



# Carbon stocks and its variations with topography in an intact lowland mixed dipterocarp forest in Brunei

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## Abstract

Tropical forests play a critical role in mitigating climate change, and therefore, an accurate and precise estimation of tropical forest carbon (C) is needed. However, there are many uncertainties associated with C stock estimation in a tropical forest, mainly due to its large variations in biomass. Hence, we quantified C stocks in an intact lowland mixed dipterocarp forest (MDF) in Brunei, and investigated variations in biomass and topography. Tree, deadwood, and soil C stocks were estimated by using the allometric equation method, the line intersect method, and the sampling method, respectively. Understory vegetation and litter were also sampled. We then analyzed spatial variations in tree and deadwood biomass in relation to topography. The total C stock was 321.4 Mg C ha<sup>-1</sup>, and living biomass, dead organic matter, and soil C stocks accounted for 67%, 11%, and 23%, respectively, of the total. The results reveal that there was a relatively high C stock, even compared to other tropical forests, and that there was no significant relationship between biomass and topography. Our results provide useful reference data and a greater understanding of biomass variations in lowland MDFs, which could be used for greenhouse gas emission-reduction projects.

**Key words:** biomass, carbon pool, carbon stocks, lowland mixed dipterocarp forest, tropical forest, topography

## INTRODUCTION

As international concerns over climate change have increased, there has been rising interest in forests, which sequester more carbon (C) than any other terrestrial ecosystem (Gibbs et al. 2007). Any forest-based project that aims to mitigate climate change requires an accurate and precise estimation of forest C (Ravindranath and Ostwald 2008). Further research on tropical forest C stock estimation is needed for the following reasons: firstly, tropical forests have a great potential for sequestering carbon di-

oxide from the atmosphere because they have the highest primary productivity and occupy the largest area of all of the global forests (Pan et al. 2011); secondly, more reference data are needed to lower the uncertainty when estimating tropical forest C stocks because complex stand structures and high species diversity make the estimation prone to many errors (Chave et al. 2004); and lastly, 15-20% of global greenhouse gas emissions are caused by C emitted into the atmosphere by tropical deforestation

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(Gibbs et al. 2007); therefore, greenhouse gas emission-reduction projects must be given priority. However, there have been few studies conducted on the estimation of tropical forest C stocks, because tropical forests are generally located in developing countries, in which adequate research funding is difficult to obtain (Malhi et al. 2009), particularly in Southeast Asia (Pan et al. 2011).

One of the typical forest types in Southeast Asia is mixed dipterocarp forest (MDF). The Dipterocarpaceae is a family of tall and fast-growing trees that dominate the upper canopy of tropical forests. These vegetation zones are called MDFs due to their overwhelming presence (Appanah and Turnbull 1998). This family plays an important role in the timber market of many Southeast Asian countries because of their excellent quality (Poore 1989). It has been documented that the floristic compositions and canopy structures of MDFs vary with precipitation, topography, and soil nutrients (Ashton and Hall 1992, Appanah and Turnbull 1998). In addition, the biomass in MDFs exhibits high variance (e.g.,  $271 \pm 19$  to  $478 \pm 38$  Mg ha<sup>-1</sup>) (Laumonier et al. 2010). Consequently, in order to decrease uncertainty in C stock estimation in MDFs, obtaining reference data is essential.

Kuala Belalong lowland MDF (i.e., this study area) has been protected by the Bruneian government; consequently, there are no records of significant disturbances, either natural or artificial (Cranbrook and Edwards 1994). Therefore, it is a completely intact primary forest. This is important, as many forests in developing countries that have been destroyed were tropical forests, and it is very difficult to find completely intact tropical forests for research purposes. For greenhouse gas emission-reduction projects, studies conducted in intact tropical forests can provide important data. In addition, the study area was established as the part of the Center for Tropical Forest Science (CTFS) project, which is a global network of forest researchers (<http://www.ctfs.si.edu>). Over 60 forest research plots in the Americas, Africa, Asia, and Europe are included in long-term research using the same methodology, for easy data sharing. Therefore, the scientific value of this study area can be considered very high. There have been approximately 260 papers published concerning Kuala Belalong lowland MDF, on various subjects: biodiversity, soil, forest structure, biogeography, etc. However, this is the first study that has investigated C stocks.

Knowing spatial variations in forest biomass is also important because carbon dioxide emissions from deforestation are determined by the original biomass of the forest that was destroyed, not necessarily by the average

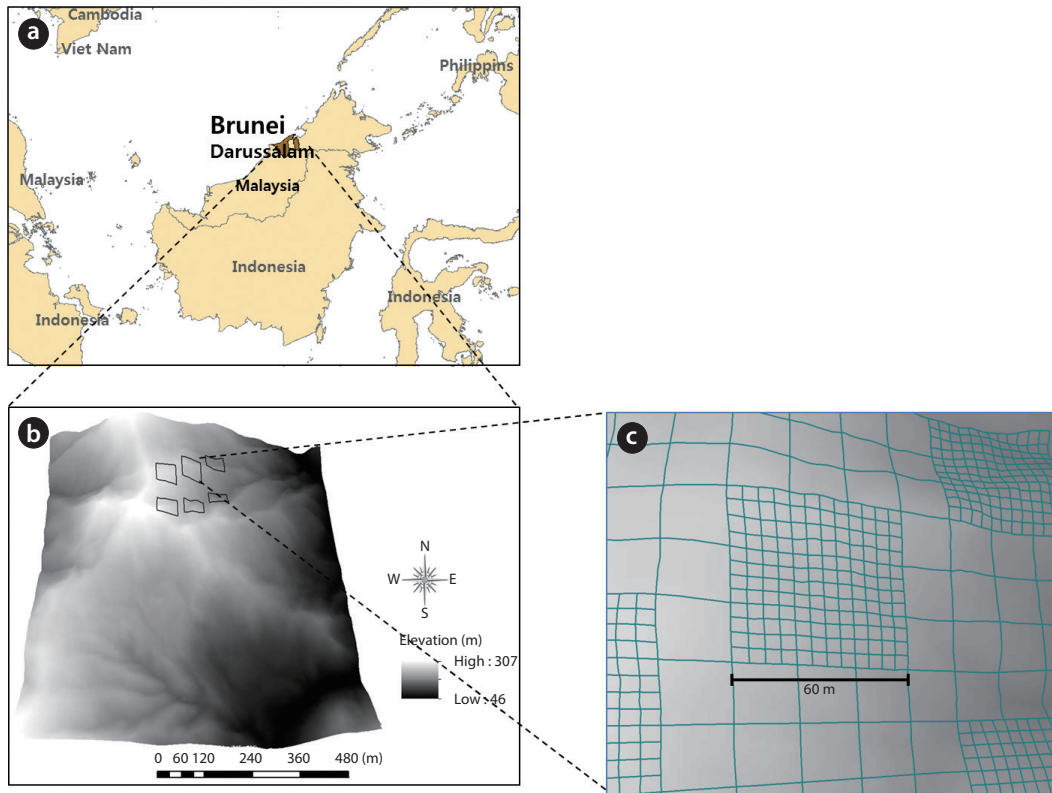
biomass for that geographical region (Houghton 2005, de Castilho et al. 2006). Consequently, it is essential to take into account several environmental factors when describing biomass variations. Tropical forests exhibit large spatial variability in tree biomass (Laurance et al. 1999, Chave et al. 2001, 2003); however, this variation is poorly understood (Houghton 2005). Therefore, investigating the effects of topography on variations in biomass is necessary to understand the forest in large-scale.

This study aimed to achieve the following objectives: 1) to provide reference data for estimating C stocks of an intact lowland MDF in Brunei; and 2) to investigate the relationship between biomass (aboveground and deadwood) and topographical factors. This is the first study that has estimated forest C stocks in Brunei and recorded not only the generally reported aboveground biomass (AGB) but also the total biomass in a forest ecosystem.

## MATERIALS AND METHODS

### Study site

The study was conducted in the undisturbed Kuala Belalong lowland MDF, which is part of the Ulu Tembulong National Park, Brunei Darussalam (04°63'50.3" N, 115°22'79.1" E) (Fig. 1a). Meteorological data that were collected from 2006 to 2010 at Semabat Agricultural Station, which is located 9 km northwest of Kuala Belalong, show that the temperature is slightly variable, with monthly mean maxima of between 31.1°C (July 2010) and 34.2°C (May 2007) and minima around 26°C. The mean annual precipitation is approximately 4,582 mm, with no distinct dry season. The soils are yellow or red and are mainly inceptisols and ultisols derived from shale parent materials (Ashton and Hall 1992), according to the United States Soil Survey Classification. A detailed description of the local climate, topography, soil, and hydrology is provided by Cranbrook and Edwards (1994). The canopy consists of the crowns of the biggest trees at 30-40 m above the ground, which are only surpassed in height by emergents that are over 60 m tall (Poulsen et al. 1996). The dominant canopy family is Dipterocarpaceae, with individuals of the genera *Shorea* (Dipterocarpaceae), *Dryobalanops* (Dipterocarpaceae), and *Koompassia* (Caesalpinaceae) being the main emergents (Ashton and Hall 1992). Small et al. (2004) found 1,062 stems (diameter at breast height (DBH)  $\geq 5$  cm) and 278 species, representing 110 genera in 49 families, in a 1-ha quadrat (1 ha = 10<sup>4</sup> m<sup>2</sup>) in this area.



**Fig. 1.** The location of Brunei Darussalam (a), six quadrats (60 × 60 m) in Kuala Belalong lowland mixed dipterocarp forest, where the study was conducted (b), and the experimental design of each 60 × 60 m quadrat (c).

## Experimental design

The study was conducted in six 60 × 60 m quadrats, separated by a distance of approximately 100 m at an elevation of between 200 and 300 m above sea level (Fig. 1b). For ease of identification, numbered poles were placed every 10 m in both directions (rows and columns), and the 10 m was measured as a linear distance that accounted for the gradient. The 60 × 60 m quadrats were divided into several sub-quadrats (Fig. 1c). Large forest plots, including the CTFS plots, were established using this design, and they share the same methods of mapping and censusing trees. A detailed description of quadrat establishment and tree measurement is given by Condit (1998).

## Living biomass and C stock estimation

The AGB (DBH ≥ 1 cm) was estimated by using the biomass estimation equation approach (Ravindranath and Ostwald 2008). DBH data were acquired from the six 60 × 60 m quadrats. We selected the following biomass estimation equation which was developed in a tropical lowland

MDF in East Kalimantan, Indonesia (Basuki et al. 2009):

$$\ln(\text{AGB}) = -0.744 + 2.188\ln(\text{DBH}) + \ln(\text{WD}), \quad (1)$$

where AGB is in kg tree<sup>-1</sup>, DBH is in cm, WD (wood density) is in g cm<sup>-3</sup>, and the correction factor is 1.047 (Sprugel 1983). A WD value of 0.6 g cm<sup>-3</sup> was found in a previous study conducted in this area (Osunkoya et al. 2007). The belowground biomass (BGB) was estimated using a BGB-AGB ratio of 0.18, obtained from the Pasoh Forest Reserve, Malaysia (Niiyama et al. 2010).

Understory vegetation (trees with a DBH < 1 cm and herbs) biomass was estimated using the harvest method (Ravindranath and Ostwald 2008) within 2 × 2 m quadrats, which were randomly established in each 60 × 60 m quadrat (n = 6). All of the collected samples were oven-dried at 70°C and weighed using an electronic scale.

To convert living biomass into C stocks, we assumed that 50% of the dry mass was C, based on the results from a study in Malaysia that had a similar species composition (Kenzo et al. 2010).

## Dead organic matter biomass and C stock estimation

Deadwood biomass was calculated as the sum of log (fallen dead wood with diameter  $\geq 10$  cm) and snag (standing deadwood with DBH  $\geq 10$  cm) biomass. The log biomass was estimated using the line intersect method (Marshall et al. 2000), which is as follows:

$$B_{\log} = WD_{\log} \times V_{\log} \quad (2)$$

$$V_{\log} = \pi^2 / 8L \sum_{i=1}^n \frac{d_i^2}{\cos \lambda_i} \quad (3)$$

where  $B_{\log}$  is the log biomass ( $\text{Mg ha}^{-1}$ ),  $WD_{\log}$  is the log WD ( $\text{g m}^{-3}$ ),  $V_{\log}$  is the log volume ( $\text{m}^3 \text{ha}^{-1}$ ),  $L$  is the length of the line transect (m),  $n$  is the number of log pieces that intersects the line transect,  $d_i$  is the diameter ( $\geq 10$  cm) of log  $i$  at the point of intersection (cm), and  $\lambda_i$  is the angle from the horizontal of the log ( $n = i$ ) crossed by the line transect (degrees). To estimate the  $V_{\log}$ , six 60 m transect lines were established in each  $60 \times 60$  m quadrat at regular intervals. The  $d_i$  and  $\lambda_i$  were measured along each transect line. To estimate  $WD_{\log}$ , all the logs were subsampled in a  $20 \times 20$  m sub-quadrat of each  $60 \times 60$  m quadrat ( $n = 6$ ). The volumes of the samples were determined using the ethanol displacement method (Saner et al. 2012). The samples were then dried in an oven to a constant weight ( $70^\circ\text{C}$ ) and weighed using an electronic scale.

The snag biomass ( $B_{\text{snag}}$ ) was the product of the WD ( $WD_{\text{snag}}$ ) and the volume of snag ( $V_{\text{snag}}$ ). Due to a lack of data for the  $WD_{\text{snag}}$ , the same value of the  $WD_{\log}$  was applied to the  $WD_{\text{snag}}$ . To estimate the  $V_{\text{snag}}$ , DBH, height, and snag structure (stem only or stem plus branches) were recorded for all snags in the same six  $60 \times 60$  m quadrats. Snag height was visually estimated, and tree  $V_{\text{snag}}$  was calculated following the methods described in Gale (2000). The  $B_{\text{snag}}$  was estimated by multiplying the  $V_{\text{snag}}$  and the  $WD_{\log}$ . To convert dead organic matter biomass into C stocks, we assumed that 50% of the dry mass was C.

Litter (twigs, leaves, and reproductive organs) biomass was also sampled within  $2 \times 2$  m quadrats, which were randomly established in each  $60 \times 60$  m quadrat ( $n = 6$ ). All of the collected samples were oven-dried at  $70^\circ\text{C}$  and weighed using an electronic scale.

## Estimation of soil organic C

Soil was sampled in August and December 2013 at 0 to 10 cm, 10 to 20 cm, and 20 to 30 cm depths using a 10-

cm long cylindrical metal corer ( $406.94 \text{ cm}^3$ ) at three random points in each six  $60 \times 60$  m quadrat ( $n = 18$ ). The samples were then air dried and sieved through a 2-mm mesh screen (US standard No. 10) for determining bulk density and concentrations of C. Soil bulk density was determined by dividing the weight of soil samples dried at  $105^\circ\text{C}$  by the volume of the metal corer. An elemental analyzer (vario Macro cube CN, Elementar, Germany) was used to measure the soil C concentration. Soil C stocks at each depth were calculated from the soil C concentration and the bulk density of each soil sample.

## Variations in living and dead wood biomass in terms of topographical characteristics

To analyze variations in biomass and topographical characteristics, each  $60 \times 60$  m quadrat was divided into nine  $20 \times 20$  m sub-quadrats. The biomass and topography were analyzed using PROC MEANS, PROC CORR, and PROC REG in SAS 9.3 software (SAS Institute Inc., Cary, NC, USA). Topographical data were obtained from LiDAR and ArcGIS.

## RESULTS AND DISCUSSION

### Living biomass

Total AGB was estimated as  $361.8 \pm 21.0 \text{ Mg ha}^{-1}$  (Table 1), which was classified as in the highest biomass class category ( $\text{AGB} > 350 \text{ Mg ha}^{-1}$ ) according to the classification criteria proposed by Saatchi et al. (2011). Only 7% in Asia, 8.7% in Africa, and 7.4% in Latin America has more than  $350 \text{ Mg ha}^{-1}$  AGB (Saatchi et al. 2011). However, this value is much lower than that recorded in the Lambir Hills National Park, Sarawak, Malaysia ( $544.8 \text{ Mg ha}^{-1}$ ; Katayama et al. 2013), which has a similar primary MDF near our study site. There could be several reasons for this: 1) the dominant tree height differs between areas. The canopy of our site was approximately 30 to 40 m in height, and the density of tall trees was not high, whereas Lambir National Park has a continuous 40 to 50 m tree layer (Katayama et al. 2013); 2) the result obtained in Lambir included lianas. In a lowland rainforest in Venezuela, the mean biomass of a liana with a 10-cm DBH is nearly four times the leaf biomass of a 10-cm DBH tree (Putz and Chai 1987). Therefore, lianas might be an important component in estimating the biomass of tropical forests; 3) lastly, environmental conditions are different. The mean annual rainfall in Lambir (2600 mm) is much lower than that at our site, the

soil has a higher sand content (62 to 72%), and the range of elevation (20 to 470 m) is greater (Katayama et al. 2013). Consequently, the AGB depends on the area, even in the same MDF; for many reasons. The specialized estimation for a particular area might be required in this case.

The stand density of the study site was  $6718.1 \pm 328.5$  stems  $\text{ha}^{-1}$  (mean  $\pm$  SE), and about half (48.1%) of the AGB was in trees with a DBH greater than 50 cm, which accounted for 0.6% of the total number of stems. The AGB of the trees with a DBH of 1.0 to 9.9 cm (that accounted for 91% of the total number of stems) accounted for 8.1% of the total AGB (Table 1). This suggests that the study site is a climax forest and has a large number of highly competitive young trees, and only a small number of big trees survive (Alder and Synnott 1992). In addition, the site has an uneven topography and an easily disaggregated soil type, which results in severe soil erosion (Cranbrook and Edwards 1994); this also might inhibit the growth of large trees. Generally, trees with a DBH of less than 10 cm are usually disregarded in AGB estimations. In this study, however, the AGB of trees with a DBH of 1.0 to 9.9 cm was also estimated, and the result (8.1% of the total AGB) was not negligible. As a result, to enhance the accuracy and precision of AGB estimations in intact tropical forests with a similar DBH profile as this area, the inclusion of trees with a DBH lower than 10 cm is essential. The total basal area of the study site was  $38.8 \text{ m}^2 \text{ ha}^{-1}$ , which is similar to that of a previous study conducted in an undisturbed Malaysian lowland MDF ( $34.5 \text{ m}^2 \text{ ha}^{-1}$ ; Sato et al. 2013).

The BGB of the study site was estimated as  $65.1 \text{ Mg ha}^{-1}$ , using a BGB-AGB ratio of 0.18. When the DBH-BGB regression equation developed in a Malaysian lowland

MDF was used for the estimation (Niyama et al. 2010), the resulting BGB was  $120.9 \text{ Mg ha}^{-1}$ . According to this result, the BGB-AGB ratio is estimated as 0.33, while values from previous studies conducted in other tropical forests were 0.14 (Chave et al. 2005), 0.19 (Jackson et al. 1996), and  $\leq 0.24$  (Cairns et al. 1997). Compared to these reported values, a ratio of 0.33 might be considered an overestimation. In fact, the Malaysian study area where the DBH-BGB regression equation was developed has a DBH distribution that is different from that in our study area, and the area is dominated by trees with a large DBH. In addition, Brown (2002) reported that tree age was also an important factor that had to be considered when using a BGB regression equation. Root biomass also differs among tropical forests, and depends on meteorological and soil characteristics (Brown and Lugo 1982, Sanford and Cuevas 1996). For these reasons, using the above DBH-BGB regression equation in our study area may not have been ideal.

The biomass of woody plants ( $\leq 1 \text{ cm}$  DBH) and herbs was  $0.2 \pm 0.1 \text{ Mg ha}^{-1}$ , and this was relatively low compared to the total living biomass ( $< 0.1\%$ ). This result is similar to that found in a previous study (Brown 1997); biomass allocation in woody plants is a typical characteristic of mature tropical forests, and understory vegetation plays important ecological roles in tropical forests. Indeed, the rate of forest tree development is higher in areas without understory cover (Parrotta 1995). Therefore, understory vegetation may have the same value as other C pools in tropical forest restoration, even though its biomass allocation is small (Lamb 1998).

**Table 1.** Estimates of number of stems, basal area (BA), and aboveground biomass (AGB) in Kuala Belalong lowland mixed dipterocarp forest

DBH class (cm)	No. of stems ( $\text{ha}^{-1}$ )			BA ( $\text{m}^2 \text{ ha}^{-1}$ )			AGB ( $\text{Mg ha}^{-1}$ )		
	Mean	SE	% of total	Mean	SE	% of total	Mean	SE	% of total
1.0-9.9	6113.9	320.1	91.0	5.3	0.2	11.9	29.2	1.2	8.1
10.0-19.9	360.2	17.9	5.4	5.4	0.3	12.2	36.7	1.9	10.1
20.0-29.9	116.2	6.2	1.7	5.4	0.3	12.3	41.0	2.2	11.3
30.0-39.9	58.8	4.4	0.9	5.5	0.4	12.5	44.7	3.0	12.4
40.0-49.9	27.8	3.1	0.4	4.3	0.5	9.7	36.0	4.3	10.0
50.0-59.9	15.3	2.7	0.2	3.6	0.6	8.1	31.3	5.6	8.7
60.0-69.9	10.2	3.0	0.2	3.3	1.0	7.4	29.7	9.2	8.2
70.0-79.9	3.2	0.5	0.0	1.5	0.3	3.3	13.6	2.4	3.8
80.0-89.9	5.6	2.3	0.1	3.1	1.3	7.1	29.9	12.2	8.3
90.0-99.9	2.3	1.3	0.0	1.6	0.9	3.7	16.1	9.0	4.4
$\geq 100.0$	4.6	0.9	0.1	5.2	1.4	11.8	53.5	14.8	14.8
Total	6718.1	328.5	100.0	44.1	2.1	100.0	361.8	21.0	100.0

DBH, diameter at breast height; SE, standard error.



## Dead organic matter

The volume of dead wood in the study site was estimated as  $122.3 \pm 25.7 \text{ m}^3 \text{ ha}^{-1}$ , and this value is similar to that obtained in a previous study ( $116 \text{ m}^3 \text{ ha}^{-1}$ ; Yoneda et al. 1990) in the MDF of Sumatra island (Table 2). Log volume was  $103.4 \pm 24.5 \text{ m}^3 \text{ ha}^{-1}$ , and it accounted for 84.5% of the entire dead wood volume. This value is 57% higher than that obtained in a previous study conducted in the same area ( $66.0 \pm 10.2 \text{ m}^3 \text{ ha}^{-1}$ ; Gale 2000). The difference in the two results might be due to the facts that: 1) the current study included logs with a DBH of 10 to 20 cm; and 2) transect lines were established mainly on ridges. Gale (2000) found that log volume tended to decrease from the ridge to the valley. In this study, snag volume accounted for 15.5% of the entire dead wood volume ( $18.9 \pm 10.8 \text{ m}^3 \text{ ha}^{-1}$ ), and this was lower than that of the previous study ( $37.7 \pm 4.7 \text{ m}^3 \text{ ha}^{-1}$ ; Gale 2000). The log WD was  $0.50 \pm 0.04 \text{ g cm}^{-3}$  ( $n = 36$ ), which is identical to the result of a previous study conducted in a Venezuelan tropical rain forest ( $0.5 \text{ g cm}^{-3}$ ; Delaney et al. 1998). Log and snag dry weights were estimated by multiplying the WD with the volume.

The total biomass of dead wood was estimated as  $61.2 \pm 12.9 \text{ Mg ha}^{-1}$ . In an old forest, such as in our study area, the inputs and outputs of dead wood are theoretically in balance, and dead wood biomass is relatively constant (Harmon and Sexton 1996). Therefore, it can be assumed that the total dead wood biomass would remain constant, as the study site was an old forest. Our results should be highly accurate, as the study areas (six of  $60 \times 60 \text{ m}$  quadrats) were large in comparison with those in other studies, e. g.,  $50 \times 50 \text{ m}$  by Delaney et al. (1998);  $30 \times 40 \text{ m}$ , Toriyama et al. (2014). The amount of dead wood in tropical forests has been poorly quantified, but is extremely variable (it can account for less than 10% to more than 40% of the total biomass; Brown 1997), and depends on various factors. Therefore, the current study's results should be highly accurate and could provide useful reference data for intact tropical MDFs.

The litter dry weight was estimated as  $6.2 \pm 1.0 \text{ Mg ha}^{-1}$ , which was 10% of the dry weight of dead wood. Twig dry weight accounted for 59.7% of the total litter, and leaves accounted for 40.1%. Almost all of the litter was composed of twigs and leaves, and the dry weight of the reproductive organs was relatively insignificant. Litter dry weight was very similar to that found in a previous study:  $5.75 \text{ Mg ha}^{-1}$  in a MDF in the Andulau Forest Reserve, Brunei (Moran et al. 2000). Patterns of litter from standing crops usually exhibit temporal variations (e.g., seasons), and tropical forests are not an exception ( $3.0$  to  $10.5 \text{ Mg ha}^{-1}$ ; Spain 1984).

However, our study site had little seasonal variation, and monthly litterfall was relatively constant, therefore, the litter from standing crops in this area might exhibit little temporal variation.

## Soil C stocks

The total soil C stocks between 0 and 30 cm in depth was estimated as  $74.2 \text{ Mg C ha}^{-1}$ , 46.5% of which was between 0 to 10 cm, 28.7% was between 10 to 20 cm, and 24.8% was between 20 to 30 cm. The soil C concentration ( $\text{g kg}^{-1}$ ) of 0-10, 10-20, 20-30 cm depths were 38.4, 19.4, 14.2, respectively, decreasing from 0 to 30 cm. Because of frequent rain, uneven topography, and a silty clay soil type, the soil of the study site is relatively shallow, and is rarely deeper than 2 m (Cranbrook and Edwards 1994). In addition, there were many roots and stones present on the soil surface, making core sampling difficult. In a previous study conducted in a primary tropical forest in Singapore (Ngo et al. 2013), the soil was 3 m deep, and soil C stocks between 0 and 300 cm in depth were estimated as  $132.5 \text{ Mg C ha}^{-1}$ . Variations in soil characteristics within our study area suggest that the optimal investigative method should be specialized for the target area (Carter 1993). Because soil C accounts for the second-largest proportion of the total C stock, accurate and precise soil C estimation is important.

**Table 2.** Estimated volume ( $\text{m}^3 \text{ ha}^{-1}$ ) and dry weight ( $\text{Mg ha}^{-1}$ ) of log and snag in Kuala Belalong lowland mixed dipterocarp forest

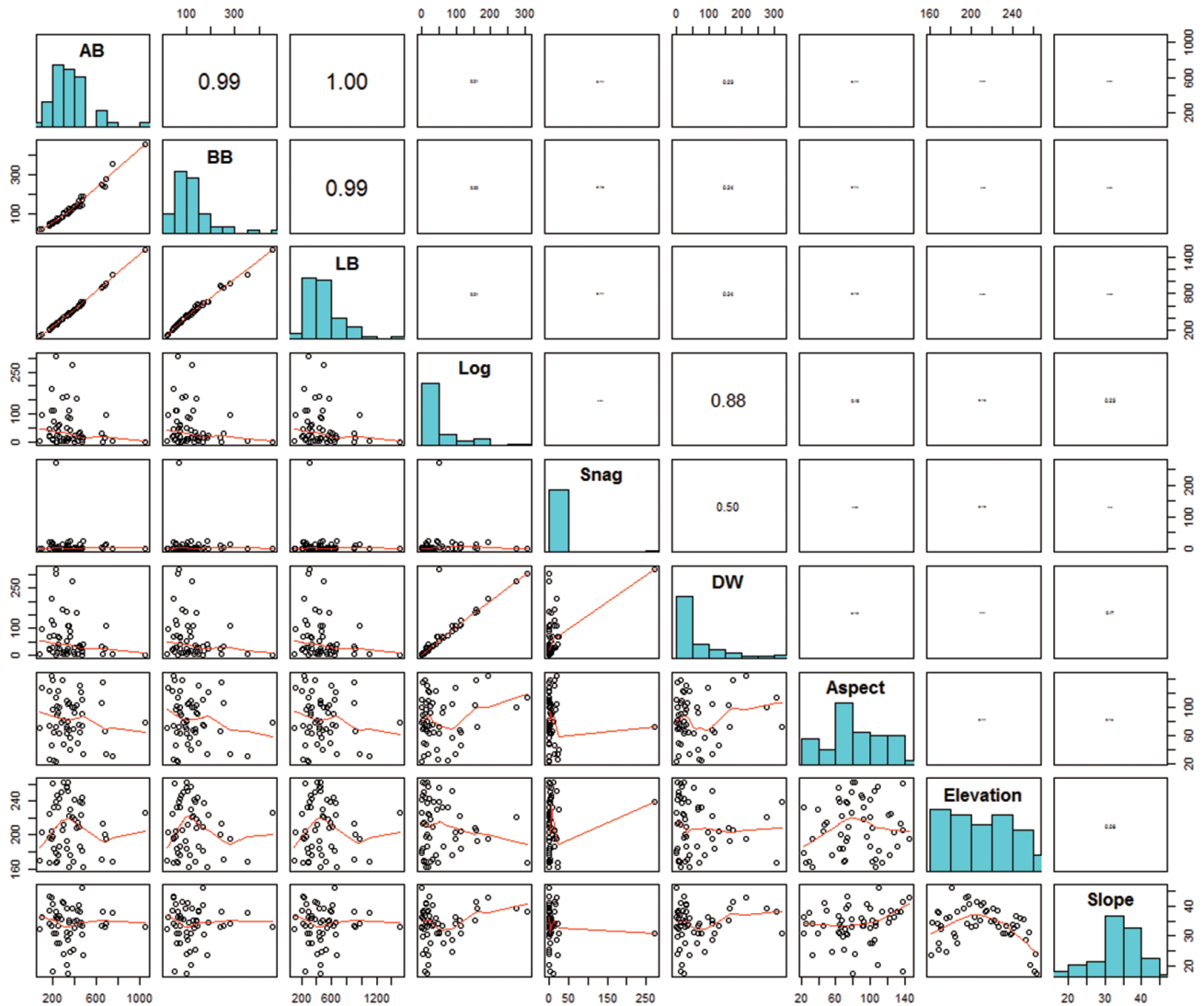
	Volume ( $\text{m}^3 \text{ ha}^{-1}$ )			Dry weight ( $\text{Mg ha}^{-1}$ )	
	Mean	SE	% of total	Mean	SE
Log	103.4	24.5	84.5	51.7	12.3
Snag	18.9	10.8	15.5	9.5	5.4
Total	122.3	25.7	100.0	61.2	12.9

SE, standard error.

**Table 3.** Estimates of carbon (C) stocks in each C pool ( $\text{Mg C ha}^{-1}$ ) in Kuala Belalong lowland mixed dipterocarp forest

Carbon pools	Mg C ha <sup>-1</sup>	% of total
<b>Living biomass</b>	<b>213.6</b>	<b>66.5</b>
Aboveground tree biomass (DBH $\geq 1 \text{ cm}$ )	180.9	56.3
Belowground tree biomass (DBH $\geq 1 \text{ cm}$ )	32.6	10.1
Woody plant (DBH $< 1 \text{ cm}$ ) and herb biomass	0.1	0.0
<b>Dead organic matter</b>	<b>33.6</b>	<b>10.5</b>
Log	25.8	8.0
Snag	4.7	1.5
Litter	3.1	1.0
<b>Soil (to 30 cm)</b>	<b>74.2</b>	<b>23.0</b>
0-30 cm	74.2	23.0
<b>Total</b>	<b>321.4</b>	<b>100.0</b>

DBH, diameter at breast height.



**Fig. 2.** Variations in aboveground tree biomass (AB), belowground tree biomass (BB), all living biomass (LB), log, snag, all dead wood biomass (DW), aspect, elevation, and slope. Numbers on the upper panels are correlation coefficients ( $P > 0.05$ ). The diagonal cells show histograms. Curves on the lower panels are weighted scatterplots.

## Total C stocks and allocation

The C stocks and allocation to each C pool are shown in Table 3. The total C stock was estimated as 321.4 Mg C ha<sup>-1</sup>. This value is higher than that found in the Bukit Timah National Park, Singapore, which has a similar stand structure (337 Mg C ha<sup>-1</sup>; Ngo et al. 2013). The C stocks of the living biomass, the dead organic matter, and the soil accounted for 67%, 11%, and 23%, respectively, of the total. This suggests that living biomass accounts for a high proportion of C, whereas that by dead organic matter and soil is low. This is typical of tropical rain forests with high primary productivities and decomposition rates (Pan et al. 2011).

## Variations in living biomass and dead wood biomass associated with topographical characteristics

Variations in biomass and topography among the 20 × 20 m quadrats ( $n = 54$ ) varied widely (Fig. 2). The total living biomass varied from 108.3 to 1509.8 Mg ha<sup>-1</sup>, which was highly variable compared to the results from a previous study (189.8 to 422.8 Mg ha<sup>-1</sup>; de Castilho et al. 2006). Dead wood biomass was also variable (0 to 321.7 Mg ha<sup>-1</sup>), and the coefficients of variation (CVs) of aboveground tree biomass, belowground tree biomass, log dead wood, and snag dead wood were 176.8%, 81.4%, 67.4%, and 37.1%, respectively. Aspect and elevation varied between

35.3° and 303°, and 161.5 to 262.5 m, respectively, and the slope ranged from 17.3° to 46°.

No statistically significant correlations were found between biomass and topographical factors (Fig. 2), and only weak, non-significant correlation was found between log biomass and slope ( $r = 0.2$ ;  $P = 0.1$ ). There are several possible reasons for this result: 1) there was no evidence of spatial variations in tree growth or mortality in our study site. In fact, the tree growth rate in the study site ( $3.3 \pm 0.14 \text{ mm yr}^{-1}$ ) and the mortality rate—estimated as the ratio of dead wood to living tree biomass ( $0.1 \pm 0.02$ )—were relatively constant, regardless of the topography. This is similar to that found in previous studies conducted in central Amazonia and Borneo (de Castilho et al. 2006, Osunkoya et al. 2007), and suggests that topography has no effect on growth and survival; 2) there may have been a possibility of topographical variation within the  $20 \times 20 \text{ m}$  quadrats. In our study, the biomass and topographical data were analyzed as  $20 \times 20 \text{ m}$  quadrat units, and in the process of producing an average for each quadrat, the variation inside each quadrat could have been missed; 3) the key factors that determine biomass variation might not have been included in this study. In many tropical forests, light is critical for tree growth and survival (King 1991, Schnitzer et al. 2005). Although other resources, such as water and nutrients, in tropical forests are usually easily available to trees, light is highly limited. There was no evidence of a relationship between canopy openness and topography in our study site. In fact, the distribution of DBH classes did not exhibit any spatial variation, suggesting that competition for light was uniform throughout the study area; 4) the result may be related to tropical forest complexity. Topography generally covaries with many other variables, such as soil type, canopy openness, and soil water availability, and it can also affect forest dynamics and nutrient cycling (de Castilho et al. 2006). It is probable that topography alone does not affect variations in biomass. However, many environmental factors closely related to biomass are affected by topography. In respect to forest dynamics, the high spatial variance in biomass suggests that forest dynamics may differ, depending on the topography. This could lead to significant differences in C fluxes, even though biomass is not directly affected by topography (Clark and Clark 2000).

## CONCLUSION

Our study quantified the C stock of the Kuala Belalong lowland MDF, Brunei Darussalam, which was 321.4 Mg

C ha<sup>-1</sup>. Living biomass, dead organic matter, and soil accounted for 67%, 11%, and 23%, respectively, of the total C stock. One of the remarkable characteristics of this forest is that it is dominated by small trees. Variations in living and dead wood biomasses were high; however, there were no significant relationships between biomass and topographical factors. Our results provide useful reference data and background information for understanding the biomass variations specialized in lowland MDFs.

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