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Ecosystem carbon storage and partitioning in a tropical seasonal forest in Southwestern China

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ABSTRACT

Tropical forests play an important role in the global carbon cycle. Despite an increasing number of studies have addressed carbon storage in tropical forests, the regional variation in such storage remains poorly understood. Uncertainty about how much carbon is stored in tropical forests is an important limitation for regional-scale estimates of carbon fluxes and improving these estimates requires extensive field studies of both above- and belowground stocks. In order to assess the carbon pools of a tropical seasonal forest in Asia, total ecosystem carbon storage was investigated in Xishuangbanna, SW China. Averaged across three 1 ha plots, the total carbon stock of the forest ecosystem was 303 t C ha^{-1}. Living tree carbon stocks (both above- and belowground) ranged from 163 to 258 t C ha^{-1}. The aboveground biomass C pool is comparable to the Dipterocarp forests in Sumatra but lower than those in Malaysia. The variation of C storage in the tree layer among different plots was mainly due to different densities of large trees (DBH > 70 cm). The contributions of the shrub layer, herb layer, woody lianas, and fine litter each accounted for 1–2 t C ha^{-1} to the total carbon stock. The mineral soil C pools (top 100 cm) ranged from 84 to 102 t C ha^{-1} and the C in woody debris from 5.6 to 12.5 t C ha^{-1}, representing the second and third largest C component in this ecosystem. Our results reveal that a high percentage (70%) of C is stored in biomass and less in soil in this tropical seasonal forest. This study provides an accurate estimate of the carbon pool and the partitioning of C among major components in tropical seasonal rain forest of northern tropical Asia. Results from this study will enhance our ability to evaluate the role of these forests in regional C cycles and have great implications for conservation planning.

1. Introduction

Carbon storage and fluxes in forests have been the focus of research in recent years because of the role of CO_2 in global climate change (Dixon et al., 1994; Houghton et al., 2009). Tropical forests have a large potential to sequester carbon primarily through reforestation, agroforestry and conservation of existing forests (Brown, 1996) and the high productivity of tropical forests may make them particularly responsive to growth enhancement from increasing atmospheric CO_2 concentrations (Prentice and Lloyd, 1998). Furthermore, old-growth tropical forests can continue to serve as carbon sinks rather than reaching a steady state C equilibrium (Luyssaert et al., 2008; Lewis et al., 2009). Thus, accurately characterizing the stocks and fluxes of carbon in tropical forests will have great implications for understanding the global carbon cycle.

While carbon storage in aboveground biomass of tropical forests is commonly measured (Jepsen, 2006), this is not the case for other components, such as roots, understory vegetation, coarse woody debris, fine litter and soil. All these components may play an important role in the carbon storage and cycling of tropical forest ecosystems. For example, soil carbon accounts for more than 60% of the total ecosystem carbon storage in tropical montane wet forest (Delaney et al., 1997). Moreover, the role of coarse woody debris (CWD) as a carbon pool is generally neglected although stocks of CWD can be huge, up to 107.8 t ha^{-1} in an eastern Brazilian Amazonian forest (Keller et al., 2004), and accounting for 42% of aboveground live woody biomass in a Costa Rican forest (Clark et al., 2002). Given the importance of these components, more knowledge from extensive field measurements is needed to give a more accurate picture of total carbon storage in tropical forests.

Our knowledge of biomass carbon pools and carbon sequestration with net primary production of tropical forests is increasing. However, most of the studies are from South and Central America

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(Delaney et al., 1997; Johnson et al., 2001; Rice et al., 2004; Malhi et al., 2009) and recently from Africa (Lewis et al., 2009), whereas precise data from Southeast Asia are rare (Houghton, 2002; Lasco et al., 2004). Furthermore, our knowledge about the tropical forests in Asia is generally restricted to the Dipterocarp forests (Laumonier et al., 2010) and we still know little about the non-Dipterocarp forests in this region. Sparse data on the biomass and carbon storage of Southeast Asian tropical forests makes it difficult to evaluate the role of these forest ecosystems in the global carbon cycle. Moreover, Southeast Asia is the region where forests are under the highest pressure and consequently the highest rate of deforestation (Mayaux et al., 2005) and there is a urgent need to characterize the total ecosystem carbon storage of different tropical forests in this region.

The primary objective of this study was to quantify the amount of carbon in major components of a tropical seasonal rain forest in Xishuangbanna, SW China. Another emphasis was on how the total C in this forest is distributed among the different components. Specifically, this study assessed carbon stocks in trees (leaves, branches, stems, and roots), lianas, understory (shrub and herb layer), woody debris, fine litter, and soil, using standard field techniques in three 1 ha permanent forest plots. We compared our results to data from other studies of tropical seasonal forests as well as to data from contrasting tropical biomes. The results of this study will increase our understanding of tropical forests in the northern edge of tropical Asia and are expected to provide valuable inputs in estimating the potential of tropical forests in China to mitigate climate change.

2. Materials and methods

2.1. Study area

The study was carried out in Xishuangbanna (21°09′–22°36′ N and 99°58′–101°50′ E), which borders Laos and Myanmar on the upper course of the Mekong River. Three plots of 1 ha size (100 m × 100 m) were established in tropical seasonal rain forest located in wet valleys. The region experiences a typical tropical monsoon climate with a rainy season between May and October and a dry season between November and April. Long-term climate data (1959–2002) were collected at the weather station (21°55′ N, 101°15′ E, 600 m a.s.l.; Xishuangbanna Tropical Rainforest Ecosystem Station). The climate of the region has the following characteristics: annual mean air temperature, 21.7 °C; mean temperature for the warmest month (June), 25.7 °C; mean temperature for the coldest month (January), 15.9 °C, and mean annual precipitation, 1539 mm (of which 87% occurs in the rainy season and 13% in the dry season). The mean relative humidity is 87%. The soil, developed from purple sandstone, belongs to Haplic Acrisol (pH(H_2O) 4.5–5.5) according to the FAO soil classification. The dominant tree species in this forest include *Pometia tomentosa* (Bl.) Tewsm. et Binn., *Terminalia myriocarpa* Van Heurck & Mull.-Arg., *Garuga floribunda* Decne. var. gamblai (King et Smith) Kalkm., and *Barringtonia macrostachya* (Jack) Kurz. The three plots are referred to as Menglun, Mengla, and Manyang. See Lü et al. (2009) and Lü and Tang (2010) for detailed background information of the three plots.

2.2. Overstory and understory sampling

All trees and lianas with a diameter at breast height (DBH) ≥2 cm were measured inside each plot from December 2004 to March 2005. Aboveground and belowground biomass of trees and woody lianas were then estimated using specific biomass regression equations (Appendix A) developed for the tropical seasonal rain forest in this region, with diameter as the independent variable (Lü et al., 2007, 2009).

For shrub layer measurements (individuals with DBH < 2 cm and height ≥1 m), ten 5 m × 5 m subplots were systematically laid out in both the left and the right side of each 1 ha plot (outside but directly adjacent the 1 ha plots) to avoid any disturbance of each permanent plot. All individuals of seedlings, saplings and woody species were destructively harvested. Fresh weight of leaves, branches, stems and roots were determined in the field. Oven-dried weights of the different plant organs were determined in the laboratory of Xishuangbanna Tropical Rainforest Research Station.

All plants with the height < 1 m were harvested in 1 m × 1 m subplots systematically located in each of the 5 m × 5 m plots within which the shrub layer was harvested. Their fresh and oven-dried weights were determined following the same methods applied to the shrub layer.

2.3. Woody debris (WD) sampling

Both the fine (2–10 cm) and coarse (≥10 cm) fractions of downed wood on the forest floor and standing dead trees with DBH ≥ 2 cm were included in this study. The fine fraction of dead wood was sampled in 25 subplots (5 m × 5 m each) systematically and evenly located in each 1 ha plot. The coarse fraction of the dead wood was surveyed in the whole 1 ha plot. For all pieces of fallen WD, the length and diameters at both ends were measured. The state of decomposition was classified in the field into three classes: sound, intermediate and rotten (Delaney et al., 1997). Unless the shape of the log was distinguishable, rotten wood that was fully incorporated into the forest floor or buried was not included in the inventory. Subsamples from each piece of coarse dead wood were collected with a saw or a machete to measure their wood density and conserved for further analysis. Volume of all CWD was calculated using the Smalian's formula (Baker et al., 2007). Mass was estimated as the product of volume and corresponding wood density.

DBH of all standing dead trees were measured in each 1 ha plot. Biomass of standing dead trees was estimated following the regression equations applied to the living trees (Delaney et al., 1997; Lü et al., 2007).

2.4. Fine litter and soil sampling

In each plot, 25 samples of fine litter, consisting of leaves, twigs (diameter < 2 cm), fruits/flowers, and barks, were collected using 1 m × 1 m quadrats. All the 25 quadrats were systematically distributed in each 1 ha plot. Samples were oven-dried at 70 °C and weighed to determine the standing crop of fine litter. Subsamples of fine litter were ground and used for analyses of total C concentrations. As the fine litter was sampled in December 2004 and January 2005, and since the litter layer generally changes throughout the year due to oscillations in litterfall and decomposition rates in response to seasonal variation of both temperature and precipitation, it is must be noted that the data collected here may not effectively represent the annual average standing crop of litterfall in the tropical seasonal forest.

Mineral soil samples were taken with a cylindrical soil sampler at eight random points within each plot. There was no organic layer present atop the mineral soil. Soil samples were taken at each 10 cm of depth to a 1 m depth in each point. Bulk density for each soil depth was determined by weighing the whole sample and drying subsamples at 70 °C. After determination of bulk density, soils were sieved with a 2 mm sieve, and homogenized for further chemical analysis.

2.5. Laboratory analysis

Fine litter and soil samples were both analyzed for total organic C concentration using the induction furnace method with a Perkin-Elmer 2400 Series II CHN/O Analyzer.

All organic matter of living plants and woody debris was converted to C equivalents by multiplying dry weight by 0.5 (Brown and Lugo, 1982).

2.6. Statistical analysis

Paired *t*-tests were used to compare the differences in carbon storage among woody lianas, the shrub layer, and the herb layer. Two-way ANOVAs were used to test the effects of plot and depth on soil carbon concentration, bulk density and soil carbon storage. Statistical significance was defined as $P < 0.05$. Statistical analysis was performed using SPSS (Version 13.0, SPSS Inc. Chicago, IL, USA).

3. Results

The ecosystem total carbon storage varied greatly among the three plots, ranging from 260 to 377 t ha^{-1}, with a mean of 303 t ha^{-1} (Table 1). The tree layer contributed more than 60% to the total ecosystem carbon storage. The mean carbon storage in tree roots was 38.6 t ha^{-1}, while the mean aboveground biomass carbon storage was 159.7 t ha^{-1}. Intermediate DBH classes (20–80 cm) contributed the most to the carbon storage in Menglun and Manyang (Fig. 1). In contrast, the larger DBH classes made the most important contribution in Mengla (Fig. 1). The contribution of understory vegetation (0.9 t ha^{-1} for shrub layer and 1.0 t ha^{-1} herb layer) to carbon storage was minor in this ecosystem (Table 1). Carbon storage in the woody lianas (1.6 t ha^{-1}) was higher than that of the shrub layer (paired *t*-test, $P = 0.044$).

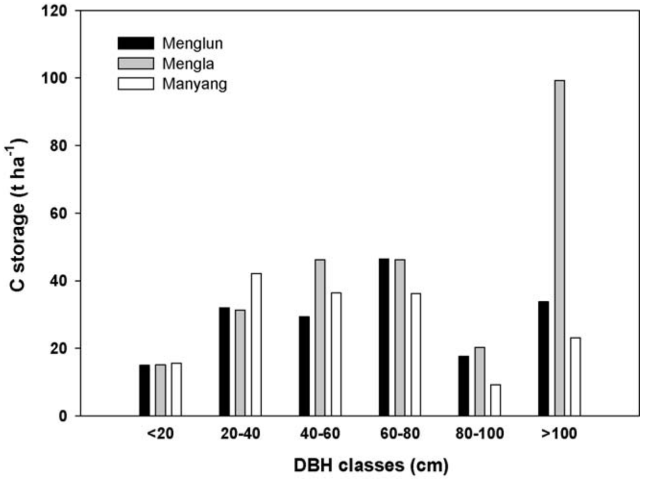

Fig. 1. Carbon storage in different DBH classes of trees in tropical seasonal rain forest of Xishuangbanna, SW China.

Table 1
Carbon distribution (t C ha^{-1}) in different components of tropical seasonal rain forest in Xishuangbanna, SW China.

Components	Menglun	Mengla	Manyang	Mean ± SE
Tree layer				
Stem	119.2	180.0	110.0	136.3 ± 22.0
Branch	18.9	24.9	19.2	20.9 ± 1.9
Leaves	2.2	2.5	2.3	2.3 ± 0.1
Roots	33.8	50.9	31.1	38.6 ± 6.2
Subtotal	174.0	258.4	162.5	198.3 ± 30.2
Shrub layer				
Stem	0.6	0.3	0.5	0.5 ± 0.1
Branch	0.1	0.1	0.1	0.1 ± 0.0
Leaves	0.2	0.1	0.1	0.1 ± 0.0
Roots	0.3	0.1	0.2	0.2 ± 0.1
Subtotal	1.1	0.6	0.9	0.9 ± 0.1
Herb layer				
Aboveground	0.4	0.8	0.5	0.6 ± 0.1
Belowground	0.3	0.4	0.7	0.5 ± 0.1
Subtotal	0.7	1.2	1.2	1.0 ± 0.2
Woody lianas				
Aboveground	1.7	1.3	1.2	1.4 ± 0.2
Belowground	0.3	0.1	0.1	0.2 ± 0.1
Subtotal	2.0	1.4	1.3	1.6 ± 0.2
Woody debris				
Standing dead tree	2.7	2.7	4.2	3.2 ± 0.5
Dead branch	1.7	2.3	1.3	1.8 ± 0.3
Fallen dead trees	1.1	7.5	3.2	3.9 ± 1.9
Subtotal	5.6	12.5	8.8	9.0 ± 2.0
Fine litter				
Leaves	0.9	0.5	0.7	0.7 ± 0.1
Twigs	0.4	0.9	0.6	0.6 ± 0.1
Flowers and fruits	0.1	0.0	0.1	0.1 ± 0.0
Subtotal	1.4	1.4	1.4	1.4 ± 0.0
Soil	87.0	101.9	84.4	91.1 ± 5.5
Total	271.8	377.4	260.5	303.3 ± 37.2

The quantity of carbon in dead wood ranged from 5.6 to 12.5 t ha^{-1}, with a mean of 9 t ha^{-1}. Across the three plots, standing and fallen dead trees contributed with 80% of the total carbon stocks of dead wood (Table 1). There were equal amounts of carbon in the fine litter across the three plots (1.4 t ha^{-1} for each) with the majority of fine litter being composed of dead leaves and twigs with little flower and fruits (Table 1).

Soil was the second largest C pool in each plot, ranging from 84.4 to 101.1 t ha^{-1}. Carbon concentration, bulk density and C storage changed significantly with depth. Both carbon concentration and carbon storage decreased with depth in a general pattern of exponential decay, whereas bulk density increased with soil depth (Fig. 2). Soil bulk density differed among the three plots (Two-way ANOVA, $F = 83.4$, $P < 0.001$), the highest recorded in Mengla and the lowest in Menglun (Fig. 2). Results from the two-way ANOVA showed that both plot ($F = 3.9$, $P = 0.021$) and depth ($F = 69.3$, $P < 0.001$) had significant effects of soil carbon concentration. Across the entire depth profile, the soil carbon concentration in Manyang was significantly lower than in the other two plots. Higher carbon concentration and bulk density resulted in higher soil carbon storage in Mengla (Fig. 2; Table 1).

4. Discussion

The total biomass C of the tree layer in this forest ranged from 163 to 258 t C ha^{-1}, of which the aboveground biomass C ranged from 132 to 207 t C ha^{-1}. These values were well within the ranges of aboveground biomass carbon stocks (25–300 t C ha^{-1}) reported for tropical forests in Asia (Brown et al., 1993; Iverson et al., 1993; Lasco, 2002). The aboveground biomass carbon storage in this forest is higher than that of non-Dipterocarp forests (120 t C ha^{-1}) in Indonesia (Hertel et al., 2009), comparable to that of lowland and hill Dipterocarp forests (135–240 t C ha^{-1}) in Sumatra (Laumonier et al., 2010), but lower than the Dipterocarp forests (230–250 t C ha^{-1}) in Malaysia (Hertel et al., 2009) and Borneo (Slik et al., 2010). Tropical seasonal rain forests in the studied sites had larger aboveground C stocks than seasonal forests in Amazon (122–141 t C ha^{-1}) (Vieira et al., 2004). The vari-

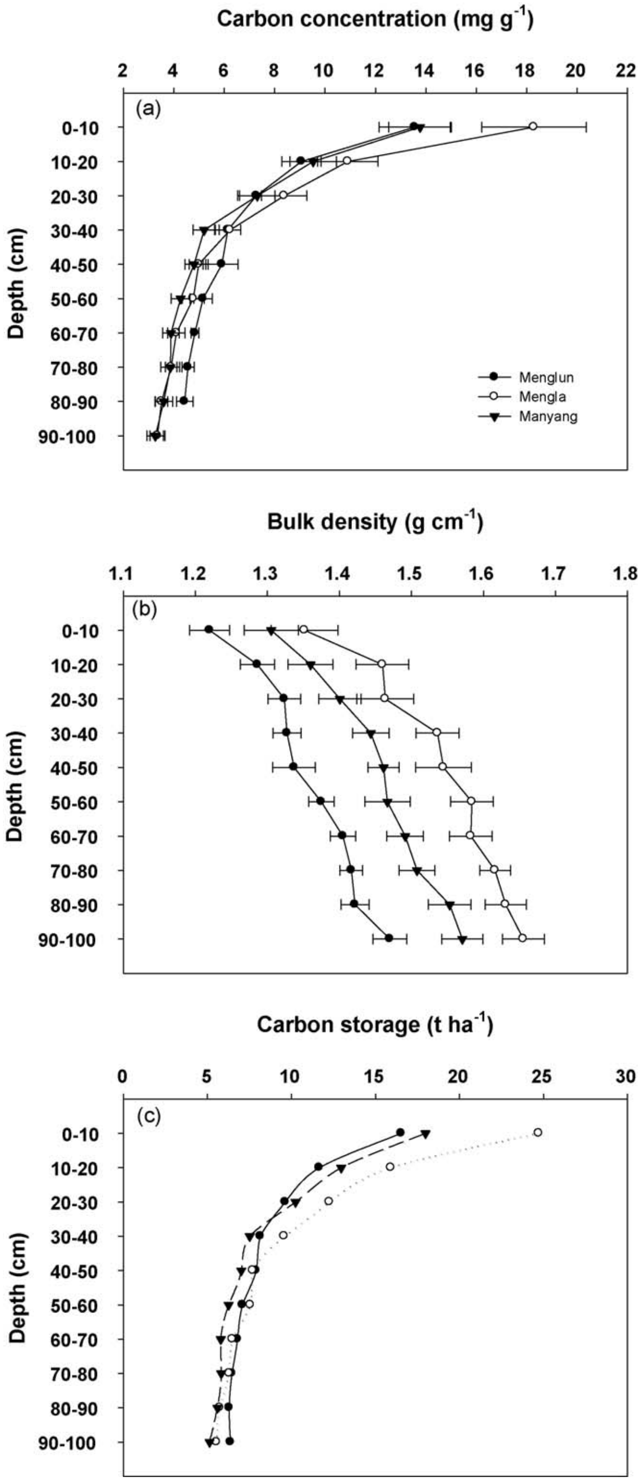

Fig. 2. General patterns of carbon concentration (a), bulk density (b) and carbon storage (c) in soil of the three plots of tropical seasonal rain forest in Xishuangbanna, SW China.

ation in aboveground biomass C stocks depends on a number of factors, such as species composition, climate, nutrient conditions, topography, forest age, disturbance, and land management history (Vieira et al., 2004; de Castilho et al., 2006; Hertel et al., 2009).

C stored in roots of the tree layer accounted for 19% of the total biomass C pools (31–51 t C ha^{-1}), which contrasts with the results from a humid tropical secondary forest in Mexico, where the belowground biomass constituted only 6–8% of the total biomass (Hughes et al., 1999). The mean value of root dry mass reported in a literature review of tropical rain forest is 49 t ha^{-1} (Jackson et al., 1996). The difference may result from specific conditions (such as water availability and soil fertility) and different species characteristics of tropical forests. The root/shoot ratios calculated in this study ranged from 0.237 to 0.245, with an average of 0.241, which was similar to the average global value (0.24) for tropical forests estimated in a meta-analysis (Cairns et al., 1997).

The contribution of large trees (DBH ≥ 70 cm) to aboveground biomass C in this forest (46 ± 13%) is higher than that of tropical forests in South America (Clark and Clark, 1996; Delaney et al., 1997; Chave et al., 2003). This result indicates that large trees play a more important role in the carbon storage of tropical forest in this area. It is notable that the contribution of large trees to biomass carbon accumulation varied greatly among plots in this area. The Mengla plot held the highest C storage in the tree layer due to the highest contribution of large trees (Fig. 2). Given the heterogeneous distribution of large trees and their importance for the estimation of biomass and carbon storage in tropical forests reported in this study and previous studies (Delaney et al., 1997), we suggest that both the size and the number of plots should be fully considered in order to give a full understanding of the biomass C storage in a particular type of tropical forests.

Compared with the tree layer, the contribution of woody lianas, the shrub layer, and the herb layer to carbon sequestration was minimal. Combined, the carbon stock of those three pools was 3.5 t C ha^{-1}, representing 1.8% of the tree layer in this study. The observed carbon stock of understory and herbaceous plants was 3.6 t ha^{-1} in a secondary tropical forest in the Philippines (Lasco et al., 2004) and it has been estimated that the biomass C of stems with DBH < 10 cm represented 1–1.5% of that in trees with DBH > 10 cm in the tropical forests of Venezuela (Delaney et al., 1997). Although the contribution of woody lianas was low in this study, they may comprise as much as 14% of the aboveground biomass in some tropical forests of Brazil (Gerwing and Farias, 2000). Our results suggest that the shrub layer, herb layer and woody lianas can be neglected during initial estimates of carbon stock in the tropical seasonal rain forest.

Fine litter (1.4 t C ha^{-1}) comprised a relatively small part of the total carbon pool in the study area (Table 1), falling outside the range (2.6–3.8 t C ha^{-1}) estimated by previous studies in the tropical areas (Brown and Lugo, 1982), but comparable to the value recorded in the secondary tropical forest in Philippines (Lasco et al., 2004). Zheng et al. (2006) reported litterfall and forest floor mass values of 10 and 5 t ha^{-1} for the tropical seasonal rain forest in Xishuangbanna. We hypothesize that the sampling time may partly explain the lower fine litter mass recorded in this study. Fine litter mass was sampled in December 2004 and January 2005 and it was a one-time measurement. In contrast, in the study of Zheng et al. (2006), forest floor mass was determined at a 3-month interval during the 2-year study period. Moreover, most of the litterfall occurs in March and April (Zheng et al., 2005), and the mean residence time for fine litter was estimated as 0.51 year in tropical forests in this area (Zheng et al., 2006). However, our result compares well with those from a long-term study conducted in this area, in which Tang et al. (in press) reported a mean value of 3.25 t ha^{-1} for the standing crop of litterfall in the tropical seasonal rain forest.

In many forests, large quantities of biomass C accumulate in the form of CWD. However, information on the quantity and dynamics of carbon stored in the woody debris in tropical forests is scarce. Our results from Xishuangbanna are in broad agreement with those from similar studies in other tropical rain forests, showing that CWD comprises a significant fraction of total carbon storage (Clark et al., 2002; Rice et al., 2004). Woody debris represented the third largest carbon pool in this tropical forest, holding less carbon than the biomass of the tree layer and the soil but more than other components. The quantities of carbon in woody debris (9 t C ha^{-1}) recorded in our study sites are in the lower end of the range reported for other tropical forests (<1 to >30 t C ha^{-1}) (Delaney et al., 1997; Clark et al., 2002; Rice et al., 2004; Baker et al., 2007; Yang et al., 2010). Low CWD storage in tropical seasonal forests in Xishuangbanna may be the result of low rates of input or high rates of decomposition. Several factors have been suggested to account for the variation in inputs and outputs of woody debris and consequently the woody debris carbon stocks in different tropical forests, including: climate, substrate quality, forest fragmentation, and fire frequency (Harmon et al., 1986; Clark et al., 2002; Yang et al., 2010). Lower stocks of CWD reflect the fact that the three plots have not been exposed to any large disturbances recently. Given the important means of CWD for carbon cycling, more research into CWD dynamics across this region is critically required.

Soils in equilibrium with a natural forest ecosystem may have high carbon stock (Lal, 2005). It has been suggested that the soil C stock may comprise as much as 50% of the terrestrial C stock in the tropical rainforest (Dixon et al., 1994). The carbon stored in the first meter of the soil in the study area (84–102 t C ha^{-1}, corresponding to 27–32% of the total ecosystem carbon storage) is within the range estimated for tropical moist and seasonal forests in Asia (Houghton, 2002) but is lower than the expected amount of carbon in the first meter of tropical soils (130–160 t C ha^{-1}) (Jobbagy and Jackson, 2000). In this study, soil organic C pools comprised 30% of the total ecosystem C pool, indicating that much more C was stored in the living and dead biomass. Consequently, total ecosystem carbon storage of tropical seasonal rain forests may be more vulnerable to deforestation and forest fragmentation caused by rubber plantations which are expanding rapidly in this area (Li et al., 2008; Ziegler et al., 2009). From a carbon storage perspective, this study gives further evidence of the important role of primary tropical seasonal rain forest in the local area. Since the results from the present study indicate tropical seasonal rain forests contain much more carbon than rubber plantations (Tang et al., 2009), the conversion of tropical forest areas to rubber plantations may not only threaten biodiversity but also certainly reduce the carbon stocks in this region.

In conclusion, the present study revealed that the tropical seasonal rain forest in Xishuangbanna can store 303 t C ha^{-1}, with 70% storing in the biomass and 30% in the mineral soil (1 m depth). Large trees contributed greatly to carbon storage in living biomass and may be the main reason accounting for the variations in the carbon stock between different locations in this area. Due to the rapid expansion of rubber plantations in the region (Li et al., 2008) the tropical forest area is shrinking, and since the carbon storage of rubber plantations is much lower (Tang et al., 2009) than the carbon stocks presented in this study, proper conservation policies are critically needed.

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Appendix A. Allometric regression equations for tree biomass in tropical seasonal rain forest in Xishuangbanna, SW China

DBH classes and sample no.	Organ	Allometric equation	Adjusted r^2
2 cm ≤ DBH ≤ 5 cm (n = 46)	Stem	$W_S = 0.0733(\text{DBH})^{2.5884}$	0.803***
	Branch	$W_B = 0.0135(\text{DBH})^{2.5158}$	0.536***
	Leaf	$W_L = 0.0394(\text{DBH})^{1.456}$	0.456***
	Root	$W_R = 0.028(\text{DBH})^{2.399}$	0.683***
5 cm ≤ DBH ≤ 20 cm (n = 55)	Stem	$W_S = 0.1086(\text{DBH})^{2.3169}$	0.894***
	Branch	$W_B = 0.0186(\text{DBH})^{2.4685}$	0.743***
	Leaf	$W_L = 0.0455(\text{DBH})^{1.6636}$	0.589***
	Root	$W_R = 0.0242(\text{DBH})^{2.4205}$	0.876***
DBH > 20 cm (n = 22)	Stem	$W_S = 0.0401(\text{DBH})^{2.6752}$	0.934***
	Branch	$W_B = 0.0829(\text{DBH})^{2.0395}$	0.835***
	Leaf	$W_L = 0.0979(\text{DBH})^{1.3584}$	0.636***
	Root	$W_R = 0.0111(\text{DBH})^{2.6801}$	0.938***

*** $P < 0.001$.

References

Baker, T.R., Coronado, E.N.H., Phillips, O.L., Martin, J., van der Heijden, G.M.F., Garcia, M., Espejo, J.S., 2007. Low stocks of coarse woody debris in a southwest Amazonian forest. Oecologia 152, 495–504.

Brown, S., 1996. Mitigation potential of carbon dioxide emissions by management of forests in Asia. AMBIO 25, 273–278.

Brown, S., Hall, C.A.S., Knabe, W., Raich, J., Trexler, M.C., Woomer, P., 1993. Tropical forests – their past, present, and potential future-role in the terrestrial carbon budget. Water Air Soil Pollut. 70, 71–94.

Brown, S., Lugo, A.E., 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14, 161–187.

Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. Oecologia 111, 1–11.

Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B., Hubbell, S.P., 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. J. Ecol. 91, 240–252.

Clark, D.B., Clark, D.A., 1996. Abundance, growth and mortality of very large trees in neotropical lowland rain forest. Forest Ecol. Manage. 80, 235–244.

Clark, D.B., Clark, D.A., Brown, S., Oberbauer, S.F., Veldkamp, E., 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. Forest Ecol. Manage. 164, 237–248.

de Castilho, C.V., Magnusson, W.E., de Araujo, R.N.O., Luizao, R.C.C., Lima, A.P., Higuchi, N., 2006. Variation in aboveground tree live biomass in a central Amazonian forest: effects of soil and topography. Forest Ecol. Manage. 234, 85–96.

Delaney, M., Brown, S., Lugo, A.E., TorresLezama, A., Quintero, N.B., 1997. The distribution of organic carbon in major components of forests located in five life zones of Venezuela. J. Trop. Ecol. 13, 697–708.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.

Gerwing, J.J., Farias, D.L., 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. J. Trop. Ecol. 16, 327–335.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., Leuschner, C., 2009. Below- and above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi, Indonesia) as compared to neotropical forests. Forest Ecol. Manage. 258, 1904–1912.

Houghton, R.A., 2002. Temporal patterns of land-use change and carbon storage in China and tropical Asia. Sci. China Ser. C 45, 10–17.

Houghton, R.A., Hall, F., Goetz, S.J., 2009. Importance of biomass in the global carbon cycle. J. Geophys. Res. Biogeol. 114, doi:10.1029/2009JG000935.

Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. Ecology 80, 1892–1907.

Iverson, L.R., Brown, S., Grainger, A., Prasad, A., Liu, D., 1993. Carbon sequestration in South/Southeast Asia: an assessment of technically suitable forest lands using geographic information systems analysis. Climate Res. 3, 23–38.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389–411.

Jepsen, M.R., 2006. Above-ground carbon stocks in tropical fallows, Sarawak, Malaysia. Forest Ecol. Manage. 225, 287–295.

Jobbagy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol. Appl. 10, 423–436.

Johnson, C.M., Vieira, I.C.G., Zarin, D.J., Frizano, J., Johnson, A.H., 2001. Carbon and nutrient storage in primary and secondary forests in eastern Amazonia. Forest Ecol. Manage. 147, 245–252.

Keller, M., Palace, M., Asner, G.P., Pereira, R., Silva, J.N.M., 2004. Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. Glob. Change Biol. 10, 784–795.

Lü, X.T., Tang, J.W., 2010. Structure and composition of the understory treelets in a non-dipterocarp forest of tropical Asia. Forest Ecol. Manage. 260, 565–572.

Lü, X.T., Tang, J.W., Feng, Z.L., Li, M.H., 2009. Diversity and aboveground biomass of lianas in the tropical seasonal rain forests of Xishuangbanna, SW China. Rev. Biol. Trop. 57, 211–222.

Lü, X.T., Tang, J.W., He, Y.C., Duan, W.G., Song, J.P., Xu, H.L., Zhu, S.Z., 2007. Biomass and its allocation in tropical seasonal rain forest in Xishuangbanna, Southwest China. J. Plant Ecol. 31, 11–22.

Lal, R., 2005. Forest soils and carbon sequestration. Forest Ecol. Manage. 220, 242–258.

Lasco, R.D., 2002. Forest carbon budgets in Southeast Asia following harvesting and land cover change. Sci. China Ser. C 45, 55–64.

Lasco, R.D., Guillermo, I.Q., Cruz, R.V.O., Bantayan, N.C., Pulhin, F.B., 2004. Carbon stocks assessment of a secondary forest in Mount Makiling Forest Reserve, Philippines. J. Trop. For. Sci. 16, 35–45.

Laumonier, Y., Edin, A., Kanninen, M., Munandar, A.W., 2010. Landscape-scale variation in the structure and biomass of the hill dipterocarp forest of Sumatra: implications for carbon stock assessment. Forest Ecol. Manage. 259, 505–513.

Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo, M.N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., Woll, H., 2009. Increasing carbon storage in intact African tropical forests. Nature 457, 1003–1006.

Li, H.M., Ma, Y.X., Aide, T.M., Liu, W.J., 2008. Past, present and future land-use in Xishuangbanna, China and the implications for carbon dynamics. Forest Ecol. Manage. 255, 16–24.

Luyssaert, S., Schulze, E.D., Borner, A., Knohl, A., Hessenmoller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. Nature 455, 213–215.

Malhi, Y., Aragao, L.E.O.C., Metcalfe, D.B., Paiva, R., Quesada, C.A., Almeida, S., Anderson, L., Brando, P., Chambers, J.Q., da Costa, A.C.L., Hutyra, L.R., Oliveira, P., Patino, S., Pyle, E.H., Robertson, A.L., Teixeira, L.M., 2009. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. Glob. Change Biol. 15, 1255–1274.

Mayaux, P., Holmgren, P., Achard, F., Eva, H., Stibig, H., Branthomme, A., 2005. Tropical forest cover change in the 1990s and options for future monitoring. Philos. Trans. Roy. Soc. B 360, 373–384.

Prentice, I.C., Lloyd, J., 1998. C-quest in the Amazon Basin. Nature 396, 619–620.

Rice, A.H., Pyle, E.H., Saleska, S.R., Hutyra, L., Palace, M., Keller, M., de Camargo, P.B., Portilho, K., Marques, D.F., Wofsy, S.C., 2004. Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecol. Appl. 14, S55–S71.

Slik, J.W.F., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E., van Valkenburg, J.L.C.H., 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. Glob. Ecol. Biogeogr. 19, 50–60.

Tang, J.W., Cao, M., Zhang, J.H., Li, M.H., in press. Litterfall production, decomposition and nutrient use efficiency varies with tropical forest types in Xishuangbanna, SW China: a 10-year study. Plant Soil, doi:10.1007/s11104-010-0414-2.

Tang, J.W., Pang, J.P., Chen, M.Y., Guo, X.M., Zeng, R., 2009. Biomass and its estimation model of rubber plantations in Xishuangbanna, Southwest China. Chin. J. Ecol. 28, 1942–1948.

Vieira, S., de Camargo, P.B., Selhorst, D., da Silva, R., Hutyra, L., Chambers, J.Q., Brown, I.F., Higuchi, N., dos Santos, J., Wofsy, S.C., Trumbore, S.E., Martinelli, L.A., 2004. Forest structure and carbon dynamics in Amazonian tropical rain forests. Oecologia 140, 468–479.

Yang, F.F., Li, Y.L., Zhou, G.Y., Wenigmann, K.O., Zhang, D.Q., Wenigmann, M., Liu, S.Z., Zhang, Q.M., 2010. Dynamics of coarse woody debris and decomposition rates in an old-growth forest in lower tropical China. Forest Ecol. Manage. 259, 1666–1672.

Zheng, Z., Li, Y.R., Liu, H.M., Feng, Z.L., Gan, J.M., Kong, W.J., 2005. Litterfall of tropical rain forests at different altitudes, Xishuangbanna, Southwest China. Acta Phytoecol. Sin. 29, 884–893.

Zheng, Z., Shanmughavel, P., Sha, L.Q., Cao, M., Warren, M., 2006. Litter decomposition and nutrient release in a tropical seasonal rain forest of Xishuangbanna, Southwest China. Biotropica 38, 342–347.

Ziegler, A.D., Fox, J.M., Xu, J.C., 2009. The rubber juggernaut. Science 324, 1024–1025.