

Carbon allocation in a Bornean tropical rainforest without dry seasons

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Abstract To clarify characteristics of carbon (C) allocation in a Bornean tropical rainforest without dry seasons, gross primary production (GPP) and C allocation, i.e., aboveground net primary production (ANPP), aboveground plant respiration (APR), and total below-ground carbon flux (TBCF) for the forest were examined and compared with those from Amazonian tropical rainforests with dry seasons. GPP ($30.61 \text{ MgC ha}^{-1} \text{ year}^{-1}$, eddy covariance

measurements; $34.40 \text{ MgC ha}^{-1} \text{ year}^{-1}$, biometric measurements) was comparable to those for Amazonian rainforests. ANPP ($6.76 \text{ MgC ha}^{-1} \text{ year}^{-1}$) was comparable to, and APR ($8.01 \text{ MgC ha}^{-1} \text{ year}^{-1}$) was slightly lower than, their respective values for Amazonian rainforests, even though aboveground biomass was greater at our site. TBCF ($19.63 \text{ MgC ha}^{-1} \text{ year}^{-1}$) was higher than those for Amazonian forests. The comparable ANPP and higher TBCF were unexpected, since higher water availability would suggest less fine root competition for water, giving higher ANPP and lower TBCF to GPP. Low nutrient availability may explain the comparable ANPP and higher TBCF. These data show that there are variations in C allocation patterns among mature tropical rainforests, and the variations cannot be explained solely by differences in soil water availability.

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Introduction

It is important to study the characteristics of carbon (C) cycling in tropical rainforests to quantify global C cycling, because gross primary production (GPP; $\text{MgC ha}^{-1} \text{ year}^{-1}$) in the tropics accounts for approximately 60 % of that in the terrestrial biosphere (Beer et al. 2010). There have been many studies on GPP in various forest ecosystems, including tropical rainforests (e.g., Kosugi et al. 2008; Malhi et al. 1998). However, there is still uncertainty about the details of C allocation; that is, how much of the C 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 at an ecosystem scale.

C allocation can vary according to environmental conditions such as water and/or soil nutrient status, according to the study of Litton et al. (2007). That study was based on synthesis of readily available data from various forest sites, although the synthesis included only a few data from mature tropical rainforests. There are variations in environmental conditions among different sites covered with vegetation in the same specific category (Vicca et al. 2012). This is also the case for sites covered with tropical rainforests (Araújo et al. 2009; Malhi et al. 2004), suggesting that there are variations in C allocation among different sites covered with tropical rainforests. An increasing knowledge of manner and variability in C allocation for forest ecosystems in different regions and under resource availability would provide us with insights into the ecological background of carbon metabolism and its possible consequences with environmental conditions. Such understanding is no doubt useful for improving simulation models of carbon assimilation and its allocation in ecosystems (e.g., Malhi et al. 2011). Modeling of C allocation is an essential part of ecosystem carbon cycling under present and changing climate conditions (Friedlingstein et al. 1999; Litton et al. 2007). Thus, it is important to clarify not only GPP, but also C allocation in various tropical rainforests to estimate spatial variations in C cycling under present and future conditions (Malhi 2012).

Most studies examining GPP and C allocation in tropical rainforests have been conducted in rainforests with dry seasons, mainly in the Amazon (e.g., Chambers et al. 2004; Malhi et al. 2009), where a dry season is defined as the month or months of the year with historical mean monthly precipitation of less than 100 mm. There are tropical rainforests without dry seasons in Southeast Asia (e.g., Bornean forests). Some studies have estimated the GPP for such forests using eddy covariance measurements (Hirano et al. 2007; Kosugi et al. 2008). However, few studies have examined C allocation because of the requirement for integrated and laborious measurements to clarify all components of C allocation. In fact, C allocation in such forests may differ from those in tropical rainforests with dry seasons. For example, higher soil water availability in forests without dry seasons might lead to less intensity of fine root competition for water. This would result in a lower ratio of total belowground C flux (TBCF; $\text{MgC ha}^{-1} \text{ year}^{-1}$) to GPP and a higher ratio of aboveground net primary production (ANPP; $\text{MgC ha}^{-1} \text{ year}^{-1}$) to GPP, because soil water availability is regarded as an important factor altering C allocation in forest ecosystems (Gower et al. 1992; Stape et al. 2008). To examine this possibility, data must be collected for the GPP and C allocation components in tropical rainforests without dry seasons.

We have been conducting integrated studies on C cycling in a tropical rainforest in the Lambir Hills National

Park, Borneo. This forest is located in a region without obvious dry seasons (Kumagai et al. 2005; Whitmore 1990). This results in conservative canopy transpiration rates for the forest throughout the year (Kumagai et al. 2005; Kume et al. 2011), implying insignificant root competition for water. In our previous studies, we examined temporal and spatial variation in soil respiration (SR; $\text{MgC ha}^{-1} \text{ year}^{-1}$, Ohashi et al. 2008) and estimated the ecosystem-scale SR of the forest (Katayama et al. 2009). Eddy covariance measurements were also conducted to estimate net ecosystem exchange (Saitoh et al. 2005). The data derived from eddy covariance measurements were used to develop and parameterize an ecohydrological model simulating C and water exchange for the forest (e.g. Kumagai et al. 2004, 2006). However, other components of C allocation (i.e., ANPP, aboveground plant respiration, and TBCF) and GPP had not been estimated. To clarify characteristics of C allocation for this forest, we (1) estimated GPP based on eddy covariance measurements and biometric measurements, (2) estimated each component of C allocation, and (3) compared the results with those reported for tropical rainforests with dry seasons in the Amazon.

Materials and methods

Study site

The study was carried out in the Lambir Hills National Park, Sarawak, Malaysia ($4^{\circ}20'N$, $114^{\circ}02'E$), situated approximately 30 km southwest of Miri. The area of the park is 6,949 ha. Approximately 85 % of the park is covered by lowland mixed-dipterocarp forest, which is a typical mature lowland tropical rainforest in Southeast Asia (e.g., Ashton and Hall 1992; King et al. 2009). The continuous tree layer is approximately 40 m above the ground, but emergent trees can reach heights greater than 50 m. The leaf area index (LAI) ranges spatially between 4.8 and $6.8 \text{ m}^2 \text{ m}^{-2}$ with a mean of $6.2 \text{ m}^2 \text{ m}^{-2}$ (Kumagai et al. 2004).

According to meteorological measurements conducted between 2000 and 2009 at our site, the mean annual temperature (MAT, $^{\circ}\text{C}$) and mean annual rainfall (MAR, mm) were 25.8°C and 2,600 mm, respectively. Rainfall occurs throughout the year without clear dry seasons (Kume et al. 2011). Monthly rainfall composited using data recorded between 1958 and 2001 was more than 100 mm in all months of the year (Kumagai et al. 2005). Thus, unlike Amazonian and African tropical rainforests, there are no obvious dry seasons under the maritime climate at our study site (Kumagai et al. 2005; Kume et al. 2008; Manfroi et al. 2006). At this site, the soils are red-yellow podzolic

Table 1 Soil characteristics in Lambir Hills National Park

Soil characteristics	Mean
Soil porosity ($\text{m}^3 \text{m}^{-3}$) ^a	0.69
pH ^b	4.03
Available P (mg kg^{-1}) in 0–5 cm depth ^b	8.21
Available P (mg kg^{-1}) in 5–50 cm depth ^b	0.25
N (%) ^c	0.12/0.14
C (%) ^c	1.21/1.91
C/N ratio ^c	9.6/13.6
Fine root biomass (Mg ha^{-1}) ^a	4.71

^a Data from Katayama et al. (2009). Those measurements were conducted for surface soil (0–5 cm depth) in the same subplot in the 4-ha plot of this study

^b Data from Ishizuka et al. (1998). Those measurements were conducted for surface soil (0–5 cm depth) at the ridge of different plot approximately 300 m away from the 4-ha plot

^c Data from Baillie et al. (2006). Those measurements were conducted for two different soil types (shale and sandstone, respectively) in surface soil (0–10 cm depth) in a different plot several kilometers away from the 4-ha plot

soils (Malaysian classification) or Ultisols (United States Department of Agriculture Soil Taxonomy), with a high sand content (62–72 %), low pH (4.0–4.3), and high porosity (54–68 %) (Table 1, Ishizuka et al. 1998; Sakurai 1999).

Measurements

Environmental factors

Solar radiation (S_r , Wm^{-2}) was measured using a pyranometer (MS401; EKO, Tokyo, Japan) between 2001 and 2005. The pyranometer was installed at the top of a crane facility (85 m above the ground surface) situated in the park. S_r data were collected every 5 s and an averaging period of 10-min was applied using a data logger (CR10X; Campbell Scientific, Logan, UT, USA).

Tree census and litterfall measurements

To estimate aboveground biomass (AGB; MgC ha^{-1}) and aboveground biomass increment (ABI; $\text{MgC ha}^{-1} \text{year}^{-1}$), a tree census was conducted over the 4-year period 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 with a diameter at breast height (dbh; cm, 1.3 m above ground) greater than 10 cm 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 dbhs for all live trees. We tagged newly recruited trees and measured

the dbhs. In the same way, we carried out the third, fourth and fifth censuses in September 2002, July 2004, and June 2005, respectively.

Litterfall (LF; $\text{MgC ha}^{-1} \text{year}^{-1}$) was collected in January 2001–December 2005 using 0.5 m^2 litter traps at 80 locations, which were placed at the intersections of 20 m grids within the 4-ha plot. We did not perform LF measurements at the center of the plot because of the location of the research crane. The traps were made of 1-mm nylon mesh and were placed 1 m above the ground. LF was collected from the traps once or twice a month. It was then oven-dried for 72 h at 50 °C and weighed.

Eddy covariance measurements

Eddy covariance measurements were conducted between June 15, 2001 and November 20, 2002. A three-dimensional sonic anemometer (DA-600; Kaijo, Tokyo, Japan) was installed at 60.2 m, i.e., 20 m above the mean canopy height. An open-path $\text{CO}_2/\text{H}_2\text{O}$ analyzer (LI-7500; Li-Cor, Lincoln, NE, USA) was placed about 30 cm away from the sonic anemometer. Wind speeds and gas concentrations time series were sampled at 10 Hz. All variances and covariances were computed over a 30-min averaging interval using the procedure described in Kumagai et al. (2004).

We measured the CO_2 concentration profile within the canopy at a location approximately 70 m away from the crane to quantify the in-canopy storage flux. Air samples drawn at 1.5, 6.5, 11.5, 21.5, 31.5, and 41.5 m above the ground surface were extracted using diaphragm pumps and an auto-solenoid switching system, and the CO_2 concentration was measured using a closed-path CO_2 infrared gas-analyzer (LI-800; Li-Cor). The CO_2 channels were automatically recorded everyday along with their N_2 gas and 510 ppmv CO_2 standards on a data logger (CR10X; Campbell Scientific). The in-canopy storage flux was determined by quantifying the rate of change of the CO_2 concentration in the air column within the canopy.

The net ecosystem CO_2 exchange between the forest and atmosphere (NEE, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated every hour, taking into account the CO_2 storage in the canopy at hourly intervals. Negative and positive NEE values indicated downward and upward CO_2 fluxes, respectively, and therefore quantified C absorption and release by the ecosystem. As a result of power system failure and exclusion of unreliable data (i.e., data recorded during rainfall, data with unreasonably high or low net ecosystem exchange values, and data recorded under low turbulence conditions), we obtained NEE data covering 30 % of the measurement period. A more complete description of the sampling procedures for eddy covariance measurements is available in Kumagai et al. (2006) and Saitoh et al. (2005).

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 at 10-m intervals in a 40 × 40 m plot situated 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 campaigns. A more complete description of the sampling procedures for SR is available in Katayama et al. (2009) and Ohashi et al. (2008).

Methods

GPP based on eddy covariance measurements

GPP based on eddy covariance measurements (GPP_{eddy}, MgC ha⁻¹ year⁻¹) was estimated using the following equation:

$$\text{GPP}_{\text{eddy}} = -\text{NEE}_{\text{day}} + \text{ER}_{\text{day}} \quad (1)$$

where NEE_{day} is NEE in the daytime (MgC ha⁻¹ year⁻¹) and ER_{day} is ecosystem respiration in the daytime (MgC ha⁻¹ year⁻¹). NEE_{day} for each year was estimated by inputting S_r data from the year into the relationship between NEE and S_r at an hourly time scale (see below). The relationship between NEE and S_r was approximated using a hyperbolic function (e.g., Falge et al. 2001; Hirata et al. 2008; Suyker and Verma 2001):

$$\text{NEE} = R + A_{\text{max}}S_r / (S_r + A_{\text{max}}/a_s) \quad (2)$$

where R = nighttime ecosystem respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$), A_{max} = maximum net photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), and a_s = initial slope of the NEE-S_r curve. R , A_{max} , and a_s were determined using the least-squares method based on all available data. ER_{day} for each year was estimated by multiplying R by the duration of the daytime of the year, where ‘daytime’ was defined as the period when S_r was greater than 5 Wm⁻². On the basis of the data for NEE and ER_{day} for each year, GPP_{eddy} for the year was determined using Eq. (1). Even if we classified NEE data according to soil moisture and VPD, and determined R , A_{max} , and a_s for each class, our conclusions did not change qualitatively. We assumed that ecosystem respiration remained constant over time based on the following two pieces of information: first, temporal variation in plant respiration is generally minor in tropical rainforests because there is little seasonal change in temperature (e.g., Cavaleri et al. 2006; Falge et al. 2002; Kosugi et al. 2008; Malhi et al. 1998). Second, there was no clear temporal variation in SR for our site (Ohashi et al. 2008).

GPP and each component based on biometric measurements

A schematic representation of the forest C allocation components is shown in Fig. 1. By measuring ABI, LF, SR, and ecosystem respiration (ER; MgC ha⁻¹ year⁻¹), other components were estimated based on a mass balance approach. GPP based on biometric measurements (GPP_{biometric}; MgC ha⁻¹ year⁻¹) can be estimated as the annual sum of C allocated to dry matter production and respiration (e.g., Litton et al. 2007),

$$\text{GPP}_{\text{biometric}} = \text{ANPP} + \text{APR} + \text{TBCF} \quad (3)$$

where APR (MgC ha⁻¹ year⁻¹) is aboveground plant respiration.

ANPP was calculated as follows:

$$\text{ANPP} = \text{ABI} + \text{LF} \quad (4)$$

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 data obtained from a forest on East Borneo Island, Indonesia. The forest type on East Borneo Island was similar to that for our site. Using these allometric equations, we estimated the biomass of the branches, stems, and foliage based on individual trees in each tree census. Using these data, the ABI was calculated as described by Clark et al. (2001a). The increment of biomass for each tree was calculated as the difference between consecutive tree censuses. If a tree died between one census and the next, no increment was assigned to it. The increment of each new tree was calculated as the difference between the estimated biomass at the end of the interval and the biomass of a tree with diameter of 10 cm. The interval between two tree census measurements was not exactly 1 year. ABI for each year during the measurement period was estimated assuming a constant biomass increment in each interval. LF for each

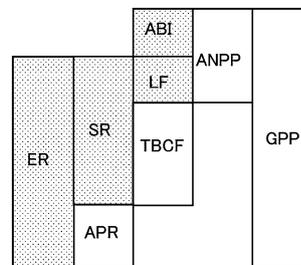


Fig. 1 Schematic illustration of carbon allocation. Dotted columns indicate components determined by measurements of CO₂ fluxes and plant biomass. Other columns indicate components estimated using mass balance equations. GPP Gross primary production, ANPP aboveground net primary production, APR aboveground plant respiration, TBCF total belowground carbon flux, ABI aboveground biomass increment, LF litterfall. All units are MgC ha⁻¹ year⁻¹

year was estimated summing monthly data for the year. For ABI and LF estimates, we assumed that the C content of the dried biomass was 50 %, like in several other studies (e.g. Clark et al. 2001b; Giardina and Ryan 2002; Malhi et al. 2004), because we did not measure the C content of the biomass and LF. Although some studies used different values for the C content, the values were very near to 50 % (e.g. 49 % for Curtis et al. (2002) and 53.1 % for Peichl et al. (2010)).

APR was calculated as follows:

$$\text{APR} = \text{ER} - \text{SR} \tag{5}$$

ER was calculated by *R* in Eq. (2) by multiplying the time length. Here, we used all available NEE data to determine the *R* value in Eq. (2). Even if we determined different *R* values for daytime and nighttime and estimated ER using these *R* values, the ER estimates did not change considerably. SR was assumed to have the same value as that determined by Katayama et al. (2009). In that study, a factor was identified that explained spatial SR variation in the 40 × 40 m plot, and SR for the 4-ha plot was estimated taking into account the spatial variation in that factor. Katayama et al. (2009) did not consider temporal variation in SR because the small variation in soil temperature and moisture meant that temporal variations in SR would be minor. Indeed, Ohashi et al. (2008) found no obvious relationship between SR and soil temperature or moisture.

According to the mass balance equation (e.g., Giardina and Ryan 2002, Litton et al. 2007), TBCF was calculated as follows:

$$\text{TBCF} = \text{SR} - \text{LF} + \text{F}_E + \Delta\text{C}_S + \Delta\text{C}_R + \Delta\text{C}_L \tag{6}$$

where *F_E* is C exported by erosion, leaching, or CH₄ efflux, Δ*C_S* is the change in the C content of mineral soil, Δ*C_R* is the increment in the C content of root biomass, and Δ*C_L* is the change in the C content of the litter layer. We assumed *F_E*, Δ*C_S*, Δ*C_R*, and Δ*C_L* were negligible, similar to many previous studies (e.g., Davidson et al. 2002; Raich and Nadelhoffer 1989). Although we did not have sufficient data such as soil organic matter and litter conditions to support this assumption, the following studies imply the validity of our assumption: Giardina and Ryan (2002) reported that *F_E* was less than 1 % of TBCF and annual changes in C storage in soil were 2.1 % of TBCF in young tropical rainforests. Telles et al. (2003) also reported that Δ*C_S* and Δ*C_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 estimating belowground C cycling for tropical rainforests. On the other hand, some studies showed that C storage in soil could be an important component of C cycling for temperate forests (Ohtsuka et al. 2007, 2010). Despite these previous studies implying

the validity of the assumption under the conditions in tropical rainforests, we could not examine the validity of the assumption based on data obtained from in situ measurements. Therefore, we stress the need for further studies examining the validity of such assumptions based on in situ measurements.

Results

GPP and each component

Figure 2 shows the relationship between *S_r* and NEE. NEE decreased with increasing *S_r*. We obtained the following coefficients for Eq. (2): *R* = 8.10, *A_{max}* = −30.49 μmol m^{−2} s^{−1}, and *a* = −0.13. The equation approximated well the relationship between *S_r* and NEE. The time-series of C allocation components are shown in Fig. 3. There was only minor year-to-year variation in the components; for example, GPP_{eddy} ranged between 30.41 and 30.96 MgC ha^{−1} year^{−1}. We determined C allocation for our site as shown in Table 2 and Fig. 4. The mean ± standard deviation (SD) of GPP_{eddy} for the 5 years from 2001 to 2005 was 30.61 ± 0.22 MgC ha^{−1} year^{−1} (Fig. 4). The mean ± SD of ANPP, APR, and TBCF for the 5 years were estimated as 6.76 ± 0.57, 8.01, and 19.63 MgC ha^{−1} year^{−1}, respectively. Consequently, the mean GPP_{biometric} for the 5 years was estimated as 34.40 MgC ha^{−1} year^{−1}. The ratios of ANPP, APR, and TBCF to GPP estimated from biometric/eddy covariance measurements were 0.20/0.22, 0.23/0.26, and 0.57/0.64, respectively.

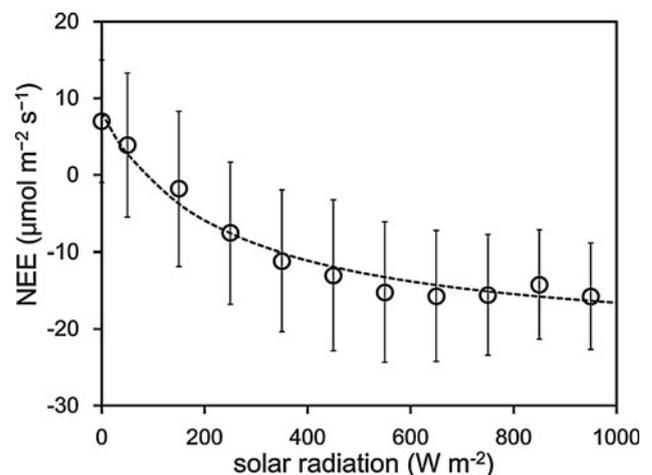


Fig. 2 Relationship between solar radiation (*S_r*, Wm^{−2}) and net ecosystem exchange (NEE, μmol m^{−2} s^{−1}). NEE data were divided into different *S_r* classes and then averaged. Error bars indicate standard deviation of NEE in each *S_r* class. Regression equation (Eq. 2, dotted line) was determined using least-squares method

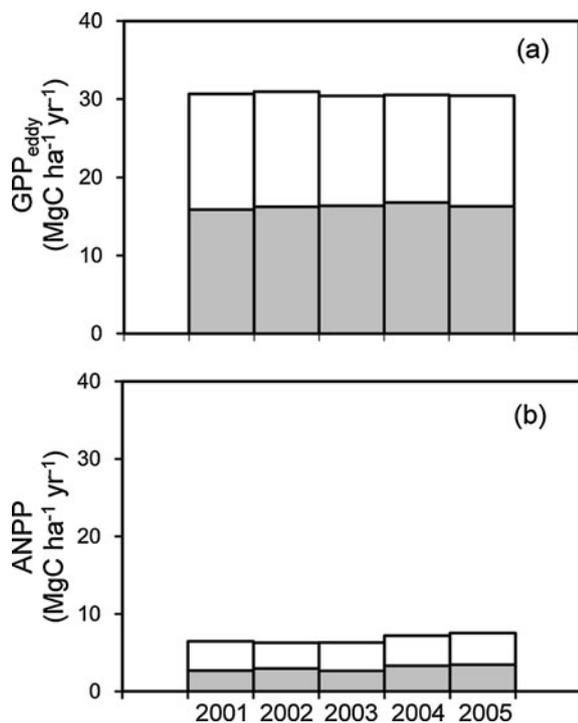


Fig. 3 **a** Time-series of gross primary production estimated by eddy covariance measurements (GPP_{eddy} , $MgC\ ha^{-1}\ year^{-1}$) and its components, i.e., ecosystem respiration in daytime (ER_{day} , $MgC\ ha^{-1}\ year^{-1}$, shaded column) and net ecosystem exchange in daytime ($-NEE_{day}$, $MgC\ ha^{-1}\ year^{-1}$, blank column). **b** Time series of aboveground net primary production (ANPP, $MgC\ ha^{-1}\ year^{-1}$) and its components, i.e., litterfall (LF, $MgC\ ha^{-1}\ year^{-1}$, shaded column) and aboveground biomass increment (ABI, $MgC\ ha^{-1}\ year^{-1}$, blank column)

Comparison with other tropical rainforests

The GPP for our site was within the range reported for tropical rainforests with dry seasons in the Amazon (Table 2). In Asian tropical rainforests without dry seasons, the reported GPP for a lowland tropical rainforest in Peninsular Malaysia ($32.43\ MgC\ ha^{-1}\ year^{-1}$, Kosugi et al. 2008) and that for a tropical peat swamp forest in Borneo ($34.34\ MgC\ ha^{-1}\ year^{-1}$, Hirano et al. 2007) were comparable to the GPP for our site.

The values for ANPP and the ratio of ANPP to GPP for our site were comparable to those for Amazonian forests (Table 2). According to an empirical relationship between GPP and ANPP across various forest ecosystems around the world ($ANPP = 0.32 \times GPP$, $R^2 = 0.88$, $n = 34$, Litton et al. 2007), ANPP for our site was estimated as $10.92\ MgC\ ha^{-1}\ year^{-1}$ with the input of $GPP_{biometric}$ obtained in this study. The ANPP measured for our study tended to be lower than this value (Fig. 5a).

The values for APR and the ratio of APR to GPP for our site were lower than those for Amazon forests (Table 2). Although APR for our site was also lower than the value

expected from the linear correlation between GPP and APR across various forest ecosystems around the world ($APR = 0.32 \times GPP$, $R^2 = 0.78$, $n = 31$, Litton et al. 2007), APR for our site was within the range of data scattering (Fig. 5b).

The values for TBCF and the ratio of TBCF to GPP for our site were considerably greater than those of Amazonian forests (Table 2). The ratio was much higher than those reported for various forest ecosystems by Litton et al. (2007). According to an empirical relationship between GPP and TBCF among various forest ecosystems around the world ($TBCF = 0.36 \times GPP$, $R^2 = 0.73$, $n = 34$, Litton et al. 2007), the TBCF for our site was estimated as $12.42\ MgC\ ha^{-1}\ year^{-1}$ with the input of $GPP_{biometric}$ (Fig. 5c).

Discussion

The GPP for our site was comparable to those reported for Amazonian forests, although there are dry seasons in Amazonian forests. The GPP in Tapajós, where MAR was the lowest among the three Amazonian forests (Table 2), was not related to rainfall intensity in the dry season, suggesting that the reduction in transpiration and, therefore, in photosynthesis, in dry seasons due to soil water deficit would not be significant, possibly because of deep roots (Hutyra et al. 2007). The comparable GPP is surprising when considering the difference in AGB between our site and the Amazonian forests (Table 2). We do not have enough data to explain the reason for this result with certainty at this stage. There are three possible explanations for the high AGB for our site: (i) high GPP, (ii) low plant respiration relative to AGB, and/or (iii) low turnover rates of biomass. The first possibility was not supported by our results. The second possibility was partly supported the lower APR for our site (see below). We cannot examine the third possibility at this stage because of the absence of data.

The ANPP for our site was comparable to those for the Amazonian forests. Furthermore, ANPP relative to GPP for our site was lower than the typical values derived from synthesis of global data (Fig. 5a). These results do not support our hypothesis that lower ANPP would be observed for our site than that for Amazonian forests because of the higher soil water availability for our site. Therefore, the difference in ANPP between our site and the Amazonian forests cannot be explained only from the viewpoint of soil water availability for our site. One possible explanation for the lower ANPP for our site might be low soil phosphorus availability. ANPP was positively correlated with soil phosphorus availability in the Amazon (Aragão et al. 2009) and Borneo (Paoli and Curran 2007), implying that soil phosphorus availability is a determinant

Table 2 Data for forest in this study (Sarawak, Malaysia) and for Amazonian forests (from Malhi et al. 2006, 2009)

Site	Forest in this study (Sarawak, Malaysia)	Amazonian forests		
		Manaus	Tapajós	Caxiuana
MAT	25.8	27.0	26.33	26.96
MAR	2,600	2,167–2,247	1,968	2,314
AGB	272.4	148–180	143.7–175	191–209
LF	3.02 ± 0.36 (0.09/0.10)	3.6 (0.13/0.12)	6.5 (0.23/0.21)	3.8 (0.13/0.10)
ABI	3.74 ± 0.29 (0.11/0.13)	2.58 (0.09/0.08)	3.76 (0.13/0.12)	2.16 (0.07/0.06)
ANPP	6.76 ± 0.57 (0.20/0.22)	6.18 (0.21/0.20) ^a	10.26 (0.36/0.33) ^a	5.96 (0.20/0.16) ^a
APR	8.01 (0.23/0.26)	14.2 (0.49/0.47)	11.2 (0.40/0.36)	14.0 (0.46/0.37)
SR	22.65 (0.66/0.74)	12.1 (0.42/0.40)	12.0 (0.43/0.38)	13.5 (0.45/0.35)
TBCF	19.63 (0.57/0.64)	8.4 (0.29/0.28)	6.7 (0.24/0.21)	10.2 (0.34/0.27)
GPP _{eddy}	30.61 ± 0.22	30.4	31.4	38.2
GPP _{biometric}	34.40	28.8 ^a	28.16 ^a	30.16 ^a

Data for Amazonian tropical rainforests (Malhi et al. 2006, 2009) are also shown. Values in parentheses are ratio of each component to GPP_{biometric} and GPP_{eddy}, respectively

MAT Mean annual temperature (°C), MAR mean annual rainfall (mm), AGB above ground biomass (MgC ha⁻¹), and mean ± standard deviation for each component of C allocation (MgC ha⁻¹ year⁻¹), LF litterfall, ABI aboveground biomass increment, ANPP aboveground net primary production, ER ecosystem respiration, APR aboveground plant respiration, SR soil respiration, TBCF total belowground carbon flux, GPP gross primary production

^a Values differ from those presented in Malhi et al. (2009) for the following reasons. This study estimated ANPP and GPP_{biometric} ignoring branch turnover and volatile organic compounds, similar to several previous studies (e.g. Malhi et al. 2006; Paoli and Curran 2007), primarily because of uncertainties in these data. In contrast, Malhi et al. (2009) estimated ANPP and GPP_{biometric} considering branch turnover and VOC. For comparison, we calculated ANPP and GPP_{biometric} for Amazonian forests ignoring branch turnover and VOC

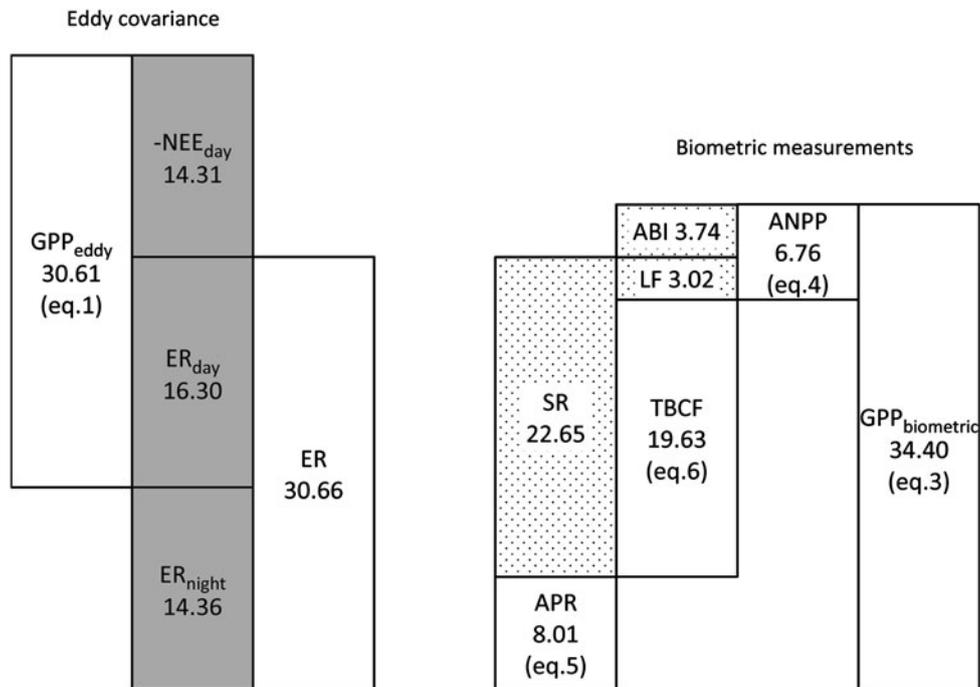


Fig. 4 Carbon allocation estimated in this study. Shaded columns indicate components directly determined by eddy covariance measurements. Dotted columns indicate components determined by biometric measurements. Blank columns indicate components estimated using mass balance equation. GPP_{eddy}, Gross primary production based on eddy covariance measurements. NEE_{day}, Net ecosystem exchange in daytime. ER_{day}, Ecosystem respiration in daytime.

ER_{night}, Ecosystem respiration in nighttime. ER, Ecosystem respiration. SR Soil respiration, APR aboveground plant respiration, ABI aboveground biomass increment, LF Litterfall, TBCF total belowground carbon flux, ANPP aboveground net primary production, GPP_{biometric} gross primary production based on biometric measurements. All units are MgC ha⁻¹ year⁻¹

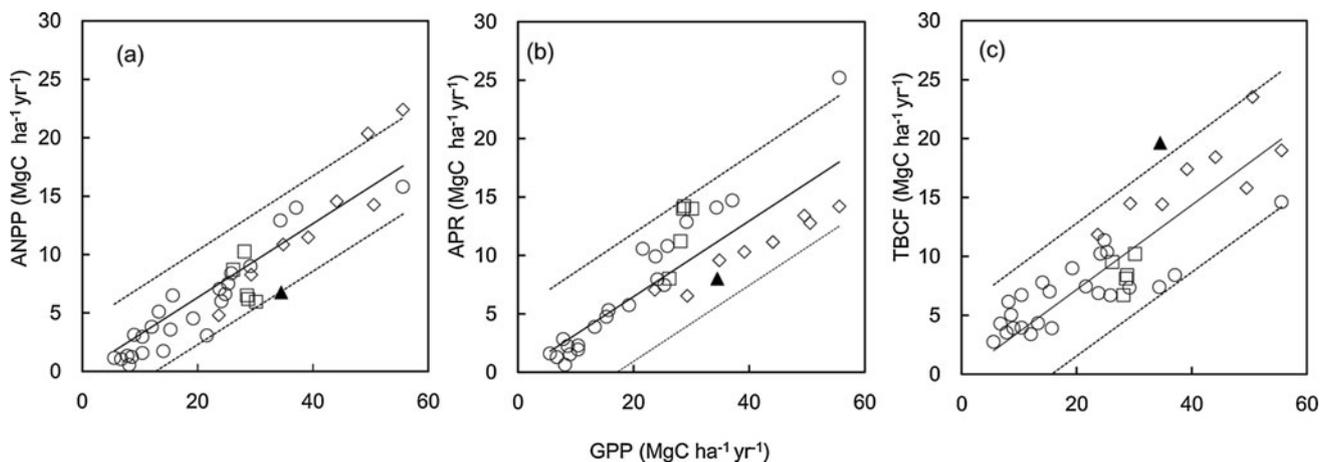


Fig. 5 Relationships of gross primary production with (a) above-ground net primary production (ANPP, $\text{MgC ha}^{-1} \text{ year}^{-1}$), (b) above-ground plant respiration (APR, $\text{MgC ha}^{-1} \text{ year}^{-1}$) and (c) total belowground carbon flux (TBCF, $\text{MgC ha}^{-1} \text{ year}^{-1}$) for tropical rainforests including this study and those in literature. Data set represents forest in this study based on $\text{GPP}_{\text{biometric}}$ (solid triangles), tropical rainforests in Amazon with dry seasons reported by Malhi et al. (2009) and represented in Table 2, and also reported by Litton et al. (open squares; 2007), young Eucalyptus plantations in Hawaii without dry seasons (open diamonds; Litton et al. 2007) and temperate and boreal forests (open circles; Litton et al. 2007). Solid

lines indicate regression lines for data of Litton et al. (2007); (a) $\text{ANPP} = 0.32 \times \text{GPP}$ ($R^2 = 0.88$), (b) $\text{APR} = 0.32 \times \text{GPP}$ ($R^2 = 0.78$) and (c) $\text{TBCF} = 0.36 \times \text{GPP}$ ($R^2 = 0.73$). Dashed lines are upper and lower 95 % confidence intervals of the regression. Regression for ANPP and APR was calculated in the present study using data of aboveground biomass increment (ABI), litterfall (LF), foliage respiration, and wood respiration presented in Litton et al. (2007), because that study did not describe relationships between GPP and ANPP or between GPP and APR. Regression for TBCF was determined by Litton et al. (2007)

of ANPP. Although soil nutrient data is limited at present and direct comparison is impossible because of different chemical analyses of soils from different depths, the amounts of available phosphorus in soil approximately 300 m away from the 4-ha plot (8.21 mg kg^{-1} in 0–5 cm depth; 0.25 mg kg^{-1} in 5–50 cm depth, Table 2) were lower than those reported from the Amazon ($9.12\text{--}20.08 \text{ mg kg}^{-1}$ in 0–30 cm soil; Malhi et al. 2009).

The APR and the ratio of APR to GPP for our site were lower than those for the Amazonian forests and the typical values derived from synthesis of global data (Table 2; Fig. 5b). This result is unexpected when assuming a positive correlation between APR and AGB. AGB was higher for our site than for the Amazonian forests, predicting higher APR for our site. Furthermore, woody tissue respiration, as determined using the chamber method, decreased in the dry season in Manaus (Chambers et al. 2004) and Tapajós (Nepstad et al. 2002), which again predicted that the higher APR for our site was because of the absence of dry seasons. Our result disagrees with this prediction. We do not have sufficient explanations for this disagreement at this stage. To solve this problem, we first need to tackle the uncertainty in APR estimates according to eddy covariance and chamber-based measurements. Note that the APR value for our site was estimated based on eddy covariance measurements, while APR values for the Amazonian forests were estimated based on chamber measurements. Piao et al. (2010) examined the relationship between plant

respiration at an ecosystem scale and the amount of biomass, and obtained contrasting results using the two different methods. Based on a meta-analysis using data for various forests worldwide, they observed a correlation between plant respiration at an ecosystem scale and biomass amounts when using respiration data based on chamber measurements obtained on an individual scale and scaled-up to an ecosystem scale. However, they did not observe this correlation when using data based on eddy covariance measurements. There are uncertainties associated with both methods: in scaling up chamber-based plant respiration measurements, it is assumed that respiration rates are similar among different individuals and biomass amount is used for scaling (Cavaleri et al. 2006), while the uncertainty in eddy-covariance based measurements results from the unreliability of nighttime fluxes, primarily because of nocturnal drainage flow (Kosugi et al. 2008). To reduce the uncertainty in estimates of plant respiration, we need further measurement studies bridging these two methods.

The TBCF for our site was higher than those for the Amazonian forests and the typical values derived from synthesis of global data (Table 2; Fig. 5c) because of the higher SR for our site. SR for our site was higher than those in the three Amazonian forests throughout the year, although the SR increased in wet seasons in the Amazon (Chambers et al. 2004; Davidson et al. 2004; Sotta et al. 2006). In general, higher soil water availability could lead

to less intensity of fine root competition for water and therefore lower SR (see the introduction). Therefore, differences in soil water availability between our site and the Amazonian rainforests cannot explain the difference in SR. Spatial variations in SR for 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} (Table 1, Katayama et al. 2009), while that in surface soil (0–10 cm) was $2.18\text{--}3.5 \text{ Mg ha}^{-1}$ in the Amazon (Nepstad et al. 2002; Silver et al. 2005). Thus, the difference in fine root biomass between our site and the Amazonian rainforests would partly explain the difference in TBCF. We do not have data for total below-ground biomass for our site. However, it would not play an important role in determining TBCF (Litton et al. 2007). Fine roots made the greatest contribution to determining TBCF because fine roots accounted more than $\approx 70\%$ of total root respiration and belowground net primary production (Burton et al. 2012; Curtis et al. 2002).

Low nutrient availability could be a possible cause for the higher fine root biomass and, therefore, TBCF for our site, as well as the lower ANPP. We recommend studies examining soil (and leaf) nutrient status in the 4-ha plot, and comparisons of such data with those obtained for other tropical forests (e.g., Malhi et al. 2009). Further, we recommend studies examining C allocation for tropical rainforests without dry seasons under various topographical conditions. The 4-ha plot where this study was conducted is located near the ridge of a gentle hill, suggesting low nutrient availability at our site (Baillie et al. 2006; Ishizuka et al. 1998; Lee et al. 2002). Comparisons of C allocation for our site with those for sites in valleys where nutrient availability is expected to be high would allow us to evaluate the contribution of nutrient availability to C allocation in tropical rainforests without dry seasons.

Conclusion

We observed a difference in C allocation between a Bornean tropical rainforest and Amazonian forests despite the similarity of forest category and GPP. This suggested that there are variations in C allocation among sites covered with mature tropical rainforests, consistent with the results of Litton et al. (2007) based on synthesis of data mainly derived from temperate or managed forests. The difference in C allocation was not explained by the difference in dry seasons, and therefore soil water availability, suggesting that other factors must be considered to explain spatial variations in C allocation among mature tropical rainforest sites. Our results suggested that soil nutrient availability

might be a factor in explaining the difference in C allocation between our site and the Amazonian sites. Thus, it is necessary to examine differences in C allocation among tropical rainforest sites with similar rainfall and soil water availability but different soil nutrient conditions. Such studies will contribute to refining the understanding and models of C allocation.

The characteristics of C cycling at this site were revealed not solely by the eddy covariance measurements, but by a combination of biometric measurements. There are numerous forest sites where eddy covariance measurements have been performed, but biometric measurements have not been sufficiently conducted (Hirano et al. 2007; Kosugi et al. 2008). Data from such sites have been compared and used to develop a comprehensive understanding of forest C cycling (Hirata et al. 2008; Malhi 2012). However, our results demonstrate aspects of C cycling that could not be clarified using only eddy covariance measurements. Thus, we recommend conducting biometric measurements at sites where only eddy covariance measurements have been performed. A greater number of sites for which such data are available would enable comparisons of C cycling including C allocation among various forest sites, and would lead to a more process-based understanding of C cycling.

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