that F_s is the representative rate of the month. We estimated daily carbon efflux of the month ($\text{gC m}^{-2} \text{ day}^{-1}$) by summing up F_s and then summed the carbon efflux from all installation period days ($\text{gC m}^{-2} \text{ period}^{-1}$) and multiplied by the respiration collar area (m^2) to estimate the total carbon efflux from the corresponding chamber ($\text{gC collar}^{-1} \text{ period}^{-1}$). The slope and intercept of the regression lines were compared between soil chamber types (SC_{NC} , SC_{50} , SC_1) using analysis of covariance (ANCOVA) with carbon loss from decomposition as a covariate.

All statistical analyses were performed using SPSS software ver. 22.0.0 (IBM Corp., Armonk, NY). For all statistical analyses, $P \leq 0.05$ was considered significant differences.

Results

N, Al, Ca, Fe, P and Si concentrations in the initial samples were significantly higher in fine roots than in coarse roots ($P < 0.05$), but no differences were observed in K, Mg, Mn and C concentrations (Table 1). N, Al, P and Si concentrations in fine roots were twofold higher than those in coarse roots. C:N and C:P ratios were significantly higher in coarse roots than in fine roots ($P < 0.05$).

Decomposition rates of coarse roots were significantly faster than those of fine roots in all chamber types through the whole experimental period (degree of freedom numerator = 1, degree of freedom denominator =

Table 1 Carbon and nutrient concentrations in coarse and fine roots. Carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), aluminium (Al), iron (Fe), manganese (Mn), silica (Si) concentration (mg gDM^{-1}) and C:N and

C:P ratios are shown. Standard deviations are noted in parenthesis ($n = 9$). Asterisks indicate statistically significant differences between the two root sizes with $P < 0.05$

	C mg g^{-1}	N mg g^{-1}	P mg g^{-1}	K mg g^{-1}	Ca mg g^{-1}	Mg mg g^{-1}	Al mg g^{-1}	Fe mg g^{-1}	Mn mg g^{-1}	Si mg g^{-1}	C mg g^{-1}	C:N gC gN^{-1}	C:P gC gP^{-1}
Coarse root	462 (14)	3.87 (0.54)	0.13 (0.02)	0.86 (0.27)	1.92 (0.79)	1.07 (0.66)	1.61 (0.66)	1.10 (0.59)	0.08 (0.04)	1.07 (0.45)	462 (14)	121.5 (17.5)	3519 (542)
Fine root	421 (10)	9.46 (1.42)	0.26 (0.07)	0.86 (0.44)	2.95 (0.79)	1.05 (0.44)	4.06 (1.48)	2.16 (0.52)	0.08 (0.04)	3.09 (0.48)	471 (10)	50.7 (6.7)	1872 (394)
		*	*		*		*	*		*	*	*	*

300, F -value = 596, $P < 0.001$). After the first 3 months, nearly 60% of the coarse root litter was lost but only 20% in the fine root litter (Fig. 1). After two years, 89% and 60% of the coarse and fine roots had disappeared. Average decomposition constants (k -values, year^{-1}) over the treatments were $0.55 \pm 0.11\text{SD}$ for coarse roots and $0.37 \pm 0.005\text{SD}$ for fine roots (Table 2).

Our results showed no impact of soil depth on the decomposition rates of coarse and fine roots (Table 3). We found a significant difference in remaining coarse roots between different soil chambers in the later stage of decomposition, T3 and T4 (Table 3, Fig. 2a). With the presence of animals and fungi, the coarse roots decomposed faster in SC_{NC} compared to SC_{50} and SC_1 in T3 and T4. With the presence of fungi, coarse

root decomposition was faster in SC_{50} compared to SC_1 in T3 (Fig. 2a). In SC_{NC} , only 25% and 17% of coarse roots remained at T3 and T4, respectively, but in SC_{50} , 32% and 20% of roots still remained at these sampling times. In addition, 36% and 24% of the coarse roots remained in SC_1 soil chambers at T3 and T4. The decomposition constant for coarse roots decreased from 0.67 to 0.45 (Table 2). We found no significant difference in the percentage of remaining fine roots between the soil chamber types (Table 3, Fig. 2b).

We found a linear correlation between carbon flux from the soil and carbon loss by root decomposition (SC_{NC} , $r = 0.73$; SC_{50} , $r = 0.73$; SC_1 , $r = 0.82$; Fig. 3). Chamber types did not affect significantly on the slope and intercept of the correlation lines (slope, $F = 1.75$, $P = 0.16$; intercept, $F = 2.42$, $P = 0.07$). The coefficient of determination was highest in SC_1 where only bacteria access the root litter. The slope of correlation line of SC_1 was 0.40, suggesting that nearly 40% of the carbon lost through decomposition was emitted as CO_2 from the soil surface.

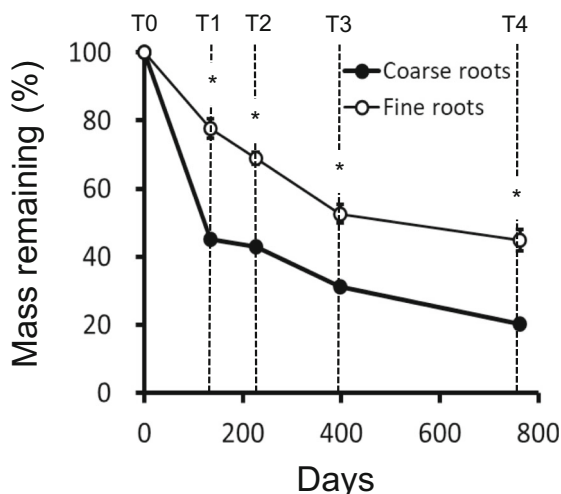


Fig. 1 Mass losses of coarse and fine root litter in soil chambers during a period of 2 years. Standard deviations are indicated ($n = 25$ –54). Asterisks indicate statistically significant differences between the two root sizes with $P < 0.05$. T0, T1, T2, T3 and T4 indicate the timing when litter bags were collected

Discussion

Impact of root diameter

Our results showed that coarse roots decomposed faster than fine roots in a tropical forest. Recently, Zhang and Wang (2015) conducted a meta-analysis of global root decomposition and found that fine roots with < 2 -mm diameter decomposed significantly faster than coarse roots with ≥ 2 -mm diameter in middle latitude areas, but their decomposition in low-latitude regions was not significantly different. Our results were totally

Table 2 Decomposition constant (k) calculated from single-exponential model

	Coarse root		Fine root	
	k	R^2	k	R^2
SC _{NC}	0.671	0.73	0.373	0.56
SC ₅₀	0.534	0.73	0.364	0.60
SC ₁	0.453	0.73	0.369	0.33

opposite to the cases in middle latitude in their study. Zhang and Wang (2015) attributed the slow decomposition rate of fine roots in low latitude to conifer roots in the fine root dataset because conifer root decomposition was slower than that of broadleaf roots. However, no conifer species were included in our root samples, suggesting conifer roots would not explain the slower decomposition of fine roots. Raich et al. (2009) showed that the fine root decomposition rate could vary widely among tropical tree species in lowland tropical forests. Since dipterocarp species are dominant in our study site, the slow decomposition of fine roots might have been partly attributed to the dipterocarp roots. Additional studies about the chemical composition and root property of dipterocarp species, which may have an influence on root-feeder, are necessary in the future.

Decomposition rates between the two root diameter classes might be due to differences in chemical properties, higher N, P, Ca, Al, Fe and Si concentrations and lower C:N and C:P ratio in fine roots compared to coarse roots. Several studies conducted in temperate forests have shown that very fine roots or lower-order roots decompose more slowly than thicker or higher-order

roots (McClaugherty et al. 1984; Sun et al. 2013; Fan and Guo 2010; Makita et al. 2015). These studies attributed this slower decomposition to associations with ectomycorrhizal (EM) fungi (Langley and Hungate 2003) and high initial N content inhibiting decomposition of litter with high recalcitrant acid-insoluble carbohydrate (McClaugherty et al. 1984; Fan and Guo 2010). Since we did not separate EM and non-EM species in our samples, the influence of mycorrhiza is unlikely to be the sole reason for our observed difference in decomposition rate between root diameter classes. Some higher chemical elements including N content detected in fine roots might indicate high levels of recalcitrant carbohydrate in fine roots in this forest. Recently, Guerrero-Ramírez et al. (2016) reported a positive impact of Mn and negative impact of Ca on root decomposition in tropical forests. In this study, we did not observe significant difference of Mn between coarse and fine roots. However, Ca concentration was higher in fine roots, which might be another reason of the slower decomposition of fine roots.

Impact of soil organisms

The coarse root decomposition rate was slower in soil chambers with 50- μ m mesh (SC₅₀) than in chambers without cover (SC_{NC}) from 398 days after chamber installation. This rate difference suggests a significant impact of soil fauna, such as ants, termites and earthworms, on coarse root litter decomposition. Soil fauna are considered the ecosystem engineers and their effect on ecosystem functions, e.g. soil turbulation, nutrient cycling and supplying of chemical substances, is widely

Table 3 Statistical results of linear mixed model analysis. The difference between sampling time (time), depth of root litter (depth) and types of soil chamber (SC type) was determined.

Variables	Coarse roots				Fine roots			
	$d.f.n$	$d.f.d$	F	P	$d.f.n$	$d.f.d$	F	P
Time	3	187	266.34	< 0.001	3	67	29.37	< 0.001
Depth	1	187	1.13	0.289	2	67	1.81	0.172
SC type	2	187	18.45	< 0.001	2	67	0.05	0.955
Time \times depth	3	187	1.20	0.311	6	67	0.24	0.962
Time \times SC type	6	187	3.76	0.001	6	67	0.40	0.879
Depth \times SC type	2	187	1.28	0.280	4	67	0.96	0.435
Time \times depth \times SC type	6	187	0.63	0.707	12	67	1.01	0.450

Degrees of freedom numerator ($d.f.n$), degrees of freedom denominator ($d.f.d$), F -value (F) and significance (P) are shown here

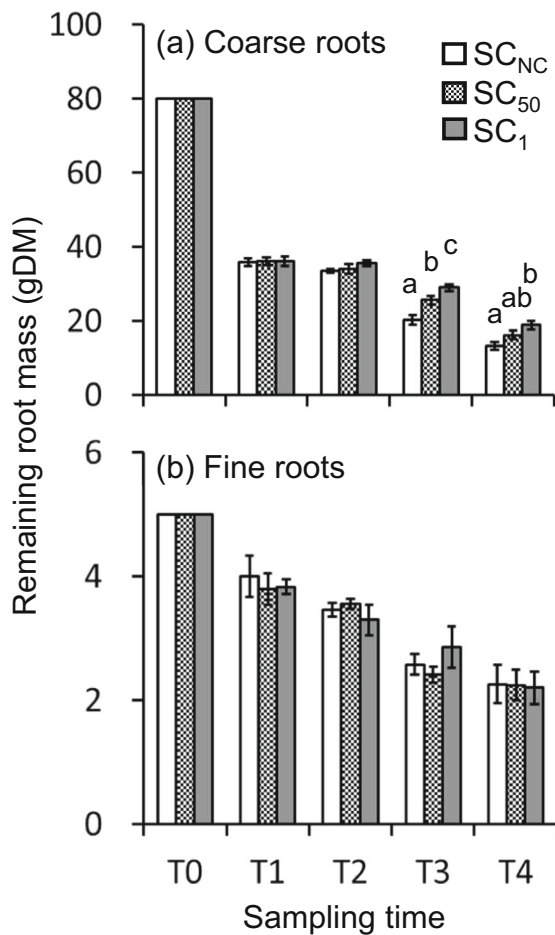


Fig. 2 Mass losses (gDM) of coarse (a) and fine (b) root litter in different types of soil chamber during the five sampling times. Standard deviations are indicated ($n = 7–18$). Different letters indicate significant differences among the soil chamber types ($P < 0.05$)

recognised (Lavelle et al. 2006). Soil fauna can also affect organic matter decomposition, but this effect has been reported mostly for leaf litter (e.g. Yang and Chen 2009; Cornelissen 1996; Makkonen et al. 2012). The impact of soil fauna on belowground decomposition has been reported by Powers et al. (2009) who found faunal impact on belowground decomposition of raffia and bay leaves in tropical forests. Our findings show that soil fauna influence not only leaf litter but also coarse root litter decomposition in a tropical forest.

Soil fauna affect decomposition directly through comminution and digestion and indirectly by activating microbial actions (Lavelle et al. 1997). They stimulate the breakdown of litters and the mixing and redistribution of litter-derived materials in the mineral soil,

thus increasing substrate availability (Briones 2014; Carrillo et al. 2011). These impacts could be more intense in moist tropical forests because of the high abundance and biodiversity of soil fauna (Gonzalez and Seastedt 2001). They access root litter in various ways, for directly feeding, for grazing microorganisms and for colonising there (Abe and Matumoto 1979; Briones 2014). Each of them might be able to coexist by having different feeding niches (Briones 2014).

Soil fauna impact can vary depending on litter quality (Hättenschwiler and Jørgensen 2010; Carrillo et al. 2011), suggesting that chemical property differences might explain the varying level of significance soil fauna have on fine (not significant) and coarse (significant) roots. Hättenschwiler and Jørgensen (2010) observed variation of impact of soil fauna, where decomposition of plant litters with low non-structural carbohydrates and high condensed tannins had no significant impact of soil fauna. In this study, therefore, the lack of influence of soil fauna on fine root decomposition could be caused by low non-structural carbohydrates that might be less attractive to soil fauna, and/or high defence chemicals such as condensed tannins. Future studies about the differences of chemical compounds between different diameter classes would be helpful to understand the mechanisms of root decomposition in this forest.

The decomposition rates of coarse roots in soil chambers with 1- μm mesh (SC₁) were slower than those of the chamber without cover (SC_{NC}) and with 50- μm mesh (SC₅₀). This indicates that not only soil animals but also soil fungi are important for root litter decomposition. Fungi and bacteria are widely considered to be the fundamental biological groups responsible for litter decomposition (Chapin et al. 2002). A previous study separated the contribution of mycorrhizal mycelium and other microbes on soil CO₂ efflux in a northern temperate forest in UK (Heinemeyer et al. 2007); in this study, CO₂ efflux decreased by nearly 30% when mycorrhizal mycelium was removed from soil microbes. However, in the present study, remaining root litter in SC₁ was 4% higher than those in SC₅₀ in T3 (36% and 32%) and T4 (24% and 20%), suggesting less contribution of fungal mycelium for root litter decomposition than for soil CO₂ efflux and in tropical forests than in northern forests.

We found that the impact of soil animals and fungi was observed from 400 days after the litterbag installation. In general, litter mass loss occurs rapidly during the early stage of decomposition, but slowed down

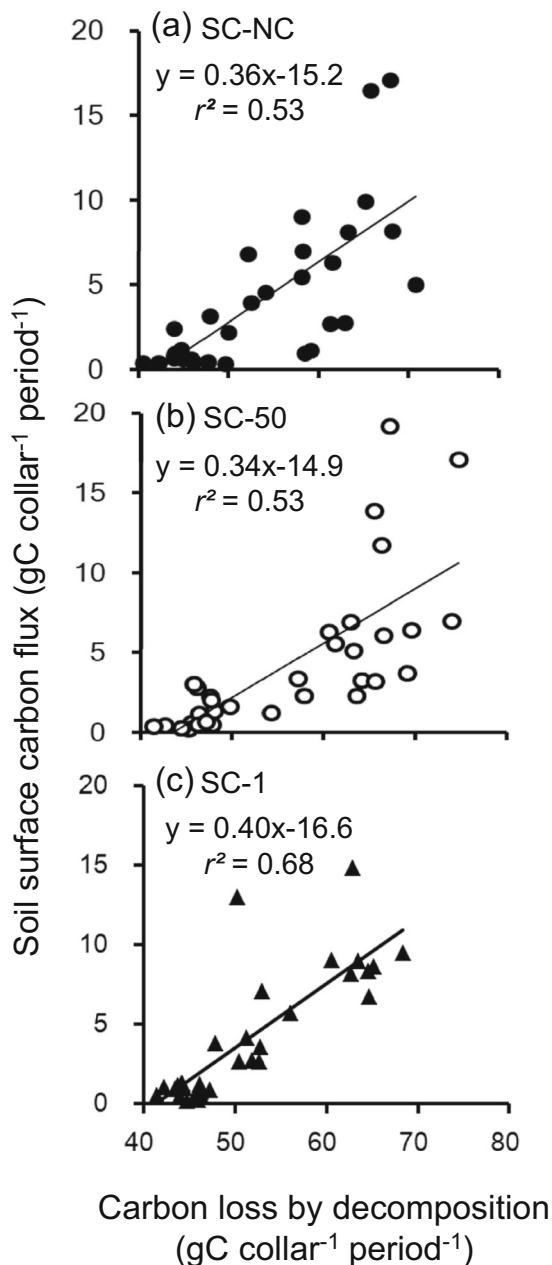


Fig. 3 Carbon loss (gC) by soil surface carbon dioxide (CO_2) flux and by root decomposition from soil chamber with different mesh sizes SC_{NC} (a), SC_{50} (b) and SC_1 (c). All regressions are significant at $P < 0.05$

thereafter because the substrate of decomposition changes from labile compounds comprising easily degraded soluble and cellulose to recalcitrant compounds that are lignified (Co teaux et al. 1995). The results of the present study suggest that soil animals and fungi may effectively support the decomposition of lignified

compounds of coarse root litter. Fungi produce a wider range of extracellular enzymes than bacteria and are therefore able to degrade highly recalcitrant detritus (Kirk and Farrell 1987; Tuomela et al. 2000). Mineralisation of lignin by bacteria is secondary important, consuming small molecular compounds produced by fungi (Romani et al. 2006). This would explain the significant impact of fungi in T3 and T4 in this study.

Our results showed no interacting impact of soil biota and soil depth even though it is expected that their density is higher in soil surface. The PVC collar installation might have limited the access of soil surface fauna and fungi, causing the lack of interaction. It also might have happened that the effect of soil fauna such as termites has retained not only near the soil surface but also in the deeper parts of the soil (Abe and Matumoto 1979).

Contribution of root decomposition to soil CO_2 efflux

In this study, carbon efflux from soil surface increased linearly with the loss of carbon caused by root decomposition. Our results suggest that 40% of the carbon lost by decomposition could be emitted as CO_2 gas from the soil surface above the chamber. This value is lower than the estimates of Tanikawa et al. (2018), where 90% of total carbon loss during conifer root decomposition was released as CO_2 in laboratory condition without soil. Metcalfe et al. (2007) found that spatial heterogeneity in litter and root mass accounted for 44% of spatial variation in soil CO_2 efflux in Amazonian tropical forests. Our results suggest that roots may contribute spatial variation in soil CO_2 efflux not only by their respiration but also their decomposition.

Our results indicate the other 60% of the carbon could be transported by the other ways, for example washing away by rainfall. The coefficient of determination was lower in SC_{50} and SC_{NC} than in SC_1 . This suggests that increases in soil biota groups in SC_{50} and SC_{NC} produce variation in carbon loss rate and pathways. For example, invasion of fungal mycelium will increase the heterogeneity of the microenvironment in the soil chamber, causing variation in root litter decomposition in the same chamber. Soil macro fauna transport dead litter to their functional domains, e.g. the myrmecosphere of ants, drilosphere of earthworms and termitosphere of termites, where decomposition follows specific pathways (Lavelle et al. 1997). The increase in soil biota diversity may have increased the variation in

soil CO₂ efflux from the forest floor, causing complexity of soil carbon dynamics.

Conclusion

In this study, we found that fine roots decompose much slower than coarse roots, which highlights the possible role of fine roots for carbon storage and slow-acting effect of nutrient supply in a tropical forest. Our results also showed significant effects of soil fauna and fungal hyphae on root decomposition, which occurred only in the later stage of coarse root decomposition. The combination of soil incubation chamber and blocking techniques using various mesh-sized nets has enhanced our understanding of the biological interactions occurring during the decomposition processes. Estimating the contribution of root decomposition to soil CO₂ efflux was a new challenge; nearly half of the decomposed carbon was emitted as CO₂ from the soil surface, but the other half was transported in other ways.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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