

Characteristics of wood CO₂ efflux in a Bornean tropical rainforest



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ARTICLE INFO

Article history:

Received 13 September 2015

Received in revised form 16 January 2016

Accepted 20 January 2016

Keywords:

Emergent trees

Ecosystem scale

Inter-individual variation

Scaling

Stem CO₂ efflux

ABSTRACT

Wood CO₂ efflux (R_{wood}) is an important carbon cycling process in forest ecosystems and is less understood in Bornean tropical rainforests compared with that in Neotropics, which have differing biotic and abiotic characteristics. Bornean tropical rainforests have particularly higher aboveground biomass because of high stand densities of tall emergent trees, and no regular seasonal dry period. These properties may reflect specific R_{wood} variation and higher annual R_{wood} at the ecosystem scale (annual- R_{wood}) in Borneo. Hence, in this study, we investigated factors that affect inter-individual variation in chamber-based R_{wood} on stem surfaces at breast height (chamber- R_{wood}) and estimated R_{wood} at the ecosystem scale (ecosystem- R_{wood}) in a Bornean tropical rainforest. Subsequently, we examined temporal variation in ecosystem- R_{wood} with environmental factors, estimated annual- R_{wood} , and then evaluated the effects of large trees on ecosystem- R_{wood} .

Stem growth rates were the most significant predictor of inter-individual variation in chamber- R_{wood} during all five measurement periods between 2012 and 2014. Accordingly, stem growth rates allowed accurate estimates of ecosystem- R_{wood} , although chamber- R_{wood} varied with diameter at breast height (DBH) and tree species in some measurement campaigns. Ecosystem- R_{wood} decreased with soil moisture. Considering the inter-individual and temporal variation, annual- R_{wood} was estimated at 7.06 ± 2.09 MgC ha⁻¹ year⁻¹. This value was comparable to those determined in Neotropical forests, even though aboveground biomass in the present study site was approximately twice of those in Neotropical sites. Large trees with DBH > 70 cm comprised 38% of aboveground biomass but accounted for only 23% of ecosystem- R_{wood} because of the small portion of woody tissue surface area of the large trees. These data indicate that the stand density of large trees can considerably affect aboveground biomass but exert less influence on variation in ecosystem- R_{wood} among various forests.

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1. Introduction

Tropical forests play important roles in global carbon cycling because of the highest photosynthesis and respiration rates of forest ecosystems (Beer et al., 2010; Malhi, 2012). Wood CO₂ efflux (R_{wood}) is a measure of carbon release from stems and branches and is an important indicator of forest ecosystem productivity, because it accounts for about 20–25% of plant respiration (Chambers et al., 2004; Malhi et al., 2009) and 13–27% of carbon assimilation from photosynthesis (Malhi et al., 2009; da Costa et al., 2013; Doughty

et al., 2013). Recent studies have estimated R_{wood} at the ecosystem-scale (ecosystem- R_{wood} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) in Neotropical rainforests (Chambers et al., 2004; Cavaleri et al., 2006; da Costa et al., 2013; Rowland et al., 2014), although studies on ecosystem- R_{wood} outside Neotropical areas remain limited (Meir and Grace, 2002). Measurements of ecosystem- R_{wood} in various kinds of tropical rainforests are important for investigations of global carbon cycling, because variation of ecosystem- R_{wood} with biotic and abiotic factors remains poorly understood.

R_{wood} on woody surface areas (chamber- R_{wood} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) is generally estimated using the chamber method, and ecosystem- R_{wood} is usually estimated by multiplying chamber- R_{wood} at breast height by woody tissue surface areas or volumes (Meir and Grace, 2002; Chambers et al., 2004). Estimates of ecosystem- R_{wood}

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still remain challenged by intra- and inter-individual variations in chamber- R_{wood} that can lead to errors in scaled estimates (Chambers et al., 2004; Malhi et al., 2009). Recently, Katayama et al. (2014) showed limited vertical variation in chamber- R_{wood} based on measurements of up to 40-m high trees in a Bornean tropical rainforest, suggesting that intra-individual variation has limited effects on estimates of whole tree stem CO_2 efflux. However, the effects of inter-individual variation remain unclear, warranting careful examination especially in old-growth tropical rainforests where tree species and sizes vary.

Multiple factors have been shown to affect inter-individual variation in chamber- R_{wood} , and various scaling methods have been suggested. In previous studies of tropical rainforests, inter-individual variation in chamber- R_{wood} was related to diameters at breast height (DBH; Cavaleri et al., 2006), stem growth rates (Ryan et al., 1994), and both (Chambers et al., 2004; Robertson et al., 2010). Subsequently, these factors were used to extrapolate chamber- R_{wood} values in individuals without direct measurements and then to estimate ecosystem- R_{wood} . In recent study of Neotropical forests, ecosystem- R_{wood} values were estimated by means of measured chamber- R_{wood} values (Rowland et al., 2014). Previous studies also reported that ecosystem- R_{wood} vary temporally with soil moisture, reflecting changes in stem growth in response to seasonal dry periods in Neotropical rainforests (Chambers et al., 2004; Malhi et al., 2014). These studies warrant investigation of factors that affect temporal variation in ecosystem- R_{wood} . Furthermore, the factors affecting inter-individual variation in chamber- R_{wood} may vary temporally. Thus, examinations of inter-individual variation in chamber- R_{wood} across measurement periods are required to investigate temporal variation in ecosystem- R_{wood} and to estimate annual R_{wood} at the ecosystem scale (annual- R_{wood} , $MgC\ ha^{-1}\ year^{-1}$).

It is well known that Bornean tropical rainforests have high aboveground biomass. Accordingly, two-fold higher stand densities of large trees (DBH > 70 cm) resulted in 60% increases in aboveground biomass compared with those in Neotropical forests (Paoli et al., 2008; Slik et al., 2010). Moreover, large trees contributed considerably to aboveground biomass and aboveground biomass increments at the ecosystem scale in Borneo (Paoli and Curran, 2007). In a recent study, higher stem growth rates were shown in larger trees than in small trees according to global analyses (Stephenson et al., 2014). These data indicate that large trees can have higher individual R_{wood} because of both effects of high chamber- R_{wood} caused by high stem growth rates and DBH, and large surface area or volume. Thus, large trees may also contribute considerably to ecosystem- R_{wood} , potentially leading to greater ecosystem- R_{wood} values in Bornean than those in Neotropical forests. Higher annual- R_{wood} in Borneo is also expected with consideration of temporal variation. There is no regular seasonal dry period but irregular short-term drought period occurs in Borneo, while there are several seasonal dry months in most Neotropical area (Malhi et al., 2006) where lower chamber- R_{wood} values were observed during dry months (Chambers et al., 2004; Malhi et al., 2014). Although higher annual- R_{wood} is expected in Borneo, the study on annual- R_{wood} has not been conducted in such forests.

In this study, we measured chamber- R_{wood} at breast heights of more than 50 individual trees of 36 species in a Bornean tropical rainforest with high aboveground biomass and no regular seasonal dry period. Measurements were performed five times under various soil water conditions. In subsequent analyses, factors affecting inter-individual variation in chamber- R_{wood} for each measurement period were identified, and ecosystem- R_{wood} was subsequently calculated. We also determined the effects of environmental factors, such as soil moisture and air temperature, on temporal variation in ecosystem- R_{wood} , and annual- R_{wood} , and its ratio to gross primary

production (GPP) were estimated accordingly. Finally, we examined the contribution of large trees to ecosystem- R_{wood} .

2. Materials and methods

2.1. 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 6949 ha park. The continuous tree layer is approximately 40 m above the ground, but the heights of trees with DBH > 100 cm often exceed 50 m (Katayama et al., 2014). The leaf area index ranges spatially between 4.8 and 6.8 $m^2\ m^{-2}$, with a mean of 6.2 $m^2\ m^{-2}$ (Kumagai et al., 2004). Between 2000 and 2009, the mean annual temperature at this site was 25.8 °C and 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 and precipitation, unpredictable dry periods sometimes occur throughout the year.

A 4 ha study plot was established surrounding a crane for ecological observation. Previously, we performed carbon cycling measurements, including eddy covariance measurements, carbon allocation (Katayama et al., 2013), and soil respiration (Katayama et al., 2009) at this site.

2.2. R_{wood} 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. Measured trees were selected randomly from 52 trees during each measurement period, and the numbers of measured trees were 48, 48, 47, 50, and 38 in January 2012, May 2013, July 2013, December 2013, and June 2014, respectively (Table A1). DBH ranged from 10 to 158 cm. The 52 samples included 36 species, and 24 of these were the Dipterocarpaceae family. 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). Diurnal measurements chamber- R_{wood} of five trees were performed every 2 h between 7:30 and 17:30 on January 1, 2014, to examine the effect of diurnal variation on the daily R_{wood} estimate based on one-time measurements during daytime.

Chamber- R_{wood} was measured using a closed-static system with an infrared gas analyzer (GMP343, Vaisala, Helsinki, Finland) attached inside a chamber. The chamber and collars were made of polyvinyl chloride. A small 8-V battery-operated fan was installed to circulate air inside the chamber, collars were attached to stems using glue and silicon sealant, and gaps between stems and collars were filled with nondrying clay. Leaks were checked after measurements by breathing around the chamber. For all measurements, incubation periods ranged from 60 to 180 s, and CO_2 concentrations within the chamber were measured every 5 s and recorded using a monitor (M170, Vaisala). Chamber- R_{wood} ($\mu\text{mol}\ m^{-2}\ s^{-1}$) was calculated using Eq. (1) as follows:

$$R_{wood} = \left(\frac{273.2}{273.2 + T_a} \right) \times \frac{V}{22.4} \times \frac{dC}{dt} \times 10^6 \times \frac{1}{A}, \quad (1)$$

where V is the chamber volume (0.3891), T_a is air temperature inside the chamber (°C), A is the projected area of the chamber ($3.849 \times 10^{-3}\ m^2$), and dC is the increment of CO_2 concentration (ppm) during the incubation time (s, dt). Eq. (1) assumes that respiration is measured under standard barometric

pressure. All measurements at each point were replicated two or three times and means were calculated. System accuracy was determined by measuring R_{wood} of some trees using a commercial respirometer (LI-6400, Li-Cor Inc., Lincoln, NE, USA) at the same time points. The relationship between R_{wood} observed using the system ($R_{wood-system}$) and LI-6400 ($R_{wood-LI6400}$) was linear ($R_{wood-LI6400} = 1.1394 \times R_{wood-system}$, $R^2 = 0.97$); thus, chamber- R_{wood} was estimated by correcting $R_{wood-system}$ using this equation.

Stem surface and air temperatures were measured concomitantly using a thermometer (Ondotori; T&D Co. Ltd., Nagano, Japan). To eliminate the effects of temperature, chamber- R_{wood} values were corrected to a reference temperature of 25 °C using Eq. (2) as follows:

$$R_{25} = R(st)Q_{10}^{(25-st)/10}, \quad (2)$$

where R_{25} is chamber- R_{wood} at 25 °C, st is the stem surface temperature (°C) where R_{wood} was measured, and Q_{10} is a temperature coefficient of R_{wood} . Because Q_{10} was not calculated from the present data, it was assumed that Q_{10} was equal to 2.0, as shown previously by Cavalieri et al. (2006) in tropical rainforests in La Selva, Costa Rica. In the present study, chamber- R_{wood} was used as R_{25} based on surface area, which was corrected at 25 °C.

Environmental observations were incorporated into analyses of temporal variation in ecosystem- R_{wood} . Air temperature was monitored on the crane at 75 m above the ground using a thermohygrograph (HMP35A, Visala) and the data was 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). Soil water content was determined at depths of 10, 30, 60, and 100 cm using time domain reflectometry sensors (CS616, Campbell) and a data logger near the crane, and mean daily soil water content (SWC, $m^3 m^{-3}$) was calculated at a depth of 0–120 cm. Measurements were initiated on 3rd September 2012, and soil moisture contents were interpolated between 1st January 2011 and 2nd September 2012 ($SWC_{estimate}$) using the relationship between cumulative 30 day rainfall (R_{cum}) and measured soil water contents ($SWC_{estimate} = 0.1631 \times R_{cum}^{0.107}$, $R^2 = 0.67$).

2.3. Tree census

A tree census was conducted in the 4-ha plot in 2012 and 2013. DBH values for trees with DBH > 10 cm were measured with a resolution of 1 mm, and differences in diameter between 2012 and 2013 were calculated as stem circumference growth rates (sg, $cm y^{-1}$) for all trees. Aboveground biomass in Borneo was estimated using DBH and a previously described allometric equation (Yamakura et al., 1986).

2.4. Scaling method and statistical analysis

To estimate annual- R_{wood} , ecosystem- R_{wood} for each measurement series was estimated from measured chamber- R_{wood} (spatial scaling), and daily ecosystem- R_{wood} in 2013 was also estimated from the relationship between the estimated ecosystem- R_{wood} and environmental factors (temporal scaling). For spatial scaling, ecosystem- R_{wood} in the 4-ha plot was estimated by two methods. In one, ecosystem- R_{wood} was estimated by multiplying mean measured chamber- R_{wood} values by woody tissue surface areas in the 4-ha plot and then dividing by the ground area, as defined by Model0. In the other, ecosystem- R_{wood} was estimated as the sum of individual R_{wood} (individual- R_{wood} , $\mu mol tree^{-1} s^{-1}$) for all trees in the 4-ha plot and divided by the ground area. Individual- R_{wood} was estimated by multiplying individual chamber- R_{wood} values by woody tissue surface areas. Chamber- R_{wood} values for all trees

were estimated by regression models. Predictors of the model included sg (continuous variable), DBH (continuous variable), and tree species (categorical variable; Dipterocarpaceae *Dryobalanops aromatica*, Dipterocarpaceae *Shorea beccariana*, Moraceae *Artocarpus anisophyllus*, and others) (Table A1). The three species for which more than three individuals were measured were selected as variables. To examine the effect of predictors on ecosystem- R_{wood} estimates, we constructed three models for chamber- R_{wood} estimate, the best-fit model, Model1, and Model2. The best-fit model was defined as the model for which predictors were determined according to the lowest AIC value from the full model. Predictor variables in Model1 were sg and DBH and the predictor in Model2 was sg. The same coefficients of sg and DBH were used across species. Woody tissue surface areas were estimated using the relationship between DBH and surface area, as previously described (Chambers et al., 2004) for Neotropical forests, and surface area of woody tissue per unit ground area (stem area index, SAI, $m^2 m^{-2}$) was calculated for comparison with previous studies. Errors in ecosystem- R_{wood} for Model0 were standard deviations of measured chamber- R_{wood} , and errors for other models were derived from 95% confidence limits for each model.

Temporal scaling was performed using a regression model with environmental factors such as SWC and air temperature. Only predictive factors with significant correlation were used for the model. Annual ecosystem- R_{wood} were estimated using the best-fit model, Model1, Model2, and Model0. Errors in annual ecosystem- R_{wood} were derived from 95% confidence limits for each model for temporal scaling. All statistical analyses were conducted using R version 3.1.3.

Although some previous studies demonstrate vertical variation in R_{wood} for scaling (Yoda et al., 1965; Damesin et al., 2002), we assumed constant R_{wood} with height because previous studies show limited vertical variation in R_{wood} based on surface area in this study site (Katayama et al., 2014). In the present study, the use of surface area for scaling individual- R_{wood} from chamber- R_{wood} was determined based on the result of a graphical technique (Levy and Jarvis, 1998; Cavalieri et al., 2006) using vertical R_{wood} data from a previous study (Katayama et al., 2014; Fig. A1).

2.5. GPP estimates

GPP was defined as the sum of aboveground plant respiration (R_{above}), aboveground net primary production (ANPP), and total belowground carbon flux (TBCF) according to a previous study (Litton et al., 2007). R_{above} is the sum of ecosystem- R_{wood} and foliage CO_2 efflux ($R_{foliage}$). Ecosystem- R_{wood} was estimated in the present study (see Section 2.4). Ecosystem- $R_{foliage}$ was estimated as the sum of leaf area densities multiplied by $R_{foliage}$ at every 5 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 24 families, 62 species, and 123 individual trees 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). $R_{foliage}$ was corrected to the respiration rate at 25 °C using Q_{10} . Q_{10} was not measured either in the present study or in previous studies in Asian tropical rainforests. Although there was high variation in Q_{10} among tree species in the Neotropics (Asao et al., 2015), Q_{10} was not different among canopy positions and the value of Q_{10} averaged among various species was 2.0 in Australia (Weerasinghe et al., 2014) and 2.3 in Costa Rica (Cavalieri et al., 2008). In the present study, Q_{10} was assumed to

be 2.3, a value reported in tropical rainforests in La Selva (Cavaleri et al., 2008) that was obtained because of a higher number of measurements. Several studies showed 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, 2014; da Costa et al., 2013; Doughty et al., 2013). Annual R_{foliage} at the ecosystem scale (annual- R_{foliage} , $\text{MgC ha}^{-1} \text{ year}^{-1}$) was estimated assuming 12 h of daytime and nighttime and a constant temperature of 25 °C each day throughout the year, and the error in annual R_{foliage} represents spatial variation according to a previous study (Metcalf et al., 2010). ANPP ($6.76 \pm 0.57 \text{ MgC ha}^{-1} \text{ year}^{-1}$) and TBCF ($19.63 \pm 6.37 \text{ MgC ha}^{-1} \text{ year}^{-1}$) were previously estimated in this study site (Katayama et al., 2013). ANPP was estimated based on tree census and litterfall measurements between 2001 and 2006 in the 4-ha plot, and the error was the standard deviation for the five years. TBCF was estimated as the difference between annual soil respiration and annual litterfall C using a steady-state assumption for soil C (Raich and Nadelhoffer, 1989). Soil respiration measurements were performed between 2002 and 2006, and the errors for soil respiration and litterfall represented spatial variation. Thus, each error of annual flux for GPP estimate was estimated based on measurements or models, resulting in different representations of variation. Error propagation was applied for all combined quantities using standard rules of quadrature according to Malhi et al. (2014), assuming that uncertainties were independent and normally distributed. Uncertainties in the estimates are described in Section 4.

2.6. Effects of large trees on ecosystem- R_{wood} and aboveground biomass

Ecosystem- R_{wood} and aboveground biomass in response to stand densities of large trees were investigated to assess the potential effects of large trees on ecosystem- R_{wood} and aboveground biomass. Large trees were defined as those with DBH > 70 cm according to Slik et al. (2013). Ecosystem- R_{wood} for various fictional stand densities of large trees was calculated as the sum of ecosystem- R_{wood} for large trees (ecosystem- $R_{\text{wood,large}}$, $\mu\text{mol m}^{-2} \text{ s}^{-1}$) and ecosystem- R_{wood} for trees with DBH < 70 cm (ecosystem- $R_{\text{wood,small}}$, $\mu\text{mol m}^{-2} \text{ s}^{-1}$). Ecosystem- $R_{\text{wood,large}}$ was estimated by multiplying mean individual- R_{wood} values for large trees obtained by the best-fit model in January/2012 with stand densities. Stand density of large trees differed between zero and actual densities (16.5 trees ha^{-1}). Ecosystem- $R_{\text{wood,small}}$ was the sum of individual- R_{wood} values for trees with DBH < 70 cm. Aboveground biomass was similarly calculated for various stand densities of large trees.

3. Results

3.1. Inter-individual variation in R_{wood}

Average \pm standard deviation (S.D.) chamber- R_{wood} values at breast height were 1.39 ± 0.74 , 0.99 ± 0.58 , 0.81 ± 0.52 , 1.23 ± 0.87 , and $0.91 \pm 0.65 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in January 2012, May 2013, July 2013, December 2013, and July 2014, respectively. Multiple regression analyses of each measurement period showed that sg and DBH were positively correlated with chamber- R_{wood} (Fig. 1), although selected variables differed for the best-fit model of chamber- R_{wood} . Among variables, sg was the most predictive of chamber- R_{wood} (Table 1), although DBH and species significantly affected chamber- R_{wood} in some cases. Specifically, chamber- R_{wood} was higher for *D. aromatica* and lower for *S. beccariana* than the other species when selected as the best-fit model. Diurnal variation patterns differed between

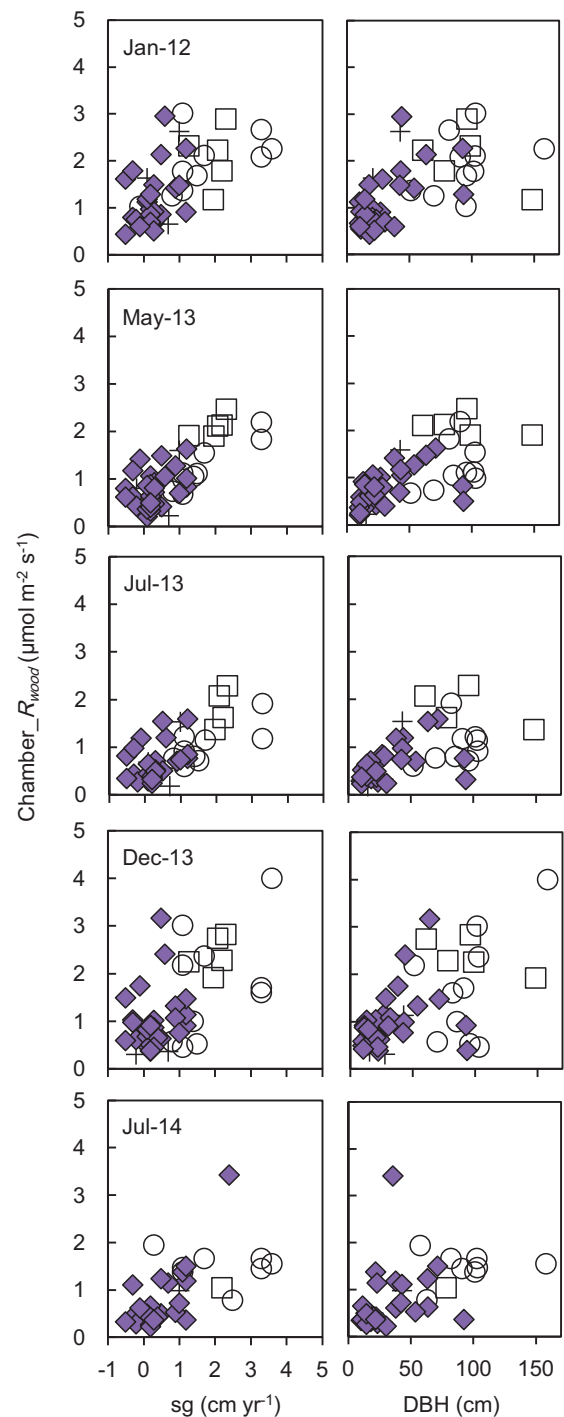


Fig. 1. Relationships of chamber- R_{wood} during each measurement period, with diameters at breast height (DBH; right) and stem growth rates (sg; left). Symbols indicate tree species: circles, DIPTEROCARPACEAE *Shorea beccariana*; squares, DIPTEROCARPACEAE *Dryobalanops aromatica*; cross, MORACEAE *Artocarpus anomophyllus*; closed diamond, other species.

individuals (Fig. A2). Chamber- R_{wood} peaked in the early afternoon for some trees but in the late afternoon for others. The mean CV of diurnal variation was $13 \pm 7\%$, and daily chamber- R_{wood} with consideration of diurnal variation was 1.09 ± 0.17 higher than those based on only one-time measurements in the daytime, suggesting an approximately 10% underestimate of chamber R_{wood} in this study.

Table 1
Statistical result of multiple regression analysis for each measurements period. The objective variable is chamber- R_{wood} . predictor variables for the best-fit model were determined according to the lowest AIC value from all predictors including stem growth rate (sg), dbh and tree species. Predictor variables of Model1 and Model2 are sg and DBH, and sg, respectively.

	Jan-12			May-13			Jul-13			Dec-13			Jul-14		
	Best-fit model	Model1	Model2	Best-fit model	Model1	Model2	Best-fit model	Model1	Model2	Best-fit model	Model1	Model2	Best-fit model	Model1	Model2
Coefficients of independent variables															
sg	0.28*	0.28*	0.47***	0.36***	0.36***	0.49***	0.32***	0.32***	0.41***	0.26*	0.30*	0.55***	0.37***	0.33**	0.37***
DBH	0.007*	0.007*	–	0.005*	0.005*	–	n.s.	0.003	–	0.007*	0.008*	–	n.s.	0.002	–
<i>D.beccariana</i>	n.s.	–	–	–0.28	–	–	n.s.	–	–	n.s.	–	–	n.s.	–	–
<i>D.aromatica</i>	n.s.	–	–	0.44	–	–	0.63**	–	–	0.58	–	–	–	–	–
<i>A.anisophyllus</i>	n.s.	–	–	n.s.	–	–	n.s.	–	–	n.s.	–	–	n.s.	–	–
Intercept	0.84***	0.84***	1.03***	0.53***	0.51***	0.64***	0.53***	0.44***	0.52***	0.61***	0.58***	0.79***	0.61***	0.56***	0.61***
AIC	84.34	84.34	87.67	34.19	45.31	47.75	36.23	43.52	43.58	106.37	107.33	110.00	63.63	65.42	63.63
R ²	0.47	0.47	0.40	0.72	0.62	0.58	0.60	0.53	0.51	0.46	0.43	0.37	0.36	0.36	0.36
N		48			48			47			50			38	

*** $P < 0.001$.

** $P < 0.01$.

* $P < 0.1$.

“n.s.” means that the factors were not selected by the best-fit model. “–” means that the factor were not used for the model.

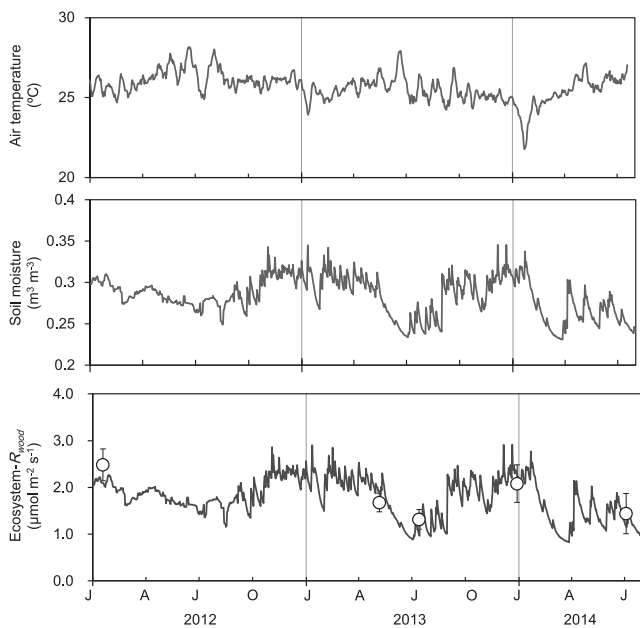


Fig. 2. Temporal variations in (a) air temperature, (b) soil moisture, and (c) R_{wood} between January 2012 and July 2014. Lines in (c) show ecosystem- R_{wood} values estimated using a linear regression model with soil moisture. Circles in (c) indicate ecosystem- R_{wood} values that were estimated using the best-fit model and error bars indicate the 95% confidence line of the model.

3.2. Temporal variations in ecosystem- R_{wood} , $R_{foliage}$, and GPP

Seasonal variations in air temperature and soil moisture were not clear, although air temperature decreased in January 2014, and soil moisture decreased in June 2013 and March 2014 (Fig. 2). On the other hand, high temporal variation in ecosystem- R_{wood} was observed (Fig. 2), with best-fit model estimates of 2.48 ± 0.34 , 1.68 ± 0.20 , 1.32 ± 0.21 , 2.08 ± 0.40 , and $1.44 \pm 0.43 \mu\text{mol m}^{-2} \text{s}^{-1}$ during January 2012, May 2013, July 2013, December 2013, and July 2014, respectively (Table 2). Estimates of ecosystem- R_{wood} from each model were significantly related to SWC except for Model2 (Table 3) but were not related to air temperature. Annual- R_{wood} between 2012 and 2013 estimated from the linear regression model with the predictor of SWC for Best-fit model, Model1, Model2, and Model0 were 7.06 ± 2.09 , 7.07 ± 2.18 , 6.68 ± 2.26 , and $8.56 \pm 2.20 \text{ MgC ha}^{-1} \text{ year}^{-1}$, respectively. Ecosystem- R_{wood} and annual- R_{wood} were comparable between the best-fit model, Model1, and Model2,

but Model0 gave higher values than the other models (Table 2), suggesting that sg is necessary for scaling, and that DBH and tree species are not. Annual- $R_{foliage}$ and GPP were 9.54 ± 0.46 and $42.99 \pm 6.74 \text{ MgC ha}^{-1} \text{ year}^{-1}$, respectively, and ratios of R_{wood} and $R_{foliage}$ to GPP were 0.17 ± 0.05 and $0.23 \pm 0.01 \text{ MgC ha}^{-1} \text{ year}^{-1}$, respectively.

3.3. Effect of large trees on R_{wood} and aboveground biomass

The number of large trees strongly influenced aboveground biomass, but less strongly influenced ecosystem- R_{wood} . Large trees were present in the study site at $16.5 \text{ trees ha}^{-1}$, accounting for only 3% of all trees ($567 \text{ trees ha}^{-1}$), they comprised 21% of total ecosystem- R_{wood} , 38% of total aboveground biomass, and 16% of total woody surface area (Fig. 3). The higher contribution of large trees (38%) to aboveground biomass than to surface area (16%) was caused by the differences in allometric equations. The allometric equation for aboveground biomass has an exponential function (Yamakura et al., 1986), whereas the allometric equation for surface area has a logarithmic function (Chambers et al., 2004). Thus, aboveground biomass exponentially increased with DBH, whereas the increase ratio of a woody surface area with DBH gradually decreased with DBH and almost saturated at high DBH on the individual scale. As chamber- R_{wood} increased with DBH, the ratio of large trees to ecosystem- R_{wood} (21%) was slightly higher than the ratio to woody tissue surface area (16%). Accordingly, decrease in stand density of large trees more strongly affected aboveground biomass than ecosystem- R_{wood} (Fig. 4). When stand densities of large trees were decreased by 55% to levels that are comparable to those in Neotropical areas ($7.5 \text{ trees ha}^{-1}$; Paoli et al., 2008), aboveground biomass decreased to 79%, and ecosystem- R_{wood} was decreased to 87%. Accordingly, AGB was decreased to 62% in the absence of large trees in this forest and ecosystem- R_{wood} was decreased to 79%, suggesting that whereas stand densities of large trees affect aboveground biomass considerably, their effects on ecosystem- R_{wood} are moderate.

4. Discussion

4.1. Inter-individual and temporal variation in R_{wood}

Sg was the most important factor affecting inter-individual variation in chamber- R_{wood} for all measurement periods, rather than DBH or tree species (Table 1). DBH and/or sg have been used for scaling in previous studies in tropical areas (Meir and Grace, 2002;

Table 2

Ecosystem- R_{wood} and annual ecosystem- R_{wood} with soil moisture estimated by different models. Multi-regression analyses were conducted for ecosystem- R_{wood} estimates. Predictor variables for the best-fit model were determined according to the lowest AIC value from all predictors including stem growth rate (sg), dbh and tree species. Predictor variables of Model1 and Model2 are sg and DBH, and sg, respectively. Annual ecosystem- R_{wood} was estimated by linear regression model which objective variables were ecosystem- R_{wood} for each model and predictor variable is SWC for each measurements period.

	Measured value	Ecosystem- R_{wood} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				Annual ecosystem- R_{wood} ($\text{MgC ha}^{-1} \text{ year}^{-1}$)			
		SWC ($\text{m}^3 \text{ m}^{-3}$)	Best model	Model1	Model2	Model0	Best Model	Model1	Model2
Jan-12	0.303 ± 0.004	2.48 ± 0.34	2.48 ± 0.34	2.37 ± 0.41	2.85 ± 1.5	7.06 ± 2.09	7.07 ± 2.18	6.68 ± 2.26	8.56 ± 2.20
May-13	0.287 ± 0.004	1.68 ± 0.20	1.65 ± 0.22	1.56 ± 0.27	2.04 ± 1.20				
Jul-13	0.239 ± 0.001	1.32 ± 0.21	1.34 ± 0.22	1.27 ± 0.27	1.67 ± 1.10				
Dec-13	0.309 ± 0.005	2.08 ± 0.40	2.08 ± 0.40	1.91 ± 0.49	2.53 ± 1.80				
Jun-14	0.253 ± 0.003	1.44 ± 0.43	1.47 ± 0.37	1.44 ± 0.43	1.88 ± 1.34				

Table 3

Statistical result of linear regression analysis for temporal variation in ecosystem- R_{wood} .

		Best model	Model1	Model2	Model0
Coefficients of independent variables					
	SWC	18.17*	17.46*	15.43	18.16*
Intercept		-3.36	-3.16	-2.68	-2.97
R^2		0.75	0.71	0.65	0.72

* $P < 0.1$.

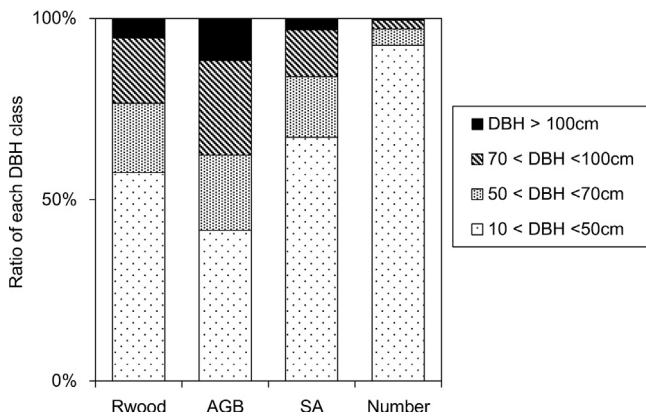


Fig. 3. Ratio of each DBH classes to ecosystem- R_{wood} , aboveground biomass (AGB), surface areas of woody tissue (SA), and numbers of trees (number).

Chambers et al., 2004; Robertson et al., 2010). DBH is an indicator of sapwood volume, and chamber- R_{wood} increases with DBH because sapwood volume directly affects maintenance respiration, reflecting increases in live cell numbers with sapwood volume (Ryan et al., 1994). Thus, strong relationships between chamber- R_{wood} and DBH have been shown previously. However, the present study suggested that DBH was not particularly important for scaling in this study, potentially reflecting differences in measured tree sizes. We measured multiple trees with DBH of > 100 cm, whereas chamber- R_{wood} was measured for trees with DBH < 100 cm in previous studies. For such large trees, sapwood volumes under the collar may not increase with DBH, probably owing to limited sapwood depth of < 10 cm (Ichie, unpublished data). At the study site, sapwood depths, which were measured by dye experiments (Ichie et al., unpublished data), did not correlate with DBH ($n = 34$, $P = 0.66$, $32 < \text{DBH} < 106$ cm), suggesting that sg is the most significant predictor of inter-individual variation in forests with very large trees.

In the present best-fit model, chamber- R_{wood} for *D. aromatica* was higher than that for *S. beccariana*, especially in July 2013 (Fig. A3). However, DBH and sg of measured trees did not differ between the two species ($P > 0.1$, respectively). Differences in chamber- R_{wood} may be reflected by the difference in sapwood depths and wood density between the two species. Sapwood depths for *D. aromatica* (5.4 ± 1.4 cm for trees with DBH of 59–96 cm, $n = 3$) were

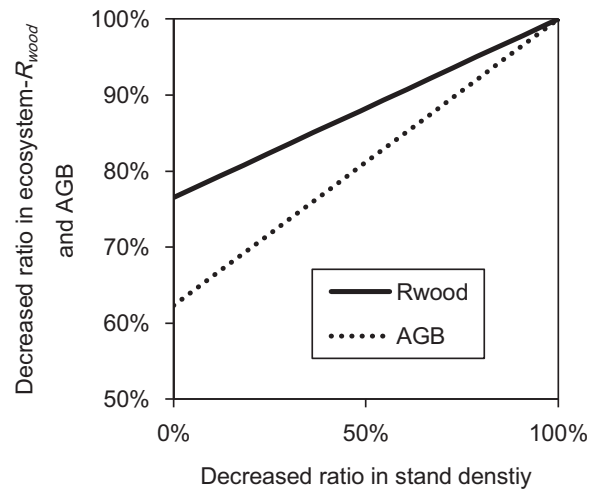


Fig. 4. Decreased ratios of ecosystem- R_{wood} and aboveground biomass (AGB) with different stand density of large trees; 100%, actual stand density of large trees ($16.5 \text{ tree ha}^{-1}$).

significantly higher than those for *S. beccariana* (3.2 ± 0.4 cm for trees with DBH of 93–102 cm, $n = 3$, $P < 0.05$; Ichie et al., unpublished data, Fig. A4). Wood density for *D. aromatica* (0.796 g cm^{-3}) was higher than that for *S. beccariana* (0.531 g cm^{-3} , Inoue unpublished data). The difference may result in higher construction respiration for *D. aromatica* than for *S. beccariana* with comparable sg because construction respiration can be estimated by sg and woody density (e.g., Ryan, 1991; Ryan et al., 1994). Hence, higher sapwood volumes and wood density may have affected species-specific chamber- R_{wood} in this study, even though these species belong to the same dipterocarp family.

The temporal variation in ecosystem- R_{wood} in the present study was associated with soil moisture despite the absence of a regular seasonal dry period (Table 3, Fig. 2). This finding may be due to growth phenology, given that R_{wood} seasonally increased in growing stems (e.g., Ryan and Yoder, 1997) and stem the growth of several tree species of Dipterocarpaceae was observed after drought (Ichie et al., 2004). R_{wood} also responded to soil moisture conditions and likely reflected stem growth phenology in Neotropical rainforests, where stem growth is highest at the start of the wet season and lowest at the start of the dry season (Chambers et al., 2004; Malhi et al., 2014). In contrast, Cavaleri et al. (2006) reported no seasonality in R_{wood} in Costa Rica, where there were no distinct dry seasons, as is the case in Bornean forests. Cavaleri et al. (2006) attributed the absence of seasonal variation in R_{wood} to the asynchrony of the phenologies of all species. Thus, stem growth phenology in response to soil water availability is likely linked with temporal variation in R_{wood} in tropical rainforests. There is also another possibility: more CO_2 respired for roots might be transported by the transpiration stream and released from the stem because of low diffusion in wet soil (Teskey et al., 2008). Continuous

measurements of chamber- R_{wood} and stem growth rates in addition to sap flux measurements are necessary for an investigation of the cause of increase in ecosystem- R_{wood} in a wet period.

The range of temporal variation in ecosystem- R_{wood} (ratio of highest to lowest ecosystem- R_{wood} , 1.89) was higher in this study site than that observed in Neotropical forests (1.30, Chambers et al., 2004). Moreover, the lowest ecosystem- R_{wood} was observed during a severe drought in June 2013, and was followed by “general flowering,” with masting at the community level at irregular intervals of one to several years (Sakai et al., 2006; Nakagawa et al., 2012). The phenomenon of general flowering is reported in aseasonal tropical rainforests in Asia and is likely triggered by unexpected droughts in Lambir (Sakai et al., 2006). Strong temporal variation in net primary production was also reported in a study in Lambir that included a period of general flowering (Kho et al., 2013), and annual aboveground biomass increments decreased in the year of general flowering, whereas litterfall of flowers and seeds significantly increased (Nakagawa et al., 2012). These studies indicate that general flowering follows dynamic temporal variation in net primary production and R_{wood} , reflecting increased carbon allocation to the canopy for reproductive organs during general flowering.

4.2. Annual- R_{wood} and impact of large trees

Annual- R_{wood} estimates based on the best-fit model were comparable to those based on Model1 and Model2, suggesting that DBH and tree species are not always necessary for estimates of ecosystem- R_{wood} in this study site. In contrast, annual- R_{wood} based on Model0 was higher than that from the best-fit model, and the difference ($1.50 \pm 3.03 \text{ MgC ha}^{-1} \text{ year}^{-1}$) was higher than the net ecosystem production in a Neotropical forest ($0.71 \pm 9.34 \text{ MgC ha}^{-1} \text{ year}^{-1}$, Phillips et al., 1998) and was more than half of the net ecosystem production in an old-growth forest ($2.4 \pm 0.8 \text{ MgC ha}^{-1} \text{ year}^{-1}$, Luyssaert et al., 2007). These data suggest that scaling by averages only may lead to large errors. Nonetheless, this difference likely reflects differences in sg distribution between sampled trees and those in the present 4-ha plot. Accordingly, average measured sg ($0.80 \pm 0.95 \text{ cm y}^{-1}$) was much higher than that in the 4-ha plot ($0.2 \pm 0.3 \text{ cm y}^{-1}$). Thus, sg distributions should be considered during scaling of averaged chamber- R_{wood} values.

Annual- R_{wood} values differed among the study sites (Table 4). This variation was not explained by aboveground biomass, although some studies have shown positive relationships between plant respiration and biomass (Kira and Shidei, 1967; Delucia et al., 2007). In the present study, possible factors affecting variation in annual- R_{wood} among forests such as SAI, chamber- R_{wood} , and sampling method are discussed using comparisons of annual- R_{wood} and biomass with those of previous studies (Table 4). Compared with annual- R_{wood} values observed in Peru (Malhi et al., 2014), annual- R_{wood} values in the present study site were similar despite the twice higher aboveground biomass. Comparable SAI and chamber- R_{wood} led to comparable annual- R_{wood} between the two study sites. Higher stand density of large trees in the present study site led to higher biomass but comparable SAI. Compared with both Brazil studies (da Costa et al., 2013; Doughty et al., 2013), annual- R_{wood} in this study site was lower despite 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 aboveground biomass but slightly lower annual- R_{wood} in Costa Rica. The reason for these results may be attributed to the difference in the sampling method; they measured chamber- R_{wood} for lianas and palms in addition to vertical variation for trees. Liana and palms accounted for 24 and 9% of total R_{wood} in the forest, and underestimates using data with no vertical measurements have often been reported (e.g., Katayama et al., 2014). These results suggest that annual- R_{wood} in the present study and previous studies may

be underestimated. Consideration of tree size 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.

GPP and annual- $R_{foliage}$ were the highest and second highest, respectively, among tropical rainforests reported in the literature, whereas ratios of R_{wood} and $R_{foliage}$ to GPP were within the range of those shown in Neotropical forests (Table 4). Most ratios of R_{wood} and $R_{foliage}$ to GPP in this study and other tropical rainforests were higher than the averages for various forest ecosystems, including boreal and temperate, and young and old-growth forests (0.16 and 0.16, respectively, Litton et al., 2007). Hence, ratios of R_{above} to GPP (0.38–0.51) were higher than the average among various forest ecosystems (0.32, Litton et al., 2007). In agreement, previous studies showed 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 lead to higher ratios in mature tropical rainforests.

We estimated annual- R_{wood} with consideration of inter-individual and temporal variation in the present study, but there are still large uncertainties in each component of the GPP estimate. For annual- R_{wood} , there are four major sources of uncertainty. First, vertical variation for smaller trees and branches was not investigated, and can lead to underestimates when measurements are conducted only at breast height (e.g., Katayama et al., 2014). Second, temporal variation was investigated in the present study, but only for five measurements campaign, resulting in large errors in annual- R_{wood} . To improve accuracy, relationships of environmental factors with tree phenology should be examined by more measurement time series. Third, the surface area of woody tissue was estimated by an equation obtained in the central Amazon (Chambers et al., 2004). It is reported that height–diameter relationships were different among continents; for a given diameter, stems were tallest in Asia, followed by Africa, America, and Australia, based on a meta-analysis (Banin et al., 2012). This result suggests that an equation for woody tissue surface area using DBH may be different and underestimated ecosystem- R_{wood} in the present study. Finally, there is considerable uncertainty whether the source of chamber- R_{wood} can include root-respired CO_2 and stem-respired CO_2 can be transported to the canopy (Teskey et al., 2008). This is often associated with diurnal variation in chamber- R_{wood} . Different diurnal variation in individual trees may be affected by this uncertainty.

There are uncertainties in other carbon fluxes used for GPP estimation. For annual $R_{foliage}$, seasonal variations in $R_{foliage}$ and LAI were not considered in the present study and the variations may lead to under- or overestimation although $R_{foliage}$ at the ecosystem scale did not vary seasonally in Peru (Malhi et al., 2014) and Brazil (Metcalfe et al., 2010). In the present study, $R_{foliage}$ at 25 °C was estimated using Q_{10} of 2.3 reported in Costa Rica. If Q_{10} value of 2.0, which was reported in Australia (Weerasinghe et al., 2014), is used for the estimate in the present study, annual- $R_{foliage}$ is estimated as $10.23 \text{ MgC ha}^{-1} \text{ year}^{-1}$, suggesting underestimation in the present study. As well, there are large uncertainties in TBCF in the present study site. TBCF was estimated as the difference between annual soil CO_2 efflux and annual litterfall-C, based on a steady-state assumption (Raich and Nadelhoffer, 1989), whereas TBCF was estimated as a sum of belowground respiration and net primary production in previous studies in Table 4. Furthermore, annual soil CO_2 efflux was estimated by measurements only in the daytime and temporal variation was not considered. This practice may lead to overestimation due to diurnal variation in soil CO_2 efflux.

Climate change is predicted to cause more frequent droughts of greater severity in tropical areas Malhi and Phillips (2004). Drought may affect phenology and carbon allocation in the present study

Table 4
Aboveground biomass, annual- R_{wood} , annual- $R_{foliage}$, annual- R_{above} , GPP and ratios to GPP in various tropical rainforests.

Site	Malaysia	Costa Rica	French Guiana	Brazil		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 (MgCha ⁻¹)	272.4	81	228	179.5	110.9	213.9	200.6	138.2	115.6
Annual- R_{wood} (MgCha ⁻¹ year ⁻¹)	7.06 ± 2.09	5.08 ± 1.35	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	1.1 (diameter < 10 cm)	1.3	1.65	1.63	–	–	1.98	2.09
Average Chamber- R_{wood}	0.81 ± 0.52 (dry) 1.39 ± 0.74 (wet) 1.07 ± 0.48 (average)	0.60 (DBH of 10 cm) 0.83 (DBH of 80 cm)	1.13 ± 0.55 (dry) 1.56 ± 0.65 (wet)	2.08 ± 0.15	2.11 ± 0.17	1.61 ± 0.12	1.94 ± 0.19	0.95 ± 0.03	1.03 ± 0.08
Scaling factors	Growth, dbh, species	Growth, diameter, Species, height, slope	Average	Growth			Growth		Growth
Samples	DBH > 10 cm	All trees, Liana, Palm	DBH > 10 cm	All trees			All trees		All trees
Annual- $R_{foliage}$ (MgCha ⁻¹ year ⁻¹)	9.54 ± 0.46	–	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} (MgCha ⁻¹ year ⁻¹)	16.60 ± 2.14	–	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 (MgCha ⁻¹ year ⁻¹)	42.99 ± 6.74	–	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	0.27 ± 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	0.16 ± 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	0.43 ± 0.11	0.38 ± 0.10	0.41 ± 0.14	0.51 ± 0.17	0.40 ± 0.10	0.41 ± 0.10
Reference	This study	Cavaleri et al., 2006	Stahl et al., 2011 Rowland et al., 2014	Doughty et al., 2013		da Costa et al., 2013 da Costa et al., 2010		Malhi et al., 2014	

site, and severe drought often induces high tree mortality (Allen et al., 2010). In Lambir Hills National Park, severe drought caused by El Nino in 1997–1998 induced high tree mortality, especially among large trees (Nakagawa et al., 2000). Recent studies also show that large trees drive forest aboveground biomass variation in moist lowland forests across the tropics (Slik et al., 2013) and higher stem growth at the plot level in Borneo (Banin et al., 2014). These observations suggest that large trees are important carbon stores. Previous studies in Lambir showed that partial variation in soil CO₂ efflux was affected by large trees (Katayama et al., 2009), and soil CO₂ efflux was higher in the presence of emergent trees (Ohashi et al., 2014). Moreover, photosynthetic ability reportedly increases linearly with height (Kenzo et al., 2015), suggesting higher photosynthesis rates for larger trees. Hence, soil CO₂ efflux and GPP might decrease with the loss of large trees due to severe droughts, whereas R_{wood} might be conserved. Taken together, future climate change 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 changes in number of large trees.

5. Conclusions

We measured chamber- R_{wood} in trees of various species and sizes in a Bornean tropical rainforest. All measurements were performed five times between 2012 and 2014, and subsequent analyses indicated that the factor of stem growth rate was

the most important determinant of inter-individual variation in chamber- R_{wood} , followed by DBH and tree species. In this study, ecosystem- R_{wood} was estimated based on the model for individual chamber- R_{wood} using the predictive factors of stem growth rate, DBH, and tree species, and the average measured chamber- R_{wood} value. Estimates of ecosystem- R_{wood} using stem growth rate only were similar to those estimated using the all factors, whereas mean measured ecosystem- R_{wood} was higher than that estimated using regression models, suggesting that spatial scaling should be conducted with consideration of factors that affect chamber- R_{wood} . Moreover, ecosystem- R_{wood} varied temporally, reflecting changes in soil moisture despite the absence of a regular seasonal dry period. These data suggest that carbon allocation may dynamically vary with time and changes in soil moisture. Annual- R_{wood} values were comparable to those in Neotropical forests, despite higher aboveground biomass in the present Bornean study site. Higher stand density of large trees caused higher aboveground biomass, but comparable ecosystem- R_{wood} compared with Neotropical forests. Although the effects of stand age or biomass on autotrophic respiration remain unclear, the present data suggests that stand structure may mediate these effects on respiration at the ecosystem scale.

Acknowledgments

We thank the Forest Department of Sarawak and the Sarawak Forestry Corporation for their permission and kind assistance in

conducting research studies at Lambir Hills National Park. We also thank Dr. Tohru Nakashizuka of Tohoku University and Dr. Takao Itoika of Kyoto University for their sincere cooperation with our work in Lambir. This work was financially supported by a the Japan Society for the Promotion of Science (JSPS) grant for the Global Center of Excellence Program (Asian Conservation Ecology as a Basis of Human–Nature Mutualism, representative: T. Yahara), the Aashi Group Foundation grant, and a Sasakawa Scientific Research Grant from The Japan Science Society.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2016.01.140>.

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