

## Annual budget and seasonal variation of aboveground and belowground net primary productivity in a lowland dipterocarp forest in Borneo

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[1] Tropical forests are thought to have among the highest values of net primary productivity (NPP) on Earth, but comprehensive data on NPP have rarely been collected for tropical forests, especially outside of the Neotropics. In this study, we quantify aboveground and belowground NPP, along with additional environmental factors over a 1–2 year period in a lowland dipterocarp forest in Borneo. The site is characterized by high annual rainfall and typically no month of the year when the forest is under water stress. We estimated the total NPP to be  $15.89 \pm 0.90 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  (mean  $\pm$  standard error) for a forest plot on clay soils and  $12.79 \pm 0.68 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  for a forest plot on sandy loam soils. Of this productivity, the allocation to aboveground NPP is  $81.8 \pm 6.0\%/80.4 \pm 6.0\%$  and to belowground NPP is  $18.2 \pm 3.7\%/19.6 \pm 2.6\%$  on clay and sandy loam, respectively. Fine root productivity ( $\text{NPP}_{\text{fine roots}}$ ) shows stronger seasonal variation relative to other components of NPP. There is evidence suggesting interannual variation in  $\text{NPP}_{\text{fine roots}}$ , leaf flush,  $\text{NPP}_{\text{litterfall}}$ , and  $\text{NPP}_{\text{ACW}}$ . This is the first attempt to describe how the biomass of a Bornean tropical forest is allocated to the various components of NPP over the seasonal cycle. The study highlights the marked seasonality of a tropical forest even under largely aseasonal environmental conditions, as well as the important effect of contrasting seasonality on different soil types.

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### 1. Introduction

[2] The magnitude and dynamics of the allocation of net primary productivity (NPP) in various tissues and organic structures in plants are essential characteristics of forest ecosystem ecology but have rarely been well quantified for tropical forests [Malhi *et al.*, 2011]. Tropical forests are among the most productive ecosystems on Earth and have been estimated to account for approximately one third of the global terrestrial NPP [Field *et al.*, 1998; Grace *et al.*, 2001; Melillo *et al.*, 1993]. In addition, tropical forests play an important role in the exchange of carbon with the atmosphere, as well as in the overall carbon balance of the terrestrial biosphere.

[3] NPP is the net production of biomass used by plants to produce various organic structures, including leaves, wood,

reproductive materials, roots, root exudation, and volatile organic compounds [Roy *et al.*, 2001]. Quantifying the biomass components that contribute to the total NPP is difficult and confounded by challenging methodologies [Clark *et al.*, 2001b]. Hence, most studies have typically investigated components that are easily measured, such as aboveground coarse wood productivity or litterfall [Chave *et al.*, 2008; Clark *et al.*, 2001b; Malhi *et al.*, 2011; Proctor *et al.*, 1983a, 1983b]. There are very few studies on belowground biomass and productivity [Fisher *et al.*, 2007; Green *et al.*, 2005; Lima *et al.*, 2010; Metcalfe *et al.*, 2008; Niiyama *et al.*, 2010; Yoda, 1978], in particular in conjunction with aboveground productivity data, and it is often estimated as some fixed proportion of aboveground biomass productivity [Clark *et al.*, 2001a]. As such, it is difficult to generate a reliable estimation of the carbon budget for tropical forest [Adachi *et al.*, 2011; Chambers *et al.*, 2004; Kira, 1978; Luyssaert *et al.*, 2007; Malhi *et al.*, 2009; Tan *et al.*, 2010]. In recent years, a larger and more comprehensive data set on tropical forest NPP has begun to emerge for the Andes-Amazon region [Aragão *et al.*, 2009; Chambers *et al.*, 2004; Girardin *et al.*, 2010]. However, estimation of NPP, particularly the allocation of NPP, is still very limited in tropical forests elsewhere, such as in Africa or Asia [Malhi, 2012; Malhi *et al.*, 2011].

[4] The dipterocarp-dominated forests of Southeast Asia are well recognized for their richly diverse and relatively tall trees [Ashton and Hall, 1992; Ashton, 1964, 2005; Whitmore, 1984], with very high aboveground biomass [Paoli *et al.*,

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2008; Proctor *et al.*, 1983a; Yamakura *et al.*, 1986]. In the island of Borneo, aboveground biomass in lowland dipterocarp forests is typically 60% more than that in Amazonian forests [Slik, 2006]. A considerable number of studies have estimated aboveground wood biomass for dipterocarp forests at several sites in Borneo [Basuki *et al.*, 2009; Burghouts *et al.*, 1992; Kenzo *et al.*, 2009; Morel *et al.*, 2011; Saner *et al.*, 2012; Yamakura *et al.*, 1986, 1996], and others have done the same for litterfall [Burghouts *et al.*, 1992, 1994; Proctor, 1984]. However, studies of the components of NPP are rare in regard to Borneo [Kitayama and Aiba, 2002; Paoli and Curran, 2007] and generally scarce in Southeast Asia [Hertel *et al.*, 2009; Kira, 1978; Ogino *et al.*, 1967; Yoneda *et al.*, 1977].

[5] The production of woody biomass has a major influence on biosphere carbon stocks, but it is largely uncertain how the future of forest carbon stocks will respond to climate change across tropical terrestrial ecosystems. It is generally acknowledged that high biomass forest often relates to high productivity and generally assumes a fairly constant mean residence time. However, a recent result emerging from Amazonian forests has suggested that woody biomass showed no apparent relationship to woody productivity [Malhi *et al.*, 2006]. There is evidence suggesting substantial variation in aboveground allocation of NPP across tropical forest sites, with a very different relationship for Asian forests [Malhi *et al.*, 2011]. The lack of data from Asian forests hinders attempts to accurately estimate and predict the allocation relationship across continents. Hence, quantification and understanding of productivity, its allocation, and their response to climate are imperative in a lowland dipterocarp forest. Moreover, to our knowledge, no studies have examined the seasonality of NPP, a topic of particular interest in the generally aseasonal climate of Borneo.

[6] The overall aim of this study is to quantify aboveground and belowground NPP and develop a better understanding of the allocation of NPP and its seasonal variation in a Bornean lowland tropical forest. The specific research questions addressed in this study are as follows:

[7] 1. What is the aboveground and belowground productivity, and how is it partitioned into wood material, leaves, flowers, fruits, fine roots, and coarse roots in a lowland dipterocarp forest in Borneo?

[8] 2. What is the seasonal variation in the components of aboveground and belowground NPP, and how are these related to the environmental factors?

[9] 3. What is the overall allocation of NPP at this site, and how does it vary between the sand and clay sites?

## 2. Materials and Methods

### 2.1. Study Site

[10] This study was carried out in a 52 ha forest dynamics plot in Lambir Hills National Park, Sarawak, Malaysia (4°12' N, 114°2'E), which is part of the Center for Tropical Forest Science (CTFS) global network of large plots [Condit, 1995; Lee *et al.*, 2004]. Within the 52 ha plot, we established two 1 ha research plots (100 × 100 m), one each on clay and sandy loam soils. The 1 ha plot was further divided into 25 subplots measuring 20 × 20 m. Lambir is an exceptionally diverse lowland mixed dipterocarp forest, with the highest recorded tree diversity in the Paleotropics [Ashton, 2005; Davies and

Becker, 1996; Lee *et al.*, 2002a; Phillips *et al.*, 1994]. Euphorbiaceae and Dipterocarpaceae are the most species-rich families at the site. The dipterocarp species have mass flowering events which occur periodically, including during our measurement period [Kettle *et al.*, 2011]. A comprehensive description of floristic and stand structure has been presented by Lee *et al.* [2002a]. The 52 ha forest dynamics plot was established in 1992 [Yamakura *et al.*, 1995]. All trees ≥1 cm in diameter at breast height (1.3 m, DBH) were mapped and identified to species, and their DBH were measured following standard methods [Condit, 1998]. The census was repeated in 1997 and every 5 years thereafter.

[11] The soils in Lambir range from sandstone sandy loam to shale-derived clay. From this gradient, four soil types have been identified in order of increasing fertility and moisture: sandy loam, loam, fine loam, and clay based on soils clustering [Davies *et al.*, 2005]. The sandstone-derived soils are humult Ultisols [Soil Survey Staff, 2006], with densely matted fine roots on the surface horizon, high sand content (typically 68% sand), low nutrients, and low water-holding capacity [Ashton and Hall, 1992; Davies *et al.*, 1998]. The shale-derived soils are clay-rich udult Ultisols [Soil Survey Staff, 2006] (typically 40% sand), with a thin litter layer on the soil surface, relatively higher fertility, and high water-holding capacity [Davies *et al.*, 1998, 2005]. Davies *et al.* [1998] showed that sandstone-derived soils typically occur on slopes and ridges, while the shale-derived soils are mostly in low-lying gullies. The altitude difference between the highest point and the lowest point is approximately 150 m, with steep, undulating, and complex bisected topography [Yamakura *et al.*, 1995]. The soils and geomorphology of Lambir have been previously described in detail [Baillie *et al.*, 2006; Ishizuka *et al.*, 1998; Tan *et al.*, 2009; Watson, 1985].

[12] To measure the main components in regard to NPP, we broadly used the protocols developed by the RAINFOR-GEM network, which are described in detail in a manual (available at <http://gem.tropicalforests.ox.ac.uk/>) [Global Ecosystems Monitoring Network (GEM), 2012] and which will facilitate direct comparison with new NPP data emerging from the African and Amazonian tropics.

### 2.2. Estimate of Aboveground Net Primary Productivity (NPP<sub>AG</sub>)

#### 2.2.1. Wood Density and Tree Height

[13] Wood density was determined for the most common species based on locally measured wood density of 11 tree species [King *et al.*, 2006] and five tree species of soil specialists and generalists [Heineman *et al.*, 2011], all of which were assessed at the Lambir site. In addition, other values of wood density measured in this region (Borneo and West Malaysia) were included: 12 species from Kuala Belalong, Brunei [Osunkoya *et al.*, 2007]; four species from East Kalimantan, Indonesia [Basuki *et al.*, 2009]; 70 species from West Kalimantan, Indonesia [Suzuki, 1999]; three species from the Pasoh Forest Reserve, Peninsular Malaysia [King *et al.*, 2006]; and three species from secondary forest near Lambir [Kenzo *et al.*, 2009]. For the remaining species, we used the average wood density of each individual species in a global wood density data set [Chave *et al.*, 2009; Zanne *et al.*, 2009]. Where data on wood density were not available for a particular tree species or an unidentified species (but genus or family known), we determined the average density to genus

or family level. For unknown tree species and those unlisted in the global data set (32 species), we used the Lambir average value of  $0.64 \text{ g cm}^{-3}$  [King *et al.*, 2006].

[14] Tree heights were derived from locally measured height data for clay and sandy loam sites in Lambir [King *et al.*, 2009]. Given that the tree species distribution in Lambir is edaphically biased to different soil types [Davies *et al.*, 2005; Palmiotto *et al.*, 2004; Russo *et al.*, 2005], tree species were determined and assigned into clay (29 trees) and sandy loam (49 trees), respectively. Regression analysis was employed to explore the relationship between tree heights and DBH. The relationship between tree height and DBH is well described by an exponential growth regression on both clay ( $r^2=0.99$ ,  $p$  value  $< 0.001$ ) and sandy loam ( $r^2=0.98$ ,  $p$  value  $< 0.001$ ). The best fit equations are as follows:

$$\text{Tree height} = 59.4726 \times (1 - 0.9805^2)(\text{clay}) \quad (1)$$

$$\text{Tree height} = 50.5623 \times (1 - 0.9764^2)(\text{sandy loam}) \quad (2)$$

where tree height was in meters, and DBH was in centimeters. Hence, trees on the sandy soil tend to be slightly shorter for a given DBH than those on the clay soil. Next, we applied these regression equations to predict the heights of all trees on clay and sandy loam sites.

### 2.2.2. Aboveground Coarse Wood Net Primary Productivity (NPP<sub>ACW</sub>)

[15] Multiple tree censuses from sandy loam and clay sites were used to determine plot-level aboveground coarse woody biomass and fluxes. Four censuses over five yearly intervals have been conducted by the CTFS following a standard protocol [Condit, 1998] on all trees  $>1$  cm DBH since 1992. All trees were identified to species [Lee *et al.*, 2002b]. Using these tree censuses from both the 1 ha clay and sandy loam sites, we determined the growth rate for all existing trees. We also separately estimated the growth and recruitment of only trees  $>10$  cm DBH for comparability with other studies.

[16] Several allometric equations for estimating biomass in tropical dipterocarp forests have been developed in the Southeast Asian region [Basuki *et al.*, 2009; Kato *et al.*, 1978; Kenzo *et al.*, 2009; Yamakura *et al.*, 1986]. Here we employed the allometric equation by Chave *et al.* [2005], which incorporates wood density and height data to directly compare with similar studies conducted at several Amazonian forest sites. In addition, recent studies in Amazonia and Borneo have shown that wood specific density is important in seeking to produce accurate estimates and capture the spatial variation of aboveground biomass at a regional scale [Baker *et al.*, 2004; Chave *et al.*, 2005; Malhi *et al.*, 2006; Slik, 2006; Slik *et al.*, 2010]. Hence, we used the allometric equation given by Chave *et al.* [2005], i.e.,

$$\text{AGB} = 0.0509 \times \rho \times \text{DBH}^2 \times H \quad (3)$$

where AGB is the aboveground dry biomass (kg);  $\rho$  is the oven-dry wood specific gravity ( $\text{g cm}^{-3}$ ); DBH is the diameter at breast height, 1.3 m (cm); and  $H$  is the height (m). NPP<sub>ACW</sub> was then estimated based on the change in woody biomass between census intervals. Biomass values were converted by assuming that dry-stem biomass has a carbon content of 47.4% [Martin and Thomas, 2011], based on a

study in Panama, which is the first to account for the volatile carbon lost when wood is dried.

[17] To capture seasonal variation of NPP<sub>ACW</sub>, we installed dendrometer bands on trees ( $\geq 10$  cm DBH), including approximately 20 randomly selected fast-growing trees ( $\geq 10$  cm DBH) on both clay and sandy loam sites. Fast-growing trees were specialist species categorized based on habitat specialization patterns for both clay and sandy loam soils [Davies *et al.*, 2005; Russo *et al.*, 2005]. Monthly (for fast-growing trees) and three monthly (all trees  $>10$  cm DBH) increments from dendrometer bands were recorded from June 2009 to September 2010. The dendrometers were installed in July 2008 on clay and sandy loam sites, but the first 10 months of data were not used to allow the dendrometer to settle onto the trees [da Silva *et al.*, 2002]. The data set was carefully checked for irregularities (e.g., measurement errors), and obvious erroneous data points were linearly interpolated. Dendrometer increments in each month were added to the initial DBH, which was measured prior to dendrometer installation, in order to estimate monthly diameter. Woody biomass was calculated using equation 3, and biomass growth rates were determined by taking the difference in biomass between months. Monthly woody growth rates for all trees were estimated based on the monthly growth rates for fast-growing trees, of which were scaled up to 1 ha to match the three monthly growth rates measured by the wider dendrometer data set. The wider dendrometer data set did not include all the trees ( $\geq 10$  cm DBH) in the 1 ha plot on clay (36 trees not included) and sandy loam (61 trees not included) sites. Hence, we scaled up to 1 ha (including nondendrometer trees) by using the full census data to determine the ratio of wood productivity of all trees over that of dendrometer trees. The multiplier (1.22 on clay and 1.08 on sandy loam) was applied to the seasonal woody growth rates of dendrometer trees. We assumed that the productivity of the dendrometer trees is representative of the wider population.

[18] Furthermore, we tried to account for any moisture-related seasonal cycle that may be caused by bark or hydraulic expansion during wet periods and contraction during dry periods. We did this by separating live trees with very low growth rates (NPP<sub>ACW</sub>  $< 0.1 \text{ kg C tree}^{-1}$ ) on clay ( $n=124$  trees) and sandy loam ( $n=197$  trees) and estimated annual seasonal growth for apparent growing trees, calculating the mean seasonal growth cycle of these trees and subtracting this cycle from all other trees. In this wet, broadly aseasonal forest, the seasonal cycle was very small. The mean seasonal NPP levels due to moisture expansion effects were calculated at  $0.001 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on clay and  $0.003 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on sandy loam, making this effect negligible. However, this correction does not allow for any correlation between the growth rate and the seasonal cycle of moisture expansion (e.g., wide-vessel trees may contract more in the dry season) (Rowland *et al.*, unpublished data).

### 2.2.3. Litterfall Net Primary Productivity (NPP<sub>litterfall</sub>)

[19] Dead organic material (woody material  $< 2$  cm diameter) was collected from litter traps measuring  $0.25 \text{ m}^2$  ( $0.5 \times 0.5$  m) installed at 1 m height above the ground in the middle of each  $20 \times 20$  m subplot on both clay and sandy loam sites (25 traps in each plot in total). Collection took place from July 2008 to August 2009. Litterfall was collected every 14 days to minimize in-trap decomposition, oven-dried at  $80^\circ\text{C}$  to constant weight, and weighed immediately after removal from the oven. NPP<sub>litterfall</sub> was then estimated as the sum of litterfall

components, separated into (i) leaves ( $\text{NPP}_{\text{leaves}}$ ); (ii) branches, twigs, and woody tissue ( $\text{NPP}_{\text{twigs}}$ ); (iii) fruits, flowers, and seeds ( $\text{NPP}_{\text{reprod}}$ ); and (iv) undefined fine debris ( $\text{NPP}_{\text{debris}}$ ). Biomass values were converted by assuming that dry-stem biomass has a carbon content of 50% [Kenzo *et al.*, 2003].

#### 2.2.4. Seasonal Leaf Productivity

[20] Canopy productivity estimated from litterfall over annual or longer-term time scales may not capture the seasonal variability in leaf production because litterfall reflects the timing of canopy biomass loss rather than biomass gain. To determine the seasonal variation of leaf productivity, we combined the litterfall data set with data on changes in leaf area index (LAI) and mean values of specific leaf area (SLA) based on the following equation [Doughty and Goulden, 2008]:

$$\text{Leaf production} = \text{dLAI}/\text{SLA} + \text{leaf litterfall} \quad (4)$$

where leaf production is in  $\text{g m}^{-2}$ , dLAI is the change in LAI ( $\text{m}^2 \text{m}^{-2}$ ) between months, SLA is the mean specific leaf area ( $\text{m}^2 \text{g}^{-1}$ ), and leaf litterfall is in  $\text{g m}^{-2}$ .

[21] We determined LAI by recording canopy hemispherical images using a digital camera (Nikon Coolpix 990) and a hemispherical lens (Nikon FC-E8 fish-eye converter) near the center of each of the 25 subplots across the 1 ha clay and sandy loam sites. Twenty images were recorded every month from August 2009 to May 2010 at 1 m above the soil surface during overcast conditions in the early morning (0630–0800 h). Monthly canopy hemispherical images were analyzed using the CAN-EYE software (available at [www4.paca.inra.fr/can-eye](http://www4.paca.inra.fr/can-eye)) [Demarez *et al.*, 2008; Weiss, 2012]. Using the CAN-EYE software, we assumed LAI as half the total developed area of leaves per unit ground horizontal surface area notwithstanding the vegetation shape [Chen and Black, 1992; Lang, 1991].

[22] The mean SLA was estimated by collecting subsamples of leaf from 11 specialist dominant tree species on sandy loam and five specialist dominant tree species on clay. Fresh leaf samples collected were scanned, and the leaf areas were analyzed using image analysis software (available at <http://rsb.info.nih.gov/ij/>) [ImageJ, 2012]. The samples were then oven-dried to constant mass. SLA is fresh leaf area divided by dry mass of leaf.

#### 2.2.5. Branch Turnover Net Primary Productivity ( $\text{NPP}_{\text{branch}}$ )

[23] The turnover of branches (branch growth and shedding not associated with tree death) can be a significant component of NPP but is rarely measured. To assess branch turnover, we conducted censuses every 3 months between August 2009 and July 2010. Fallen coarse woody materials (woody material >2 cm diameter, including bark) were collected from four  $100 \text{ m} \times 1 \text{ m}$  transects established along the boundary within each 1 ha plot. Initial collection of coarse woody materials was considered as dead wood stock rather than production of new branch material. Branches that were easily lifted were cut to only include the transect-crossing component, removed, and weighed directly. Heavier and larger branches that could not be removed were recorded for dimensions (diameter, height, and length) and were allocated a wood density value based on their decomposition stage. In subsequent censuses, new branchfall material was noted. Care was taken to discard any branchfall associated with tree mortality, as that component is already included in the mortality data and whole-tree allometric equation.

#### 2.2.6. Net Primary Productivity Loss to Leaf Herbivory ( $\text{NPP}_{\text{herbivory}}$ )

[24] Foliar herbivory alters nutrient cycles and carbon inputs in the terrestrial ecosystems and hence influences the feedback from producers and decomposers to aboveground and belowground productivity [Bardgett and Wardle, 2003]. Although leaf herbivory contributes a substantial fraction of losses [Coley and Barone, 1996],  $\text{NPP}_{\text{herbivory}}$  is often unaccounted for in tropical forests [Clark *et al.*, 2001b]. In this study, we did not directly quantify herbivory for canopy leaves. We adopted an average herbivory rate of  $0.0135\% \text{ d}^{-1}$  according to synchronous and continuous leafing patterns across 40 tree species in Lambir [Kurokawa and Nakashizuka, 2008]. This involved measuring the percentage loss in area for each leaf sampled from the canopy and comparing the damaged leaf area (evidence of leaf being eaten) to the intact leaf shape from scanned images. The herbivory rate for each tree was estimated based on accumulated damage by the life span of the leaf to correct for potential underestimation [Kurokawa and Nakashizuka, 2008]. Hence, the production lost to leaf herbivory was calculated by multiplying  $\text{NPP}_{\text{leaves}}$  (leaf litterfall) by the herbivory rate. Given that this estimation may be associated with substantial sampling uncertainty and varies between the canopy and the understory level, we assigned a 50% error ( $\pm 0.10$ ) to the multiplying factor.

### 2.3. Estimate of Belowground Net Primary Productivity ( $\text{NPP}_{\text{BG}}$ )

#### 2.3.1. Coarse Root Net Primary Productivity ( $\text{NPP}_{\text{coarse roots}}$ )

[25]  $\text{NPP}_{\text{coarse roots}}$  is the least measured and estimated woody biomass component because it is difficult to sample large biomass below the stem without destructive sampling of trees. Coarse roots were defined as roots exceeding 5 mm in diameter [Niiyama *et al.*, 2010]. To estimate coarse root biomass, we used an allometric equation for coarse root biomass developed from a large-scale root excavation study in the Pasoh Forest Reserve in Peninsular Malaysia [Niiyama *et al.*, 2010], a similar lowland dipterocarp forest to our study site, i.e.,

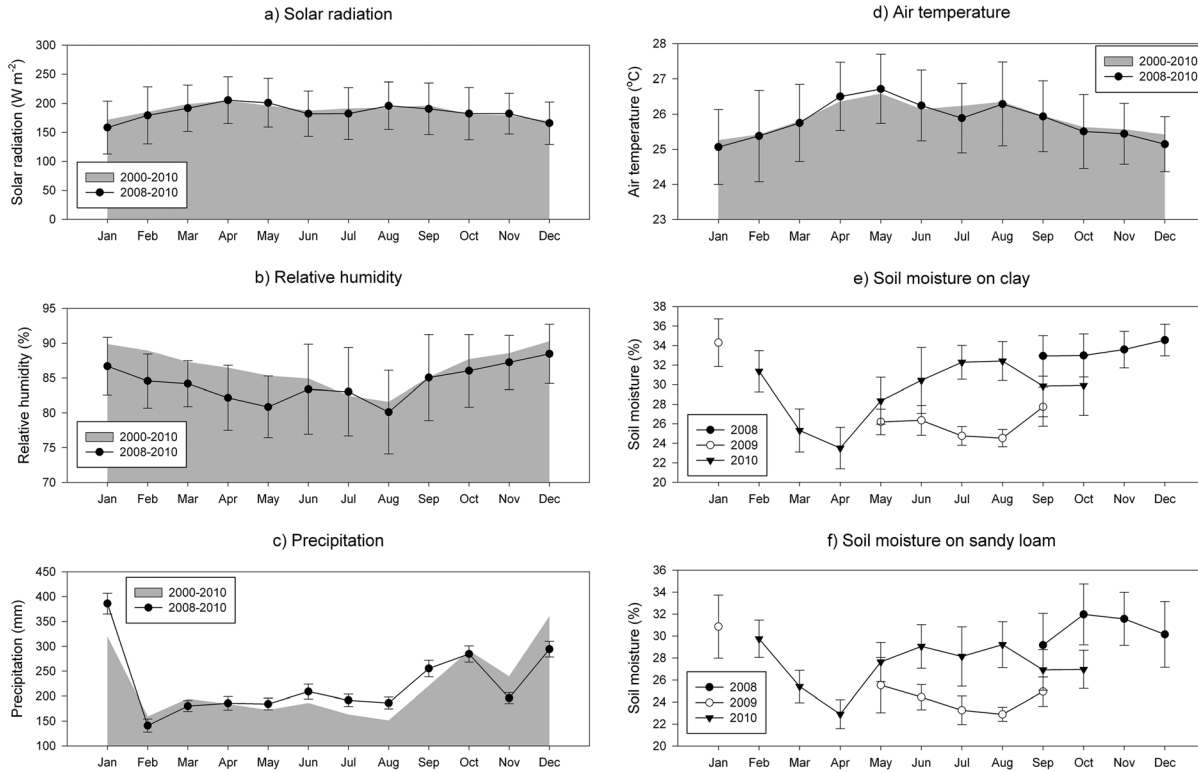
$$\begin{aligned} \text{Dry mass coarse root}(\text{tree} \geq 2.5 \text{ cm DBH}) \\ = 0.023 \times \text{DBH}^{2.59} \end{aligned} \quad (5)$$

$$\begin{aligned} \text{Dry mass coarse root}(\text{tree} < 2.5 \text{ cm DBH}) \\ = 0.079 \times \text{DBH}^{1.04} \end{aligned} \quad (6)$$

where coarse roots per tree is in kilograms [coarse root in equation (5) corrected for lost roots], and DBH is in centimeters).

#### 2.3.2. Fine Root Net Primary Productivity ( $\text{NPP}_{\text{fine roots}}$ )

[26] Production of fine roots was quantified using ingrowth cores. Nine ingrowth cores made from mesh nets (mesh size:  $1 \text{ cm}^2$ ) of 14 cm diameter and 40 cm height were installed to 30 cm in each site, in a  $3 \times 3$  grid across each 1 ha plot, starting in May 2008. The mesh nets were extracted every 3 months from September 2008 to October 2009, with new ones being installed at the same time. Roots were extracted manually from the extracted soil cores in four 10 min time steps [Metcalfe *et al.*, 2007]. Root-free soil was repacked into the mesh net and placed back into the soil. These cores were reinserted and compacted with care to replicate the natural



**Figure 1.** Monthly mean (a) solar radiation ( $\text{W m}^{-2}$ ), (b) relative humidity (%), (c) precipitation (mm), (d) air temperature ( $^{\circ}\text{C}$ ), and soil moisture (%) on (e) clay and (f) sandy loam in Lambir (meteorological data from canopy crane) over the observation period between 2008 and 2010. The shaded area is meteorological data between 2000 and 2010. Each point of soil moisture in Figures 1e and 1f is the average of point measurements obtained from both clay and sandy loam sites ( $n=25$ ) from September 2008 to October 2010. Errors are plotted as standard deviation of the mean.

soil conditions, horizon structure, and bulk density as closely as possible. We fitted a logarithmic curve to the first 40 min of the extracted root and predicted cumulative root mass up to 100 min [Metcalfe *et al.*, 2007]. On average, 38% and 49% of uncollected fine root mass on clay and sandy loam soils, respectively, was predicted in each ingrowth cores, which is comparable to the correction suggested by Metcalfe *et al.* [2007] for Amazonian forest data. Fine root production was estimated by scaling to a 1 ha area.

[27] Given that fine root production was estimated between 0 and 30 cm from the soil surface, we corrected the estimation up to 100 cm depth to reduce the discrepancies of fine root production measured from different soil depths. The depth correction applied here assumed that the ratio of fine root to coarse root biomass was invariant with depth and that fine root productivity per unit fine root biomass was invariant [Malhi *et al.*, 2009]. Following a similar approach employed by Malhi *et al.* [2009], the correction factor was calculated using the root profile biomass in the Pasoh Forest Reserve [Yoda, 1978]. We extrapolated root biomass up to 100 cm based on the following equation [Yoda, 1978]:

$$W_R = W_{R0} \exp(-\varepsilon z) \quad (7)$$

where  $W_R$  is the dry mass of fine roots in  $\text{Mg ha}^{-1} \text{cm}^{-1}$ ,  $W_{R0}$  is the biomass density of fine roots at surface soil given as a constant value at  $1.5 \text{ Mg ha}^{-1} \text{cm}^{-1}$ ,  $\varepsilon$  is given as a constant

value of 0.073, and  $z$  is the soil depth in centimeters. Hence, the multiplying correction factor for the soil depth between 30 and 100 cm was 1.125.

## 2.4. Statistical and Error Analysis

[28] We analyzed the data in this study to determine NPP components and allocations for aboveground and belowground biomass over time. Using the monthly estimates, we plotted the results to look for seasonal variations. The Student's  $t$  test was used to compare differences in the annual and monthly means between clay and sandy loam sites. Statistical analysis was conducted using R statistical software (version 2.13.0; R Development Core Team), and the results were plotted using SigmaPlot 10.0 (Systat Software, Inc.).

[29] We presented mean estimates with standard deviations (SD; reported as mean  $\pm$  SD) and standard errors (SE; reported as mean  $\pm$  SE). The propagation of errors were based on the quadrature of absolute errors for addition/subtraction and the quadrature of proportional errors for fractions [Aragão *et al.*, 2009; Malhi *et al.*, 2009], with the assumptions that the uncertainties are independent and normally distributed.

## 3. Results

### 3.1. Meteorology

[30] We analyzed meteorological data for the two periods 2000–2010 (a context period) and 2008–2010 (the measurement

**Table 1.** Aboveground Coarse Wood Biomass for All Trees on Clay and Sandy Loam Sites Between 1992 and 2008

	Mean Aboveground Biomass (Mg C ha <sup>-1</sup> )				
	1992	1997	2003	2008	Average
Clay	234.8	207.5	216.0	227.4	221.4
Sandy loam	259.2	270.2	250.2	263.4	260.7

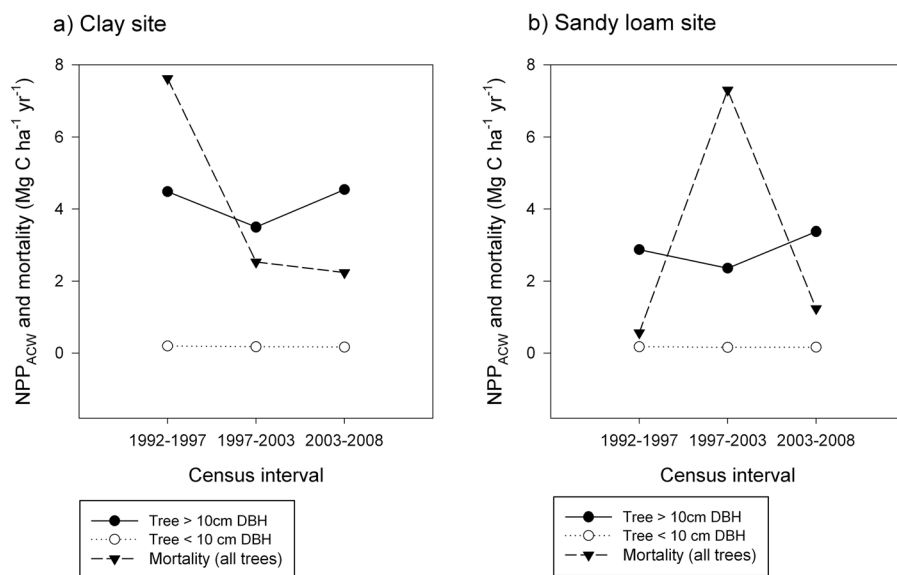
period) (from an 80 m canopy crane approximately 3 km away from our study site). Lambir is characterized by little seasonality in climate [Kumagai *et al.*, 2005]. The strongest seasonality is manifested in terms of rainfall, with a strong wet season associated with the northeastern monsoon from September to January and a drier season from February to August (Figure 1c). However, even the drier season has mean monthly rainfall around 150 mm month<sup>-1</sup>, well above the 100 mm month<sup>-1</sup> typically transpiring from tropical forest canopies [Fisher *et al.*, 2009], indicating that the site does not experience water stress at any time of the year. It should be noted, however, that the region does experience strong El Niño-associated droughts about once per decade [Malhi and Wright, 2004; Walsh and Newbery, 1999]. Total mean annual precipitation over the 10 year period was 2630 mm, and over the 3 year observation period, it was 2694 mm. The other meteorological variables show moderate seasonality associated with the precipitation seasonality. In the very wet season, solar radiation is slightly lower (Figure 1a), relative humidity is slightly higher (Figure 1b), and air temperature is 1°C–2°C cooler. Soil moisture, sampled once per month, shows little coherent variation over the year, as would be expected from a wet site where the time since the last rain event is probably the biggest influence on measured values. Mean annual solar radiation is  $187.3 \pm 12.6 \text{ W m}^{-2}$  (mean  $\pm$  SD), mean annual relative humidity is  $86.5 \pm 1.6\%$ , and mean annual air temperature (on the 80 m crane, the ground level will be about 0.4°C warmer) is  $25.9 \pm 0.3^\circ\text{C}$ . Over our measurement period, soil moisture was

significantly higher on clay (mean =  $29.5 \pm 2.2\%$ ) than on sandy loam (mean =  $27.4 \pm 2.1\%$ ).

### 3.2. Forest Structure and Biomass

[31] The average (basal area weighted) wood density was  $0.61 \pm 0.05 \text{ g cm}^{-3}$  (mean  $\pm$  SE) on clay and  $0.62 \pm 0.04 \text{ g cm}^{-3}$  on sandy loam. The mean height of trees ( $\geq 10 \text{ cm DBH}$ ) estimated following the most recent census (2008) was  $19.6 \pm 0.4 \text{ m}$  (mean  $\pm$  SE) on the clay site and  $19.5 \pm 0.3 \text{ m}$  on the sandy loam site. The mean height of canopy trees ( $\geq 40 \text{ cm DBH}$ ) was  $41.0 \pm 0.9 \text{ m}$  on clay and  $37.8 \pm 0.5 \text{ m}$  on sandy loam. This is substantially higher than the mean heights of 20–25 m for trees greater than 40 cm DBH reported for humid Amazonian forests (Y. Malhi, *et al.*, The productivity, metabolism and carbon cycle of two lowland tropical forest plots in SW Amazonia, Peru, Plant Ecol. Divers., in press, 2014). Height was not significantly different between clay and sandy loam sites ( $t=0.37$ ,  $p$  value = 0.71,  $t$  test).

[32] The average aboveground woody biomass (trees  $\geq 10 \text{ cm DBH}$ ) between 1992 and 2008 was  $216.7 \text{ Mg C ha}^{-1}$  on the clay site and  $254.7 \text{ Mg C ha}^{-1}$  on the sandy loam site (Table 1). For smaller trees ( $< 10 \text{ cm DBH}$ ), the mean value was  $4.7 \text{ Mg C ha}^{-1}$  on clay and  $6.0 \text{ Mg C ha}^{-1}$  on sandy loam. For larger trees ( $\geq 40 \text{ cm DBH}$ ), the mean value was  $170.2 \text{ Mg C ha}^{-1}$  on clay and  $178.1 \text{ Mg C ha}^{-1}$  on sandy loam. The number of trees ( $> 10 \text{ cm DBH}$ ) on clay ( $429 \text{ stems ha}^{-1}$ ) was substantially lower than that on sandy loam ( $642 \text{ stems ha}^{-1}$ ). Looking at the longer-term data, we can see that aboveground coarse woody biomass (trees  $\geq 10 \text{ cm DBH}$ ) showed moderate variation, with a notable decline in growth (Figure 2) on both the clay site ( $202.5 \text{ Mg C ha}^{-1}$ ) and the sandy loam site ( $244.5 \text{ Mg C ha}^{-1}$ ) over the period 1997–2003 (Table 1), which may be associated with the strong 1997/1998 El Niño drought. The clay site showed smaller variation in overall biomass.



**Figure 2.** The mean aboveground coarse woody biomass (NPP<sub>ACW</sub>) and mortality for trees greater than 10 cm diameter breast height (DBH) (solid circle), less than 10 cm (open circle), and mortality for all trees (solid triangle) on (a) clay and (b) sandy loam soils over three census intervals between 1992 and 2008.

**Table 2.** Summary of the Total Annual Average Net Primary Productivity (NPP) for Aboveground and Belowground Components on Both the 1 Ha Clay and Sandy Loam Sites<sup>a</sup>

	Clay			Sandy Loam		
	Mean	Standard Error	Fraction (%)	Mean	Standard Error	Fraction (%)
NPP <sub>ACW</sub> ( $\geq 10$ cm DBH)	4.17	0.42	26.2	2.87	0.29	22.4
NPP <sub>ACW</sub> ( $< 10$ cm DBH)	0.14	0.01	0.9	0.13	0.01	1.0
NPP <sub>litterfall</sub>	7.89	0.43	49.7	5.99	0.46	46.8
NPP <sub>leaves</sub> <sup>b</sup>	5.52	0.37	70.0 <sup>c</sup>	4.35	0.29	72.6 <sup>c</sup>
NPP <sub>twigs</sub> <sup>b</sup>	1.39	0.17	17.6 <sup>c</sup>	0.70	0.11	11.7 <sup>c</sup>
NPP <sub>reprod</sub> <sup>c</sup>	0.25	0.06	3.2 <sup>c</sup>	0.47	0.10	7.8 <sup>c</sup>
NPP <sub>debris</sub>	0.73	0.11	9.3 <sup>c</sup>	0.47	0.06	7.8 <sup>c</sup>
NPP <sub>herbivory</sub> <sup>d</sup>	0.27	0.05	1.7	0.21	0.05	1.6
NPP <sub>branch</sub> <sup>d</sup>	0.53	0.09	3.3	1.08	0.11	8.4
NPP <sub>coarse root</sub>	0.93	0.37	5.9	0.65	0.26	5.1
NPP <sub>fine roots</sub>	1.96	0.55	12.3	1.86	0.30	14.5
NPP <sub>AG</sub>	13.00	0.61	81.8	10.28	0.56	80.4
NPP <sub>BG</sub>	2.89	0.66	18.2	2.51	0.40	19.6
NPP <sub>Total</sub>	15.89	0.90	100.0	12.79	0.68	100.0

<sup>a</sup>All fluxes are reported in  $\text{Mg C ha}^{-1} \text{yr}^{-1}$ . Reported errors are the sample standard error of the mean.

<sup>b</sup>Woody material  $< 2$  cm diameter.

<sup>c</sup>Reproductive materials (e.g., flowers, fruits, and seeds).

<sup>d</sup>Woody material  $> 2$  cm diameter, including fallen stem and bark.

<sup>e</sup>Fraction of NPP<sub>litterfall</sub>.

Key: NPP<sub>ACW</sub>, aboveground coarse wood NPP; NPP<sub>litterfall</sub>, litterfall NPP; NPP<sub>leaves</sub>, leaves NPP; NPP<sub>twigs</sub>, twigs NPP; NPP<sub>reprod</sub>, reproductive materials NPP; NPP<sub>debris</sub>, undefined fine debris; NPP<sub>herbivory</sub>, NPP lost to leaf herbivory; NPP<sub>branch</sub>, branch turnover NPP; NPP<sub>coarse root</sub>, coarse roots NPP; NPP<sub>fine roots</sub>, fine root NPP; NPP<sub>AG</sub>, aboveground NPP; NPP<sub>BG</sub>, belowground NPP.

### 3.3. Aboveground Coarse Wood Net Primary Productivity and Seasonal Pattern

[33] Over the long term, the mean NPP<sub>ACW</sub> of trees ( $> 10$  cm DBH) was  $4.17 \pm 0.42 \text{ Mg C ha}^{-1} \text{yr}^{-1}$  on the clay site and  $2.87 \pm 0.29 \text{ Mg C ha}^{-1} \text{yr}^{-1}$  on the sandy loam site. For smaller trees ( $< 10$  cm DBH), it was  $0.14 \pm 0.01 \text{ Mg C ha}^{-1} \text{yr}^{-1}$  on the clay site and  $0.13 \pm 0.01 \text{ Mg C ha}^{-1} \text{yr}^{-1}$  on the sandy loam site (Table 2). Consequently, the total NPP<sub>ACW</sub> was  $4.32 \pm 0.43$  and  $3.00 \pm 0.30 \text{ Mg C ha}^{-1} \text{yr}^{-1}$  on clay and sandy loam, respectively. Dividing the aboveground biomass by NPP<sub>ACW</sub>, we estimated the mean C residence time to be 52 years on clay and 89 years on sandy loam. The forest on the sandy loam plot was significantly less dynamic and productive.

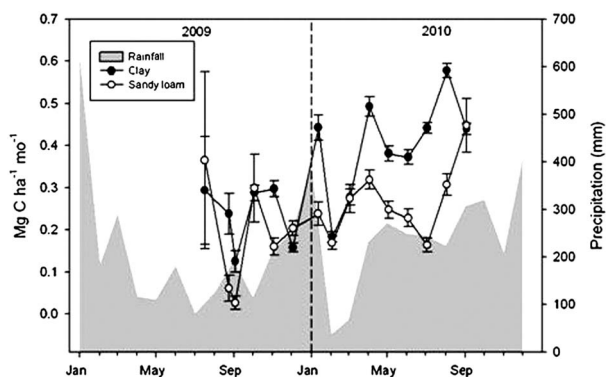
[34] Over the 15 month measurement period, we found little evidence of seasonality in growth rates. In fact, the signal appeared dominated by interannual variability, with higher growth rates in the 2010 drier season (June–September) than in the equivalent 2009 season (Figure 3). The mean monthly NPP<sub>ACW</sub> based on dendrometers was  $0.35 \pm 0.04 \text{ Mg C ha}^{-1} \text{month}^{-1}$  on clay and  $0.24 \pm 0.03 \text{ Mg C ha}^{-1} \text{month}^{-1}$  on sandy loam. In summary, the clay soil plot is characterized as a plot with relatively low biomass, more small trees, and high growth rates and tree turnover rates. The sandy soil plot has high biomass, more medium and large trees, slower growth rates, and slower tree turnover.

### 3.4. Seasonal Variation of Litterfall Net Primary Productivity

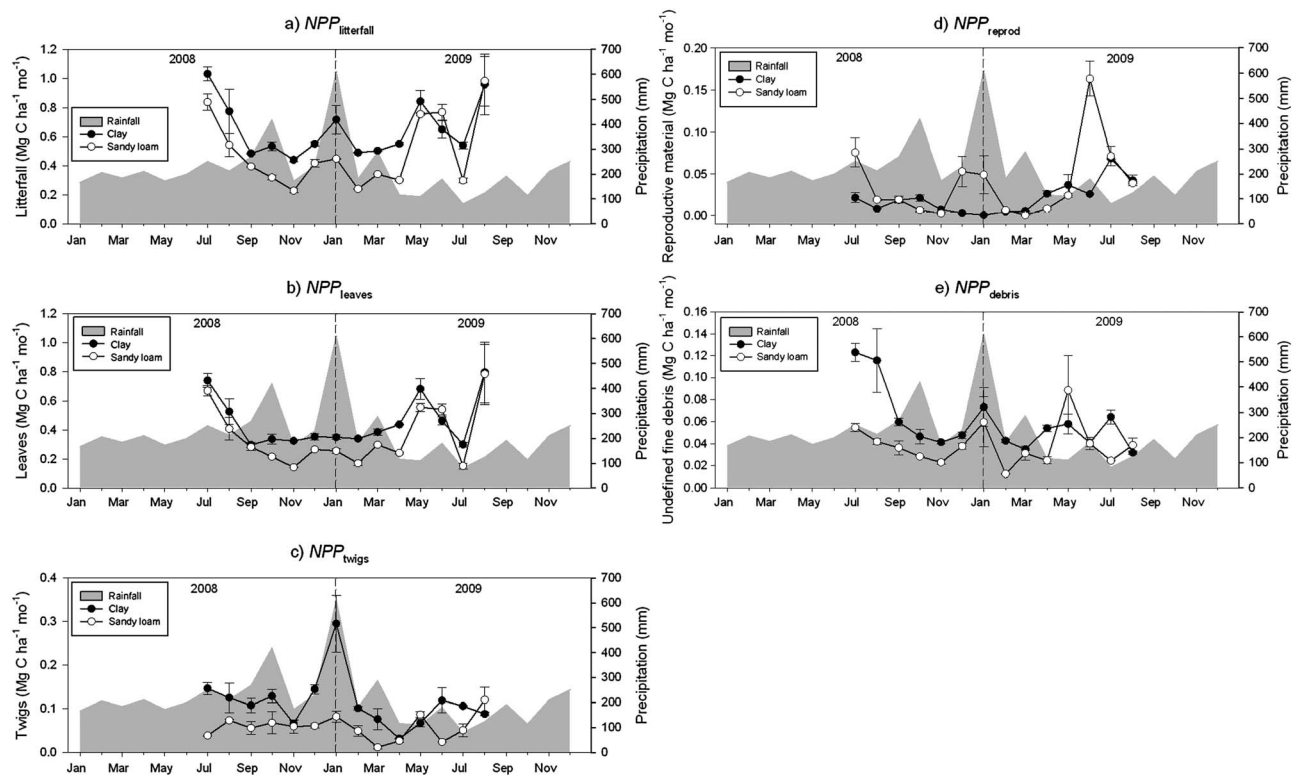
[35] NPP<sub>litterfall</sub> was  $7.89 \pm 0.43 \text{ Mg C ha}^{-1} \text{yr}^{-1}$  on clay and  $5.99 \pm 0.46 \text{ Mg C ha}^{-1} \text{yr}^{-1}$  on sandy loam (Table 2). The fractions of litterfall (clay/sandy loam) were partitioned into  $70.0 \pm 11.5\%/72.6 \pm 7.4\%$  leaves,  $17.6 \pm 3.4\%/11.7 \pm 2.0\%$  twigs,  $3.2 \pm 0.8\%/7.8 \pm 1.8\%$  reproductive materials, and  $9.3 \pm 1.5\%/7.8 \pm 1.2\%$  undefined fine debris.

[36] NPP<sub>litterfall</sub> and NPP<sub>leaves</sub> presented some evidence of seasonality, with higher rates typically during the drier period

on both clay and sandy loam (Figures 4a and 4b). Given that litterfall collection was at a different period and incomplete for a full year cycle, the evidence of seasonal variation may be tentative. However, there were contrasting trends between both years from July to August, suggesting some effects due to mass flowering of dipterocarps that occurred in June 2009 (Figures 4a and 4b). NPP<sub>reprod</sub>, NPP<sub>twigs</sub>, and NPP<sub>debris</sub> showed very little seasonal and interannual variation, with several periodic peaks on both clay and sandy loam sites (Figures 4c–4e). Similar seasonality in litterfall rates was observed in northern Borneo, with no apparent relationship to dry and wetter months [Burghouts *et al.*, 1992; Saner *et al.*, 2012].



**Figure 3.** The monthly aboveground coarse wood net primary productivity (NPP<sub>ACW</sub>) for all trees ( $> 10$  cm DBH) measured using dendrometer on clay and sandy loam sites between June 2009 and September 2010. Each point is the average monthly growth scaled up using three monthly dendrometer data and based on growth rates estimated from the monthly dendrometer data for fast-growing trees. The shaded area is the monthly rainfall from 2009 to 2010.



**Figure 4.** The seasonal variation of monthly NPP for (a) litterfall, the sum of all litter components production ( $NPP_{\text{litterfall}}$ ); (b) leaves, estimated for leaf fall only ( $NPP_{\text{leaves}}$ ); (c) branches, twigs, and woody materials ( $NPP_{\text{twigs}}$ ); (d) reproductive materials ( $NPP_{\text{reprod}}$ ); and (e) undefined fine debris ( $NPP_{\text{debris}}$ ) on clay and sandy loam sites between 2008 and 2009. Monthly rainfall (mm) is the shaded plot area from January 2008 to December 2009. Each point is the average litterfall collections ( $n=2$ ) per month. Errors are plotted as the standard error of the mean.

### 3.5. Seasonal Pattern of Leaf Production

[37] The means of LAI recorded from August 2009 to May 2010 were  $5.2 \text{ m}^2 \text{ m}^{-2}$  on clay and  $5.6 \text{ m}^2 \text{ m}^{-2}$  on sandy loam. LAI decreased over time on the clay site but showed no overall trend in regard to the sandy loam site (Figure 5a). We determined SLA based on dominant species, with DBH in the range of 1.0–80.0 cm and tree height between 6.0 and 44.0 m on clay and sandy loam sites. The mean SLA was  $14.8 \pm 1.8 \text{ m}^2 \text{ kg}^{-1}$  on clay and  $8.1 \pm 0.3 \text{ m}^2 \text{ kg}^{-1}$  on sandy loam. This is comparable to previously reported SLA with similar species and heights [Osada *et al.*, 2003; Paoli, 2006; Yoda, 1983].

[38] Using monthly changes of LAI (dLAI) and the estimated SLA for dominant species for both sites, we estimated the seasonal variation in leaf production from August 2009 to May 2010. Since our litterfall collection period did not fully coincide with LAI image recording, we substituted leaf litterfall data between September and December 2009 with data from September to December 2008 and assumed that there was little variation in the leaf fall between 2008 and 2009 ( $t=141$ ,  $p$  value  $> 0.05$ ). There was no evidence of a seasonal pattern in leaf flush or leaf fall at the clay site. At the sandy loam site, there was a suggestion of higher leaf production in the drier-wet transition (August–December). However, with the lack of concurrence of LAI and leaf fall data, such evidence should be regarded as tentative.

### 3.6. Branch Turnover Net Primary Productivity

[39] The  $NPP_{\text{branch}}$  levels for woody material ( $>2$  cm diameter) were significantly higher on the sandy loam site

( $1.08 \pm 0.11 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ) (mean  $\pm$  SE) than on the clay site ( $0.53 \pm 0.09 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ) ( $t=2.8$ ,  $p$  value  $< 0.05$ ) (Table 2). Branch turnover showed little seasonality over time on both clay and sandy loam sites (Figure 6). However, there was a sharp peak in June 2010 on the clay site to a value of  $2.28 \pm 0.14 \text{ Mg C ha}^{-1} \text{ month}^{-1}$  when a large tree fall caused substantial damage to adjacent trees and branches over a large area. In the absence of a longer data-collection period, this single event has a disproportionate effect on our estimated NPP. When this event is included in the clay site,  $NPP_{\text{branch}}$  is  $2.16 \pm 0.14 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ . However, when it is replaced with an average value from the rest of the period,  $NPP_{\text{branch}}$  is  $0.53 \pm 0.09 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ . For our overall calculations, we decided that the latter value was the better estimate of the mean long-term branch turnover.

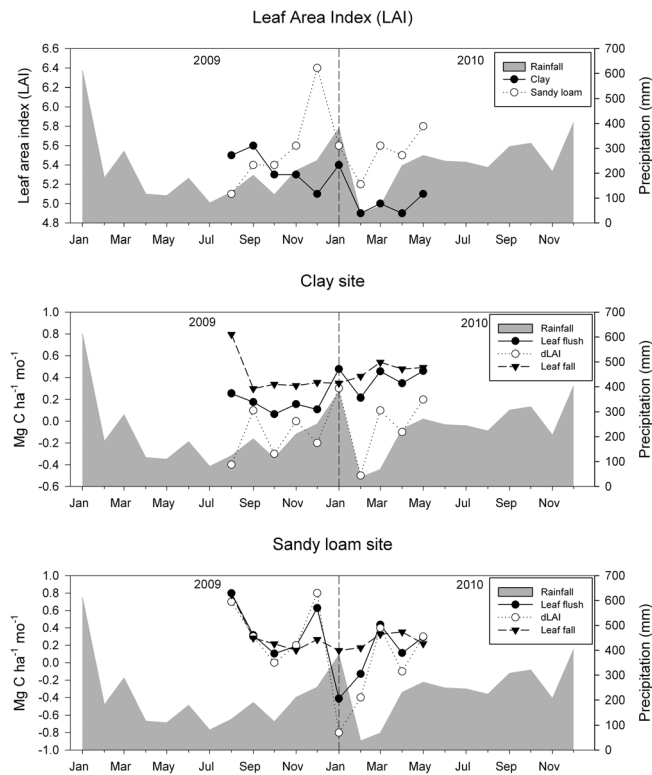
### 3.7. Net Primary Productivity Lost to Leaf Herbivory

[40]  $NPP_{\text{herbivory}}$  was  $0.27 \pm 0.14 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on clay and  $0.21 \pm 0.11 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on sandy loam. Our estimated levels of  $NPP_{\text{herbivory}}$  were relatively higher than that in an earlier study in Pasoh, which was estimated based on caterpillar frass droppings [Kira, 1978].

### 3.8. Coarse Root Net Primary Productivity

[41] The average coarse root biomass was  $48.5 \text{ Mg C ha}^{-1}$  on the clay site and  $57.6 \text{ Mg C ha}^{-1}$  on the sandy loam site. This was calculated using coarse root allometry derived for Pasoh, and the ratio of coarse root over aboveground coarse wood biomass was 0.22 on both clay and sandy loam.





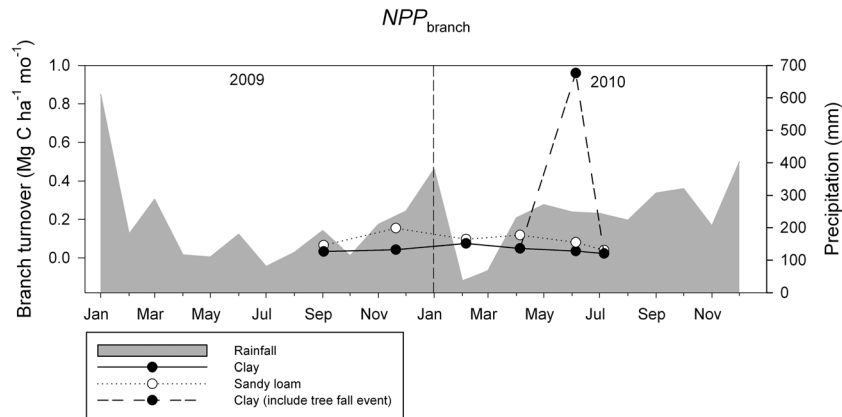
**Figure 5.** Seasonal variation of (a) leaf area index (LAI), (b) monthly leaf fall and production on clay, and (c) monthly leaf fall and production on sandy loam from August 2009 to May 2010. Substituted data between September 2009 and December 2009 are based on the rate of leaf fall from September 2008 to December 2008, since the data for the later period were unavailable. The shaded area is the monthly rainfall from 2009 to 2010.

This is comparable to the general ratio value of 0.21 applied in the Amazonian forests [Malhi *et al.*, 2009]. Using multiple censuses, we estimate  $NPP_{\text{coarse roots}}$  to be  $0.93 \pm 0.37 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on clay and  $0.65 \pm 0.26 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on sandy loam (Table 2). Similarly, the ratio of  $NPP_{\text{coarse roots}}$  to  $NPP_{\text{ACW}}$  was 0.22 on clay and 0.21 on sandy loam.

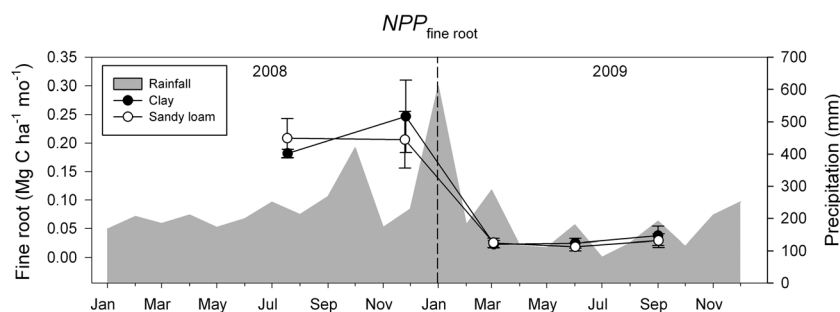
### 3.9. Fine Root Net Primary Productivity

[42] To our knowledge, this is the first attempt to quantify  $NPP_{\text{fine roots}}$  in a lowland dipterocarp forest.  $NPP_{\text{fine roots}}$  was

$1.74 \pm 0.49 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on clay and  $1.65 \pm 0.27 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on sandy loam following cumulative prediction up to 100 min. Using the depth correction factor,  $NPP_{\text{fine roots}}$  was  $1.96 \pm 0.55$  on clay and  $1.86 \pm 0.30$  on sandy loam (Table 2).  $NPP_{\text{fine roots}}$  was higher toward the wetter period between late July and December 2008 and declined during the drier period between March and September 2009 (Figure 7). The values in September 2008 and September 2009 were significantly different, indicating substantial interannual variability.



**Figure 6.** Monthly branch turnover net primary productivity ( $NPP_{\text{branch}}$ ) on clay and sandy loam sites from August 2009 to July 2010. The monthly  $NPP_{\text{branch}}$  for a particular large tree fall event in May 2009 along a sampling transect on the clay site is plotted with a dashed line.



**Figure 7.** Seasonal pattern for fine root NPP ( $NPP_{\text{fine roots}}$ ) on clay and sandy loam sites between September 2008 and October 2009. Three monthly  $NPP_{\text{fine roots}}$  is estimated based on the logarithmic curve to predict for extraction of fine root mass beyond 40 min (10 min time step extraction method). Each point is the average  $NPP_{\text{fine roots}}$  from nine ingrowth cores. Errors are plotted as the standard error of the mean.

### 3.10. Allocation of Net Primary Productivity

[43] By summing up the components described above, we estimated the total NPP ( $NPP_{\text{Total}}$ ) to be  $15.82 \pm 0.90 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on the clay site and  $12.85 \pm 0.69 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on the sandy loam site (Table 2).  $NPP_{\text{AG}}$  was  $12.93 \pm 0.61 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on clay and  $10.34 \pm 0.57 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on sandy loam.  $NPP_{\text{BG}}$  was  $2.89 \pm 0.67 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on clay and  $2.51 \pm 0.40 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  on sandy loam.  $NPP_{\text{AG}}$  contributed  $81.7 \pm 6.0\%$  and  $80.5 \pm 6.0\%$  of the  $NPP_{\text{Total}}$  on the clay and sandy loam sites, respectively.

[44] Out of  $NPP_{\text{Total}}$ ,  $NPP_{\text{leaves}}$  contributed the largest fraction of  $49.9 \pm 3.9\%$  and  $46.6 \pm 4.9\%$  on clay and sandy loam, respectively. This is followed by aboveground coarse wood productivity of  $26.8 \pm 3.0\%$  on clay and  $23.8 \pm 2.6\%$  on sandy loam.  $NPP_{\text{fine roots}}$  contributed between  $12.4 \pm 3.6\%$  and  $14.5 \pm 2.5\%$ , while  $NPP_{\text{coarse root}}$  contributed approximately  $5.9 \pm 2.4\%$  on clay and  $5.1 \pm 2.0\%$  on sandy loam. Hence,  $NPP_{\text{BG}}$  contributed  $18.3 \pm 4.3\%$  and  $19.5 \pm 3.3\%$  of  $NPP_{\text{Total}}$ . The NPP on the clay site was consistently higher than that on the sandy loam site, with significantly higher values in regard to the productivity of woody biomass, leaves, twigs, and litter debris. Only reproductive NPP ( $NPP_{\text{reprod}}$ ) was higher on the sandy site, and there was no significant difference in  $NPP_{\text{fine roots}}$  between the sites.

## 4. Discussion

### 4.1. Seasonal Variation of the Allocation of NPP

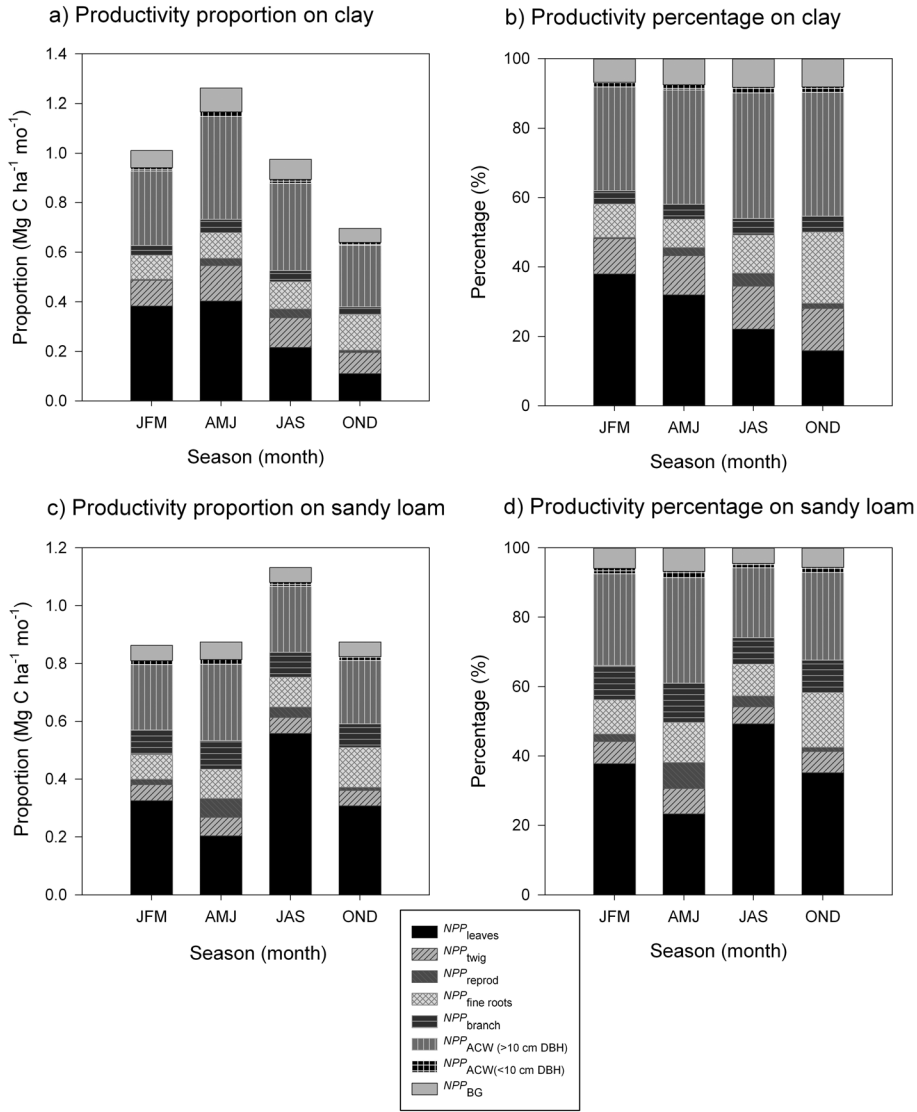
[45] We found moderate evidence of seasonality in the budget and allocation of NPP but some evidence of strong interannual variation in the components of NPP. In addition, the allocation of NPP in this forest is inherently different between soil types and may be different from tropical forests elsewhere.

[46] In this study, we have made several assumptions in order to capture a complete picture of seasonality in relation to the components of NPP. Given that the seasonal productivity of twigs, branch, and smaller trees are not available, we have assumed that these terms are proportional following the same seasonal cycle of  $NPP_{\text{ACW}}$  ( $>10 \text{ cm DBH}$ ). Hence, seasonal production is multiplied by the ratios of the annual production of these terms (Table 2). On the other hand, we have assumed that  $NPP_{\text{reprod}}$  is equal to the measured loss of flowers, fruits, and seeds because these components probably have canopy lifetime of less than 3 months.

[47] Figure 8 illustrates the seasonal proportion and fraction of NPP components. This quantification is the first attempt to explore the variation of NPP components and the allocation over the seasonal cycle for a paleotropical lowland forest. Clay and sandy loam sites show contrasting productivity patterns over the year. For the first half of the year on the clay site, NPP increases to a high of approximately  $1.3 \text{ Mg C ha}^{-1} \text{ month}^{-1}$  (April–June) following the wetter period. Productivity progressively declines to approximately  $0.7 \text{ Mg C ha}^{-1} \text{ month}^{-1}$  (October–December) in the second half of the year, which is typically in the end of the drier period (Figure 8a). The wetter conditions on clay may have provided favorable conditions on this soil, and tropical clay substrates tend to have higher nutrient retention and hence encourage higher production. This is supported by previous studies that reported higher productivity and allocation for tropical forests on high soil fertility [Aragão *et al.*, 2009; Cleveland *et al.*, 2011; Paoli and Curran, 2007; Russo *et al.*, 2005; Vicca *et al.*, 2012]. On the sandy loam site, however, productivity is the highest in the less wet period (July–September) at approximately  $1.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  and is generally consistent at approximately  $0.9 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  in other months over the year (Figure 8c). In addition, anisohydric plants in Lambir have higher productivity under moist conditions [Kumagai and Porporato, 2012]. This supported our findings that that higher moisture availability increases productivity, with a potential lag in response to a wetter period.

[48] On the clay plot, the largest allocation is to  $NPP_{\text{leaves}}$ , with the highest allocation at almost 40% during the wetter period (Figure 8b). It later progressively declines to the lowest point of about 10% between October and December. Similar patterns with smaller proportions are allocated for twigs, reproductive materials, fine roots, and branch. Productivity tends to decline in the drier period, and this reduces the allocation to leaves but increases the allocation to reproductive materials and fine roots. The proportions of aboveground and belowground wood are fairly consistent with slightly larger proportions allocated to aboveground coarse wood in the second half of the year.

[49] In the sandy loam site, the seasonal allocation varies over time (Figure 8d). Contrary to clay, productivity is highest (about  $1.1 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ ) toward the end of the drier period between July and September. Lower productivity occurs during the wetter period at approximately  $0.9 \text{ Mg C ha}^{-1} \text{ month}^{-1}$ . When productivity is highest, a larger



**Figure 8.** The seasonal allocation of net primary productivity (NPP) and its components on clay in (a) absolute value of proportion and (b) percentage and on sandy loam in (c) absolute value of proportion and (d) percentage.

allocation is invested in the production of leaves. However, when productivity is low during the wetter period, the allocation is mostly to aboveground coarse wood and fine roots. Similarly, on the sandy loam, the proportion of reproductive materials is larger during the drier period.

[50] These contrasting patterns suggest that the seasonal allocation of NPP is different on clay and sandy loam sites. During the wetter period, the proportion of leaves is larger on clay, but more allocation is in the aboveground coarse wood and fine root on sandy loam (Figures 8b and 8d). In the drier period, there is a shift of allocation from leaves to aboveground coarse wood and reproductive materials on clay, while on the sandy loam site, a large proportion is allocated to leaves, reproductive materials, and aboveground coarse wood. Because spatial distributions of tree species in Lambir are edaphically biased [Davies *et al.*, 2005; Palmiotto, 1998; Potts *et al.*, 2002] and show contrasting growth and mortality rates on different soil types [Itoh *et al.*, 2012; Russo *et al.*,

2005], the seasonal allocation of NPP is likely affected by nutrient and water availability in the soil coupled with a different demographic trade-off.

[51] The allocation of  $NPP_{BG}$  to  $NPP_{fine\ roots}$  shows strong effects in the wetter period. On the less nutrient-poor clay soil, where soil retains high volumetric water content, the allocation to fine roots is significantly higher ( $t=31.7$ ,  $p < 0.0001$ ) (Figure 8b). Higher nutrient and water availability is often associated with greater fine root growth rates [Kochsiek *et al.*, 2013; Lima *et al.*, 2010; Metcalfe *et al.*, 2008]. Green *et al.* [2005] found that fine root biomass is positively correlated with precipitation, but they found no relationship with soil nutrients. While  $NPP_{AG}$  may be linked to soil fertility,  $NPP_{BG}$  is strongly explained by the availability of water [Cavelier *et al.*, 1999; Green *et al.*, 2005; Sánchez-Gallén and Alvarez-Sánchez, 1996]. In contrast, higher  $NPP_{fine\ roots}$  on sandy loam soil during the drier period may be explained by the lower water-holding capacity that may have increased

**Table 3.** The Mean ( $\pm$ Standard Error) Total NPP of Tropical Forests in Asia and the Amazon

Site	Forest Type	Total NPP (Mg C ha <sup>-1</sup> yr <sup>-1</sup> )	Reference
<i>Asia</i>			
Malaysia: Lambir	Lowland dipterocarp	15.9 $\pm$ 0.9 <sup>a</sup>	This study
Malaysia: Lambir	Lowland dipterocarp	13.0 $\pm$ 0.7 <sup>b</sup>	This study
Malaysia: Pasoh	Lowland dipterocarp	13.7 $\pm$ 1.4 <sup>c</sup>	Kira [1978]
Malaysia: Pasoh	Lowland dipterocarp	12.8 $\pm$ 1.3 <sup>c</sup>	Kira [1987]
Thailand: Khao Chong	Seasonal evergreen	14.3 $\pm$ 1.4 <sup>c</sup>	Kira et al. [1967]
Thailand: Central Thailand	Deciduous dipterocarp/dry evergreen	6.1 $\pm$ 0.6 <sup>c</sup>	Ogino et al. [1967]
Indonesia: Sulawesi	Premontane	6.7 $\pm$ 0.3	Hertel et al. [2009]
China	Tropical forest	7.2 $\pm$ 1.6	Ni et al. [2001]
China: Fujian	Subtropical forest	11.2 $\pm$ 0.6	Yang et al. [2003]
China: Xishuangbanna	Tropical seasonal	8.8 $\pm$ 0.9 <sup>c</sup>	Tan et al. [2010]
India: Western Ghats	Wet evergreen	11.9 $\pm$ 2.0	Swamy et al. [2010]
	Estimated mean	11.0 $\pm$ 0.3	
<i>Amazonia</i>			
Brazil: Caxiuana	Moist old growth	11.6 $\pm$ 0.7	Aragão et al. [2009]; Malhi et al. [2009]
Brazil: Tapajós	Moist old growth	14.4 $\pm$ 0.9	Aragão et al. [2009]; Malhi et al. [2009]
Brazil: Manaus	Moist old growth	10.8 $\pm$ 1.0	Aragão et al. [2009]; Malhi et al. [2009]
Colombia: Agua Pudre	Moist lowland	11.5 $\pm$ 0.5	Aragão et al. [2009]
Colombia: Zafire	Moist lowland	9.3 $\pm$ 1.3	Aragão et al. [2009]
	Estimated mean	11.5 $\pm$ 0.4	

<sup>a</sup>Clay soil site.<sup>b</sup>Sandy loam soil site.<sup>c</sup>Ten percent standard error assigned [Aragão et al., 2009; Malhi et al., 2009].

root productivity to maintain soil water access [Aragão et al., 2009] and reduced allocation to aboveground growth [Kochsiek et al., 2013]. The allocation to fine roots appears to be slightly higher on sandy loam than on clay (Figure 8), but the allocation is not significantly different between plots ( $t=0.37$ ,  $p>0.05$ ). However, any observed seasonal patterns should be interpreted with a high degree of caution as data were only collected over one annual cycle, and there is evidence of strong interannual variability. In addition, our measurements were conducted during one of the driest period between 2000 and 2010 and also incorporated a mass flowering event.

#### 4.2. Overall Allocation of NPP

[52] NPP<sub>Total</sub> is consistent with results from several sites in the Southeast Asian region (Table 3). Our estimation is, however, relatively higher than the average NPP<sub>Total</sub> across several Amazonian sites [Aragão et al., 2009; Malhi et al., 2009] and the montane forests [Girardin et al., 2010; Hertel et al., 2009; Kitayama and Aiba, 2002]. This higher estimation in our study is partly due to an extensive measurement of NPP components (e.g., coarse roots and lost to leaf herbivory), which have not been measured in previous studies. The average ratio of NPP<sub>AG</sub> and NPP<sub>BG</sub> was 0.81 and 0.17 on clay and sandy loam, respectively.

[53] The allocation of NPP<sub>AG</sub> between stem and canopy shows a substantial difference between clay and sandy loam. The allocation pattern on clay is similar to that reported in Kalimantan, suggesting a saturating function between NPP<sub>fine roots</sub> and NPP<sub>ACW</sub> at high NPP sites [Paoli and Curran, 2007], as observed in our study on the clay soil. The allocation pattern on sandy loam is quite similar to that in the Neotropics [Malhi et al., 2011]. Hence, there is substantial variation in the patterns of allocation in lowland dipterocarp forest, with no fixed ratio [Malhi et al., 2011].

Furthermore, the allocation between three major components of NPP is partitioned into (canopy:wood:fine root) 8:4:2 on clay and 6:3:2 on sandy loam. Overall, the highest fraction of NPP is allocated to woody material and the least to fine roots [Malhi et al., 2011].

[54] NPP<sub>herbivory</sub> loss is usually unaccounted for because it is often a small and negligible contribution [Clark et al., 2001b]. Kira [1978] showed that grazing by caterpillars may consume approximately 0.15 Mg C ha<sup>-1</sup> yr<sup>-1</sup>. The rate of consumption derived from the rate of fecal droppings by caterpillars was estimated based on the efficiency of assimilation given as 13%. However, we estimate higher rates using herbivory rates measured from the canopy in Lambir [Kurokawa and Nakashizuka, 2008]. In fact, herbivory damage in the canopy is generally lower [Coley and Barone, 1996; Kurokawa and Nakashizuka, 2008], suggesting a higher level of damage if measured in the understory. Our estimates are within the range between two mature tropical forest sites in Amazonia, namely, the Tambopata site on fertile soils in Peru (0.70–0.76 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) (Malhi et al., in press, 2014) and the Caxiuana site on infertile soils in Brazil (0.20 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) [Doughty et al., 2013]. The proportion of NPP<sub>herbivory</sub> to NPP<sub>Total</sub> is still small, at less than 2%.

#### 5. Conclusion

[55] Our study provides a detailed description of the NPP budget and its seasonal allocation in a lowland dipterocarp forest. We find that the NPP in a dipterocarp forest is large and that considerable production is allocated to aboveground NPP. Productivity and the seasonal allocation of NPP are relatively different on clay and sandy loam. There is evidence that the dry-wet seasonality may shift the allocation of NPP on clay and sandy loam, even though this forest does not experience a significant water stress season. It is important

to note, however, that these results are taken from two geographically close plots and that further similar studies are needed before we can generalize about the productivity and carbon cycle of the old world tropical forests.

## Notation

Abbreviation	Description
NPP <sub>AG</sub>	Aboveground net primary productivity.
NPP <sub>ACW</sub>	Aboveground coarse wood net primary productivity.
NPP <sub>branch</sub>	Branch turnover net primary productivity.
NPP <sub>litterfall</sub>	Litterfall net primary productivity.
NPP <sub>leaves</sub>	Leaf fall net primary productivity.
NPP <sub>twig</sub>	Branches, twigs, and woody tissues net primary productivity.
NPP <sub>reprod</sub>	Reproductive organs (fruits, flowers, and seeds) net primary productivity.
NPP <sub>debris</sub>	Undefined fine debris net primary productivity.
NPP <sub>herbivory</sub>	Net primary productivity loss to leaf herbivory.
NPP <sub>BG</sub>	Belowground net primary productivity.
NPP <sub>coarse root</sub>	Coarse root net primary productivity.
NPP <sub>fineroots</sub>	Fine root net primary productivity.

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