

Carbon allocation of tropical rainforest in Lambir, Borneo

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Abstract It is important to understand the characteristics of carbon cycling in tropical rainforests in order to quantify global carbon cycling. Knowledge about carbon allocation, that is, how much of the carbon assimilated by photosynthesis is allocated to aboveground and belowground tissues, and how much is used for biomass production and respiration on an annual time scale and on an ecosystem scale, can improve our ability to predict the effects of global climate changes on carbon dynamics. Recently, studies on carbon allocation in the Neotropics have been increasing, while there are few such studies in Asian tropical rainforests. There are important biotic and abiotic differences between the tropical rainforests in Borneo and Neotropical rainforests, such as higher stand density of large trees, larger biomass, and absence of distinct dry seasons in the rainforests in Borneo. These factors may cause differences in the carbon allocation patterns between Borneo and the Neotropics. The goal of this study is to clarify characteristics of carbon allocation in Lambir Hills National Park, which is covered with typical Bornean mature tropical rainforests. We estimated above-ground net primary production (ANPP), woody tissue respiration (R_{wood}), foliage respiration ($R_{foliage}$), total below-ground carbon flux (TBCF) and gross primary production (GPP) in the Lambir Hills tropical rainforest, and compared the values with those from Neotropical tropical rainforests. We found that the aboveground biomass (AGB) in the Lambir Hills tropical rainforest was approximately twice higher than that in Neotropical rainforests. ANPP, R_{wood} and $R_{foliage}$ were comparable despite the higher biomass. The comparable R_{wood} despite higher aboveground biomass was partly caused by higher stand density of large trees in the Lambir Hills tropical rainforest. TBCF in the Lambir Hills tropical rainforest was much higher than those of Neotropical forests. This was unexpected, since the higher water availability in the Bornean tropical rainforest would suggest less fine root competition for water, giving higher ANPP and lower TBCF. Low nutrient availability may explain the comparable ANPP and higher TBCF. Our results suggested that large trees and

belowground resources considerably affected carbon cycling.

Keywords ANPP, Carbon allocation, GPP, TBCF, Tropical rainforest, Woody tissue respiration

Introduction

It is important to study carbon allocation; that is, how much of the carbon assimilated by photosynthesis is allocated to aboveground and belowground tissues, and how much is used for biomass production and respiration, on an annual time scale and on an ecosystem scale. Many studies have examined carbon allocation in Neotropical rainforests (e.g. Malhi et al. 2009), while studies in Asian tropical rainforests are still limited. Each component of carbon allocation can vary depending on biotic and abiotic factors such as biomass amount, water and/or soil nutrient status (e.g. Litton et al. 2007). Various factors may result in different carbon allocation between Asian and Neotropical rainforests. Thus, it is necessary to examine carbon allocation in a Bornean tropical rainforest, which is a typical lowland Asian tropical rainforest dominated by dipterocarp trees, to understand variations in carbon allocation among tropics.

Soil water availability is regarded as an important factor altering carbon allocation in forest ecosystems (Gower et al. 1992; Stape et al. 2008). There is an important difference in seasonality of rainfall between Borneo and Neotropics; There are no seasonal dry seasons in Borneo (Kumagai et al. 2005), whereas there are several seasonal dry months in most Neotropical areas (Malhi et al. 2006). The absence of regular dry seasons in Borneo may affect aboveground net primary production (ANPP; $\text{MgC ha}^{-1} \text{ year}^{-1}$) and total belowground carbon flux (TBCF; $\text{MgC ha}^{-1} \text{ year}^{-1}$). Higher soil water availability may cause lower intensity of fine root competition for water in Borneo, and thus increase ANPP and decrease TBCF.

It is also well known that aboveground biomass (AGB) in Borneo is higher than that in Neotropics. This is caused by the two-fold higher stand density of large trees with DBH > 70 cm (Paoli et al. 2008; Slik et al. 2010). This biotic characteristic may affect woody tissue respiration (annual- R_{wood} ; $\text{MgC ha}^{-1} \text{ year}^{-1}$), a component of carbon allocation. Large trees contribute considerably to AGB and aboveground-biomass increments (AGI) at the ecosystem scale in Borneo (Paoli et al. 2007). This indicates that large trees can have higher individual R_{wood} because of both high woody tissue respiration per unit area (chamber- R_{wood}) related to high stem growth rates and DBH (Ryan et al. 1994), and larger surface area or volume. Large trees contribute considerably to R_{wood} at the ecosystem scale (ecosystem- R_{wood}). So we expect greater ecosystem- R_{wood} values in Bornean forests than in Neotropical forests. Absence of seasonal dry seasons may also result in higher annual- R_{wood} , considering the lower chamber- R_{wood} values observed during dry months in the Neotropics (Chambers et al. 2004; Malhi et al. 2014).

To determine the characteristics of carbon cycling, we have conducted integrated studies on carbon cycling in a tropical rainforest in Lambir Hills National Park, Borneo. This forest is located in a region without obvious dry seasons (Kumagai et al. 2005). In the forest, we have measured components of carbon allocation including annual- R_{wood} , ANPP, and soil respiration (SR; $\text{MgC ha}^{-1} \text{ year}^{-1}$). In this paper we report the results and compare them with those reported from tropical rainforests with dry seasons in the Amazon.

Materials and methods

Study site

This study was conducted in Lambir Hills National Park, Sarawak, Malaysia (4°12'N, 114°02'E) at about 20 km southwest of Miri, Sarawak on the island of Borneo. Lowland mixed-dipterocarp forest, which is a typical mature lowland tropical rainforest type in Southeast Asia, covers 85% of this park of 6949 ha. The continuous canopy layer of the forest is approximately 40 m above the ground, but the heights of trees with DBH (the diameter at breast height) > 100 cm often exceed 50 m (Katayama et al. 2014). The leaf area index ranges spatially between 4.8 and 6.8 m² m⁻², with a mean of 6.2 m² m⁻² (Kumagai et al. 2004). Between 2000 and 2009, the mean annual temperature at this site was 25.8°C. Rainfall was distributed throughout the year, with a mean annual rainfall of 2600 mm (Kume et al. 2011). The monthly rainfall between 1958 and 2001 averaged more than 100 mm (Kumagai et al. 2005). Although there is no clear seasonality in temperature or precipitation, unpredictable dry periods sometimes occur at different times of the year. A 4 ha permanent plot has been established surrounding a canopy crane for ecological observations.

Measurements

Environmental factors

Air temperature was monitored on the crane at 75 m above the ground using a thermohygrograph (HMP35A, Visala) and the data were logged using a programmable data logger (CR10X, Campbell Scientific, Utah, USA). Rainfall was monitored using a tipping bucket rain gauge (RS102, Ogasawara Keiki, Tokyo, Japan) with a data logger (HOBO event, Onset Computer, USA) at the top of the crane (85.8 m above the ground). Mean daily soil water content (SWC, m³ m⁻³) was calculated at a depth of 0–120 cm for the analyses of R_{wood} .

Tree census and litterfall measurements

To estimate aboveground biomass (AGB; MgC ha⁻¹) and aboveground-biomass increment (ABI; MgC ha⁻¹ year⁻¹), tree censuses were conducted every year over 4 years in a 4-ha plot, in which the crane facility was located in the center. The first tree census was conducted in May–July 2000. All trees greater than 10 cm in diameter at breast height (DBH; cm, 1.3 m above ground) were tagged and mapped. The DBH values were measured with a resolution of 1 mm. The second tree census was carried out in August 2001. We identified dead trees and measured DBH for all live trees. We tagged newly recruited trees and measured the DBH. In the same way, we carried out the third, fourth and fifth censuses in September 2002, July 2004, and June 2005, respectively. DBH and stem growth rate for individual trees for the analyses of R_{wood} were obtained from tree census data in 2012 and 2013.

Litterfall-C (LF; MgC ha⁻¹ year⁻¹) was measured in January 2001–December 2005 using 80 0.5-m² litter traps placed at the intersections of 20 m grids within the 4-ha plot. Litterfall was collected from the traps once or twice a month. It was then oven-dried for 72 h at 50 °C and weighed.

Woody tissue respiration measurements

Chamber- R_{wood} was measured five times at breast height during 9–28 January 2012, 5–8 May 2013, 13–14 July 2013, 24 December 2013–2 January 2014, and 29 June–7 July 2014, mainly in

the 4-ha plot. Trees for the measurement were selected randomly from 52 sample trees during each measurement period. The 52 sample trees included 36 species, and 24 of them were of the family Dipterocarpaceae. DBH of the sample trees ranged from 10 to 158 cm. The numbers of the trees measured were 48, 48, 47, 50, and 38 in January 2012, May 2013, July 2013, December 2013, and June 2014, respectively. To minimize the effects of diurnal variation in R_{wood} , measurements were conducted between 8:30 and 15:00 according to a previous study (Katayama et al. 2014).

Chamber- R_{wood} was measured using a closed-static system with an infrared gas analyzer (GMP343, Vaisala, Helsinki, Finland) according to Katayama et al. (2013). Ecosystem- R_{wood} was estimated based on the relationships of chamber- R_{wood} with the stem growth rate, DBH and tree species, and scaled by the woody surface area (Katayama et al. 2016). Annual R_{wood} at the ecosystem scale was estimated based on the soil water content using a linear regression model following Katayama et al. (2016).

Soil respiration measurements

SR rates were measured using a commercial respirometer (LI-6400, Li-Cor). This equipment is primarily a photosynthetic measurement system. However, it can be used to measure SR rates by attaching a soil chamber (LI-6400-09; volume, 962 cm³ and diameter, 9.5 cm). We measured SR rates at the 25 intersections of the 10-m grids of a 40 × 40 m subplot demarcated in the 4-ha plot. The measurements were conducted from February 2002 to October 2006 at 2–5 month intervals. In total, there were 35 measurement campaigns. A more complete description of the sampling procedures for SR is available in Katayama et al. (2009) and Ohashi et al. (2008).

Data Analysis

GPP (GPP, MgC ha⁻¹ year⁻¹) was estimated as the annual sum of the carbon allocated to dry matter production and respiration (e.g. Litton et al. 2007),

$$\text{GPP} = \text{ANPP} + R_{above} + \text{TBCF} \quad (1)$$

where R_{above} (MgC ha⁻¹ year⁻¹) is aboveground plant respiration.

ANPP was calculated as follows:

$$\text{ANPP} = \text{ABI} + \text{LF} \quad (2)$$

ABI was calculated using AGB estimated from the tree censuses. For AGB estimates, we used allometric equations developed by Yamakura et al. (1986) based on the data obtained from a forest in the eastern part of Borneo Island, Indonesia. The type of forest was similar to that of our site. Using these allometric equations, we estimated the biomass of the branches, stems, and foliage of individual trees for each tree census. ABI was calculated using the data following Clark et al. (2001a). LF for each year was estimated by summing monthly LF of the year. For ABI and LF estimations, we assumed that the carbon content of the dried biomass was 50 % (after several previous studies (e.g. Clark et al. 2001b; Giardina and Ryan 2002; Malhi et al. 2004)), because we did not measure the carbon content of the biomass or LF.

R_{above} was calculated as follows:

$$R_{above} = R_{wood} + R_{foliage} \quad (3)$$

$R_{foliage}$ is foliage CO₂ efflux. Ecosystem- $R_{foliage}$ was estimated as the sum of leaf area densities multiplied by $R_{foliage}$ at every 5 m height from the ground (0 m) to the canopy top (50 m). Leaf area densities were estimated using the plant area index (PAI) profile and total leaf areas. The PAI profile was reported by Kumagai et al. (2006), who measured vertical variation in the plant area

index at four points using a pair of canopy analyzers (LAI-2000, Li-Cor, Lincoln, Nebraska) in this study site. Subsequently, total leaf areas at the ecosystem scale were estimated using the equation described by Yamakura et al. (1986). $R_{foliage}$ was reported by Kenzo et al. (2015), who measured foliage dark respiration rates in 123 individual trees of 62 species of 24 families, and from the ground to a height of 52.5 m in this study site using a commercial respirometer (LI-6400, LI-COR Inc., Lincoln, NE). Several studies have shown lower $R_{foliage}$ in the light than in the dark (Atkin et al. 2000). Thus, to accommodate light inhibition of $R_{foliage}$, daytime $R_{foliage}$ was calculated as 67 % of night time $R_{foliage}$ according to previous studies (Malhi et al. 2009; da Costa et al. 2013; Doughty et al. 2013; Malhi et al. 2014). Annual $R_{foliage}$ at the ecosystem scale (annual- $R_{foliage}$, MgC ha⁻¹ year⁻¹) was estimated assuming that there were 12 hours each for daytime and nighttime, with a constant temperature of 25 °C each day throughout the year. The error in annual- $R_{foliage}$ represents spatial variation, according to a previous study (Metcalf et al. 2010).

TBCF was calculated based on the mass balance equation (e.g. Giardina and Ryan 2002; Litton et al. 2007) as follows:

$$TBCF = SR - LF + F_E + \Delta C_S + \Delta C_R + \Delta C_L \quad (4),$$

where F_E is carbon exported by erosion, leaching, or CH₄ efflux, ΔC_S is the change in the carbon content of mineral soil, ΔC_R is the increment in the carbon content of root biomass, and ΔC_L is the change in the carbon content of the litter layer. We assumed F_E , ΔC_S , ΔC_R , and ΔC_L were negligible, as in previous studies (e.g. Davidson et al. 2002; Raich and Nadelhoffer 1989). Although we did not have sufficient data of factors such as soil organic matter and litter conditions to support this assumption, the assumption is thought to have been supported by some previous studies: Giardina and Ryan (2002) reported that F_E was less than 1 % of TBCF and that annual changes in carbon storage in soil were 2.1 % of TBCF in young tropical rainforests; Telles et al. (2003) also reported that ΔC_S and ΔC_L were relatively small compared to SR and LF for tropical rainforests; Giardina and Ryan (2002) and Malhi et al. (2009) reported that the change in fine root biomass was negligible for belowground carbon cycling in tropical rainforests. However, some studies conducted in temperate forests showed that carbon storage in soil could be an important component of carbon cycling (Ohtsuka et al. 2007, 2010). Therefore, we stress the need for further studies examining the validity of such assumptions based on *in situ* measurements.

Results and Discussion

ANPP

AGB was 272.4 MgC ha⁻¹, which was much higher than the values in the Neotropics. Large trees with DBH > 70 cm accounted for 38 % of total AGB (Fig. 1), suggesting that higher stand density of large trees caused higher AGB in Lambir. Large trees were present in the study site at the density of 16.5 trees ha⁻¹, while average stand density of large trees in Neotropical areas was 7.5 trees ha⁻¹ (Paoli et al. 2008). ABI and LF were estimated to be 3.74 and 3.02 MgC ha⁻¹ year⁻¹, respectively. Large trees accounted for 29 % of ABI (Fig. 1), suggesting that large trees, again, affected ABI considerably. The mean ± S.D. of ANPP was estimated to be 6.76 ± 0.57 MgC ha⁻¹ year⁻¹. The ANPP of our site was slightly lower than those for Neotropical forests (Table 1). This result does not support our hypothesis that the higher soil water availability of our site would cause lower ANPP than that for Neotropical forests. Therefore, the difference in ANPP between our site and the Neotropical forests cannot be explained only from the viewpoint of soil water availability. One possible explanation for the lower ANPP of our site is low soil phosphorus

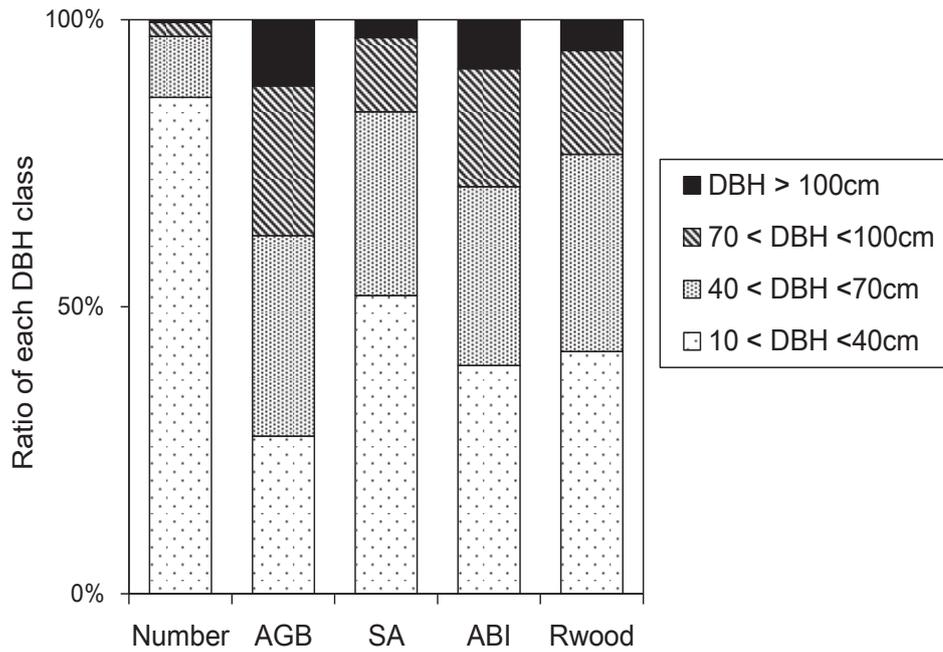


Fig. 1 Proportion of DBH classes in the number of trees (number), aboveground biomass (AGB), woody tissue surface area (SA), aboveground biomass increment (ABI), and woody tissue respiration (R_{wood}) in the 4-ha plot.

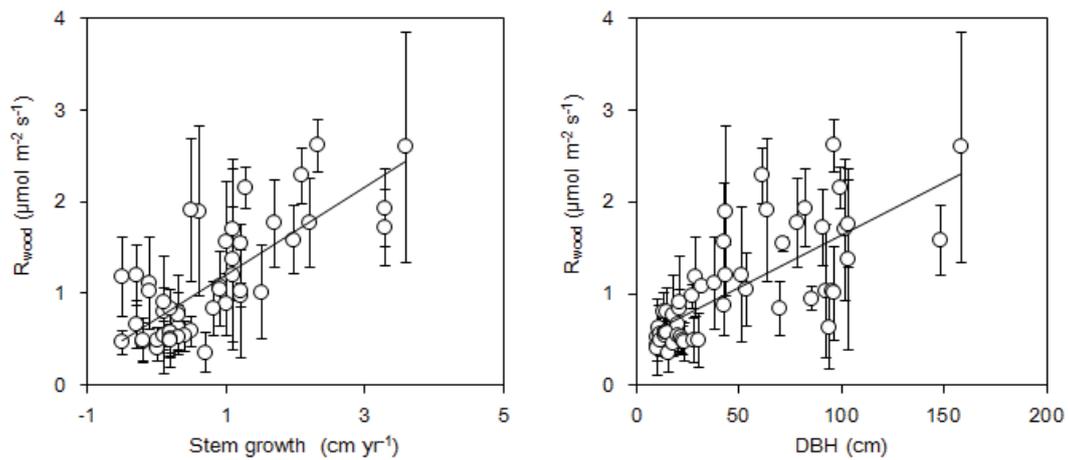


Fig. 2 Relationships of chamber- R_{wood} with stem growth rate (left) and DBH (right). Both relationships were significantly positive ($P < 0.001$).

Table 1. Aboveground biomass, annual- R_{wood} , annual- $R_{foliage}$, annual- R_{above} , ANPP, TBCF GPP and ratios to GPP in various tropical rainforests.

Site	Malaysia		Costa Rica		French Guiana		Brazil			Peru		
	Borneo		La Selva		Paracou		Caxiuana tower	Caxiuana Terra preta	Caxiuana Control	Caxiuana Dry	TAM-05 (Nutrient poor)	TAM-06 (Nutrient rich)
Aboveground biomass ($MgC\ ha^{-1}$)	272.4	81	5.08 ± 1.35		228		179.5	110.9	213.9	200.6	138.2	115.6
Annual- R_{wood} ($MgC\ ha^{-1}\ year^{-1}$)	7.06 ± 2.09	1.1 (diameter < 10 cm)	5.44 ± 0.99		5.44 ± 0.99		8.71 ± 1.07	8.46 ± 2.82	10.21 ± 4.49	11.17 ± 4.96	5.43 ± 1.77	7.62 ± 2.48
Surface area index ($m^2\ m^{-2}$)	2.01		1.3		1.3		1.65	1.63	--	--	1.98	2.09
Average Chamber- R_{wood}	0.81 ± 0.52 (dry)	0.60 (DBH of 10cm)	1.13 ± 0.55 (dry)		1.13 ± 0.55 (dry)		2.08 ± 0.15	2.11 ± 0.17	1.61 ± 0.12	1.94 ± 0.19	0.95 ± 0.03	1.03 ± 0.08
	1.39 ± 0.74 (wet)	0.83 (DBH of 80cm)	1.56 ± 0.65 (wet)		1.56 ± 0.65 (wet)							
Scaling factors	Growth, dbh, species	Growth, diameter, Species, height, slope	Average		Average		Growth	Growth	Growth	Growth	Growth	Growth
Samples	DBH > 10cm	All trees, Liana, Palm	DBH > 10cm		DBH > 10cm		All trees	All trees	All trees	All trees	All trees	All trees
Annual- $R_{foliage}$ ($MgC\ ha^{-1}\ year^{-1}$)	9.54 ± 0.46	--	11.59 ± 0.54		11.59 ± 0.54		5.02 ± 1.58	5.09 ± 1.67	5.69 ± 2.14	9.26 ± 3.63	8.86 ± 2.84	6.43 ± 2.07
Annual- R_{above} ($MgC\ ha^{-1}\ year^{-1}$)	16.60 ± 2.14	--	17.03 ± 0.55		17.03 ± 0.55		13.73 ± 4.4	13.55 ± 4.49	15.9 ± 6.63	20.43 ± 8.59	14.29 ± 4.61	14.05 ± 4.55
ANPP	6.76 ± 0.57	--	--		--		9.35 ± 0.49	8.75 ± 0.59	6.78 ± 0.14	5.71 ± 0.20	9.96 ± 0.83	11.59 ± 1.62
TBCF	19.63 ± 6.37	--	--		--		9.01 ± 1.22	13.3 ± 1.62	16.5 ± 4.03	14.3 ± 4.20	11.26 ± 1.11	8.85 ± 1.06
GPP ($MgC\ ha^{-1}\ year^{-1}$)	42.99 ± 6.74	--	37.57		37.57		32.08 ± 3.46	35.68 ± 3.65	39.18 ± 1.81	40.44 ± 6.39	35.47 ± 3.55	34.47 ± 3.53
R_{wood} / GPP	0.17 ± 0.05	--	0.14		0.14		0.27 ± 0.09	0.24 ± 0.08	0.26 ± 0.12	0.28 ± 0.13	0.15 ± 0.05	0.22 ± 0.08
$R_{foliage} / GPP$	0.23 ± 0.01	--	0.31		0.31		0.16 ± 0.05	0.14 ± 0.05	0.15 ± 0.06	0.23 ± 0.10	0.25 ± 0.08	0.19 ± 0.06
R_{above} / GPP	0.40 ± 0.06	--	0.45		0.45		0.43 ± 0.11	0.38 ± 0.10	0.41 ± 0.14	0.51 ± 0.17	0.40 ± 0.10	0.41 ± 0.10
ANPP/GPP	0.16 ± 0.03	--	--		--		0.29 ± 0.03	0.25 ± 0.03	0.17 ± 0.02	0.14 ± 0.02	0.28 ± 0.03	0.34 ± 0.06
TBCF/GPP	0.46 ± 0.16	--	--		--		0.28 ± 0.05	0.37 ± 0.14	0.42 ± 0.12	0.35 ± 0.12	0.32 ± 0.04	0.26 ± 0.04
Reference	This study	Cavaleri et al. 2006	Stahl et al. 2011		Stahl et al. 2011		da Costa et al. 2013	Doughty et al. 2013	da Costa et al. 2013	Malhi et al. 2014		
			Rowland et al. 2013		Rowland et al. 2013		da Costa et al. 2010					

availability. ANPP was reported to be positively correlated with soil phosphorus availability in the Amazon region (Aragão et al. 2009) and Borneo (Paoli et al. 2007). The amounts of available phosphorus in soil approximately 300 m away from the 4-ha plot (8.21 mg kg⁻¹ at 0–5 cm depth; 0.25 mg kg⁻¹ at 5–50 cm depth; Ishizuka et al. 1998) were considerably lower than those reported from the Amazon region (9.12–20.08 mg kg⁻¹ in 0–30 cm soil; Malhi et al. 2009).

Aboveground plant respiration

Chamber- R_{wood} was strongly correlated with stem growth rate and DBH spatially (Fig. 2), and ecosystem- R_{wood} was positively correlated with soil moisture content temporally. Annual- R_{wood} between 2012 and 2013 estimated from the linear regression model was 7.06 ± 2.09 MgC ha⁻¹ year⁻¹. Annual- $R_{foliage}$ was 9.54 ± 0.46 MgC ha⁻¹ year⁻¹. Annual- R_{wood} in our study site was comparable to those in the Neotropics even though AGB is much higher in our study site. This is partly caused by higher stand density of large trees in our study site. Large trees were present in our study site at the density of 16.5 trees ha⁻¹. Large trees accounted for only 3 % of all trees in number (567 trees ha⁻¹), but they comprised 23% of total ecosystem- R_{wood} , 38 % of total AGB, and 16 % of total woody surface area (Fig. 1). The higher contribution of large trees (38 %) to AGB than to surface area (16 %) was caused by the differences in allometric equations. AGB increases exponentially with DBH (Yamakura et al. 1986). On the other hand, surface area increases logarithmically (Chambers et al. 2004), and the increase of the ratio of a woody surface area with DBH gradually decreased with DBH and almost plateaued at high DBH on the individual scale. As chamber- R_{wood} increased with DBH, the ratio of large trees to ecosystem- R_{wood} (23 %) was slightly higher than the ratio to woody tissue surface area (16 %). Accordingly, a decrease in stand density of large trees more strongly affected AGB than ecosystem- R_{wood} . If stand densities of large trees were lower by 55 % a level that is comparable to that in Neotropical areas (7.5 trees ha⁻¹; Paoli et al. 2008), AGB would be 79 % of the actual estimate and ecosystem- R_{wood} be 87 %. If large trees were absent, AGB would decrease to 62 % and ecosystem- R_{wood} to 79%. This shows that stand densities of large trees considerably affect AGB, whereas their effect on ecosystem- R_{wood} is moderate.

The variation in annual- R_{wood} among forests (Table 1) was not explained by AGB, although some studies have shown positive relationships between plant respiration and biomass (Kira and Shidei 1967; DeLucia et al. 2007). Here we discuss possible factors affecting variation in annual- R_{wood} , such as surface area of woody tissue index (SAI, m² m⁻²), chamber- R_{wood} , and sampling method (Table 1). Annual- R_{wood} values observed in Peru (Malhi et al. 2014) were similar to those of our site, despite the twice higher AGB of our site. This is because of the similar SAI and chamber- R_{wood} of the two study sites. The higher stand density of large trees in the present study site is associated with higher biomass, but it does not affect SAI. Compared with the findings of two studies in Brazil (da Costa et al. 2013; Doughty et al. 2013), annual- R_{wood} in this study site was lower despite the higher biomass. Lower chamber- R_{wood} and slightly higher SAI in this study site resulted in lower annual- R_{wood} . Cavaleri et al. (2006) reported much lower AGB but only slightly lower annual- R_{wood} in Costa Rica. The reason for the difference can be attributed to the different sampling methods: they measured chamber- R_{wood} for lianas and palms in addition to vertical variation for trees. They reported that liana and palms accounted for 24 and 9 % of total R_{wood} in the forest, and suggested that estimation using data without vertical measurements, which are often reported, causes underestimation (e.g. Katayama et al. 2014). Therefore annual- R_{wood} in the present study, as in many previous studies, may be underestimated. Consideration of tree size

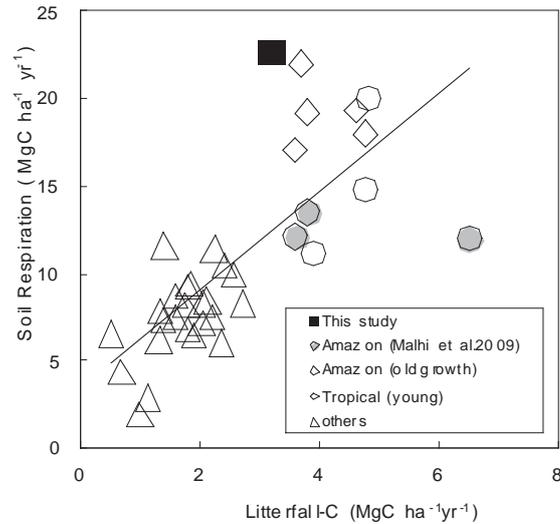


Fig. 3 Regression of annual soil respiration and annual litterfall carbon (Litterfall-C) for tropical and temperate forests from Davidson et al. (2002) and Malhi et al. (2009) and this study. The line represents the linear regression based on all data. The regression is expressed as soil respiration = $3.39 + 2.84 \times$ litterfall-C.

distributions, in addition to differences in SAI, chamber- R_{wood} and sampling design, may be the key to understanding the relationship between ecosystem- R_{wood} and biomass across various forests.

Annual- $R_{foliage}$ was the second highest among tropical rainforests reported in the literature, whereas the ratios of R_{wood} and $R_{foliage}$ to GPP were within the range of those reported in Neotropical forests (Table 1). Ratios of R_{wood} and $R_{foliage}$ to GPP in this study and in most other tropical rainforests were higher than the averages of various forest ecosystems, including boreal and temperate, and young- and old-growth forests (0.16 and 0.16, respectively, Litton et al. 2007). Hence, the ratios of R_{above} to GPP (0.38–0.51) were also higher than the average of various forest ecosystems (0.32, Litton et al. 2007). This agrees with the result of previous studies showing that ratios of plant respiration to GPP were higher in tropical forests than in temperate forests (Luyssaert et al. 2007, Piao et al. 2010). Although the causes of these differences remain unclear, high temperatures (Piao et al. 2010), biomass (Kira and Shidei 1967), and stand ages (DeLucia et al. 2007) may be responsible for higher ratios in mature tropical rainforests.

Total belowground carbon flux

We found significant positive correlations between the soil respiration and forest structural parameters such as the mean DBH, total basal area, and maximum DBH within 6 m of the measurement points. The most important factor was the mean DBH within 6 m of the measurement points, which had a significant linear relationship with soil respiration. Annual SR and LF were estimated as 22.65 and 3.02 MgC ha⁻¹ year⁻¹, respectively. Accordingly, TBCF was estimated as 19.63 MgC ha⁻¹ year⁻¹. The TBCF for our site was higher than those for the Neotropical forests (Table 1) because of the higher SR for our site. Figure 3 shows the relationship between annual LF and annual soil respiration in various tropical and temperate forest ecosystems with a linear regression based on a global dataset (Davidson et al. 2002). The figure shows that

significantly larger LF and soil respiration were observed in tropical forests than in temperate forests and that the soil respiration measured at our site was the second largest when compared with tropical forests in the Amazon, Costa Rica, and Hawaii and temperate forests (data are cited from Davidson et al. 2002; Malhi et al. 2009). On the other hand, the LF at our site was the smallest among the tropical forests. Consequently, soil respiration at our site is extremely large at a given LF in terms of the global dataset. In addition, SR for our site was higher than that for forests in the Neotropics, where there is a seasonal dry period. In general, higher soil water availability could lead to lower intensity of fine root competition for water and therefore lower SR (e.g. Litton et al. 2007). Therefore, differences in soil water availability between our site and the Neotropical rainforests cannot explain the difference in SR. Spatial variations in SR within our site were related to spatial variations in fine root biomass, implying that fine root biomass is a determinant of SR and, therefore, TBCF for our site. Fine root biomass in surface soil (0–5 cm) for our site was 4.7 Mg ha^{-1} (Katayama et al. 2009), while that in surface soil (0–10 cm) was $2.18\text{--}3.5 \text{ Mg ha}^{-1}$ in Amazon forests (Nepstad et al. 2002; Silver et al. 2005). The higher fine root biomass may be due to the poor nutrient condition. Thus, soil nutrient condition would partly explain the difference in TBCF.

Gross primary production

GPP was $42.99 \pm 6.74 \text{ MgC ha}^{-1} \text{ year}^{-1}$, which was the highest reported among tropical rainforests. This highest GPP might be caused by high LAI and the absence of regular seasonal dry seasons. We should admit, however, that there are considerable uncertainties in the estimate of GPP due to different factors such as lack of diurnal measurements of soil respiration. It will be necessary to measure continuous carbon flux including eddy covariance.

Conclusion

Our results showed that higher density of large trees considerably influenced carbon cycling in our study site. First, twice higher stand density of large trees compared to that in the Neotropics caused approximately twice higher AGB in our study site. Second, the higher stand density caused comparable annual R_{wood} despite much higher AGB. This is partly because higher stand density of large trees can considerably affect AGB, while it exerts less influence on annual R_{wood} . Third, soil respiration was high where large trees were located. These results suggest that future climate changes can alter carbon cycling through the change in carbon allocation not only by the physiological and phenological response to drought for large trees, but also by changes in the density of large trees. Furthermore, an abiotic factor also affected carbon allocation: poor nutrient condition caused slightly lower aboveground net primary production and higher annual soil respiration compared with those in the Neotropics. These results indicate the importance of studying carbon allocation in various tropical regions under different climate and soil conditions.

We have measured many components of carbon cycling, as we showed in this paper. We have already got detailed data for analyzing the belowground carbon cycling in Lambir, and they will be published soon. In addition, we have conducted eddy covariance measurements to determine the exchange of $\text{CO}_2/\text{H}_2\text{O}$ above the canopy. Continuous measurements of soil respiration and biogenic volatile organic compounds (BVOC) sampling from leaves have also just been started. We will also try to examine seasonal variations in carbon allocation with tree phenology. These studies of carbon cycling can improve our understanding not only for

biogeoscience but also for ecosystem ecology. Such studies are definitely necessary, especially for Lambir, which has biotic and abiotic characteristics quite different from those of the Neotropics.

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