ECOSYSTEM CARBON STORAGE OF TROPICAL FORESTS OVER LIMESTONE IN XISHUANGBANNA, SW CHINA

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Received August 2011

TANG JW, YIN JX, QI JF, JEPSEN MR & LÜ XT. 2012. Ecosystem carbon storage of tropical forests over limestone in Xishuangbanna, SW China. Tropical forests are recognised for their high biodiversity and the roles they play in carbon (C) storage and their influence on climate. Tropical forests over limestone take up 40% of the total area of tropical Asia. Nevertheless, C cycling in tropical forests over limestone is poorly quantified. There is a need for robust measurement of ecosystem carbon storage in tropical forests over limestone. We assessed the ecosystem C stocks, not only aboveground biomass but also belowground biomass, forest floor and mineral soil (to 1 m depth) in a tropical forest over limestone on the northern edge of tropical Asia. Mean total ecosystem C stock was estimated as 214 ± 28 t C ha^{-1} (± SE). The contribution of plant biomass in storing C was substantial, accounting for 80% of the total ecosystem C storage. The mean C stock of tree layer was 155 ± 24 t C ha^{-1}. Soil C stocks in tropical forests over limestone in this area (50 ± 10 t C ha^{-1}) were much lower than those in tropical forests from South-East Asia. Higher percentage of C stock in plant biomass while lower percentage in mineral soil indicated that C stocks of the tropical forests over limestone would be more vulnerable to vegetation destruction than other tropical forests on non-limestone substrate. This study gave an accurate estimation of C stocks of different components in tropical forests over limestone in Xishuangbanna and highlighted the important role they play in C sequestration.

Keywords: Aboveground C storage, belowground C storage, carbon stocks, C cycling

TANG JW, YIN JX, QI JF, JEPSEN MR & LÜ XT. 2012. Simpanan karbon ekosistem hutan tropika yang tumbuh di kawasan batu kapur di Xishuangbanna, barat daya China. Hutan tropika terkenal dengan kepelbagaian yang tinggi dan juga peranannya dalam menyimpan karbon (C) serta pengaruhnya terhadap iklim. Hutan tropika yang tumbuh di atas batu kapur meliputi 40% keluasan Asia tropika. Bagaimanapun, kitaran C di hutan tropika yang tumbuh di kawasan batu kapur tidak ditaksirkan dengan menyeluruh. Oleh itu adalah perlu untuk mengira simpanan C ekosistem hutan tropika di kawasan batu kapur. Kami menilai stok C ekosistem bukan setakat dalam biojisim atas tanah tetapi juga biojisim bawah tanah, lantai hutan dan tanah mineral (sehingga kedalaman 1 m) di kawasan batu kapur di pinggir utara Asia tropika. Jumlah stok C ekosistem dianggarkan 214 ± 28 t C ha^{-1} (± SE). Sumbangan biojisim pokok dalam menyimpan C adalah penting dan mencapai 80% daripada jumlah simpanan C ekosistem. Min stok C lapisan pokok ialah 155 ± 24 t C ha^{-1}. Stok C tanah di hutan tropika batu kapur di kawasan ini (50 ± 10 t C ha^{-1}) jauh lebih rendah daripada hutan tropika Asia Tenggara. Peratusan simpanan C yang lebih tinggi dalam biojisim pokok dan peratusan yang lebih rendah dalam tanah mineral menunjukkan bahawa stok C hutan tropika di kawasan batu kapur lebih terdedah kepada kerosakan tanaman berbanding dengan hutan tropika lain yang tumbuh atas substrat bukan batu kapur. Kajian ini memberi anggaran tepat untuk stok C pelbagai komponen di hutan tropika batu kapur di Xishuangbanna dan menunjukkan peranan penting hutan ini dalam pensekuesteran C.

INTRODUCTION

Tropical forests store up to half of the C stored in vegetation (Houghton 2005), representing a major reservoir of global C. However, the absolute and relative distribution of C stocks in tropical forests is known to vary with forest type, soil nutrient availability, climate, topography and disturbance regime. The large variation in tropical forest C stock estimates among different studies contributes greatly to the uncertainty of C flux estimation (Chave et al. 2008). Accurate

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estimation of C stocks in tropical forests is of great relevance for understanding C cycle at both regional and global scale.

Tropical forests over limestone are an important component of land cover in the tropics and for this reason they play an important role in carbon balance of this region. In South-East Asia, karsts cover an area of about 400,000 km^2 (Day & Urich 2000) and tropical forests over limestone are fairly common. Forests over limestone are seen as arks of biodiversity and often contain high levels of endemism (Clements et al. 2006). Moreover, tropical forests over limestone can store huge amounts of C in both aboveground biomass and soil (Proctor et al. 1983). Compared with those of tropical forests on non-carbonate lithogies, however, the C storage and partitioning for tropical forests over limestone are rarely known.

Several generalised allometric equations for tropical forests have been established (Brown et al. 1989, Chave et al. 2001, 2005) and widely used. However, application of such generalised equations to individual sites may lead to large errors in biomass estimates especially when the species concerned is poorly represented by the generalised models. Consequently, local allometric models are needed to give an accurate estimation (Chambers et al. 2001). Apart from aboveground vegetation, belowground tree root biomass, forest floor and mineral soil may all contribute considerably to ecosystem C storage. The estimations of total C stocks in tropical forests obtained from aboveground biomass tend to largely underestimate total C stocks (Sierra et al. 2007). An accurate estimation of the magnitude of C stocks in different components of forest ecosystems in tropical climates is, therefore essential. Furthermore, most studies of tropical forest C storage are based on aboveground biomass estimates multiplied by a carbon conversion factor (commonly 0.45 or 0.5). Such an approach yields a rather rough estimate for C content in different tree species and plant fractions. Interspecific variation in C concentration should be given full consideration to reduce the error associated with C stock estimation (Elias & Potvin 2003).

In a recent study, we reported the ecosystem C stocks in tropical season rainforests in Xishuangbanna, SW China (Lü et al. 2010) and found that the stocks were comparable with tropical forests in Indonesia and Malaysia. However, we still lack information about the C stocks in the tropical forests over limestone in this area. The focus of this study was to quantify the ecosystem above- and belowground C stocks of tropical forests over limestone in Xishuangbanna, SW China, based on locally estimated allometric equations and measured C concentrations in plant fractions of dominant species. The C stocks were assessed by a stratified sampling of tree, shrub and herb layers, woody lianas, coarse woody debris, litter and mineral soil. Results of this study, especially those from destructive sampling of belowground roots and actual C concentration measurement, will help fill a major gap in the related literature on the storage and distribution of C in tropical forests over limestone.

MATERIALS AND METHODS

Study site

The study area lies within the prefecture of Xishuangbanna, Yunnan province of SW China. Located between 21° 09' and 22° 36' N and 99° 58' and 101° 50' E, this region is characterised by typical tropical monsoon climate. Mean annual precipitation (1959–2006) is 1539 mm, with 80% falling between May and October and mean annual air temperature is 21.7 °C. Situated on limestone hills, the soil in the study area was derived from a hard limestone substrate of Permian origin with a pH of 6.8 (0–10 cm, Cao et al. 2006). Detailed soil characteristics in each plot are given in Table 1.

Table 1 Characteristics of soil profiles in four plots of the tropical forests over limestone in Xishuangbanna, SW China

Plot	Soil depth (cm)	Soil bulk density (g cm^{-3})	C content (%)	Soil moisture (%)
1	34.3	0.87 ± 0.02	3.46 ± 0.28	28.53 ± 1.59
2	33.8	0.86 ± 0.01	2.67 ± 0.21	26.11 ± 2.83
3	68.8	0.89 ± 0.01	2.78 ± 0.18	30.37 ± 3.67
4	22.5	0.99 ± 0.03	2.66 ± 0.33	26.67±4.47

Soil bulk density, C content and soil moisture represented 0–10 cm soil depth; data are means ± SE

Field inventory

We established four 50 m × 50 m plots in tropical forests over limestone at different locations (Figure 1) ensuring that within plot variation in slope and aspect was minimised. The forests are primary forests located at the well-protected natural reserve without any anthropogenic disturbance.

All trees and lianas with diameters at breast height (dbh, 1.3 m) greater than 2 cm were identified, labelled and their dbh and height recorded. For buttressed trees, dbh was measured just above the highest buttress.

The dbh was used to estimate tree biomass using allometric equations reported in the literature for five dominant species and mixed equations for three other species (74 sample trees for the equation of 2 cm ≤ dbh ≤ 5 cm; 45 samples for the equation of 5 cm < dbh ≤ 20 cm; 12 sample trees for the equation of 20 cm < dbh) in the tropical limestone forest in this region (Qi & Tang 2008). The dbh and length were used to estimate woody lianas biomass using allometric equations developed by Zheng et al. (2006). C concentrations of different fractions of woody lianas in this area were reported in Lü et al. (2010).

In each plot, ten 5 m × 5 m subplots were systematically established in both the left and the right side of each plot to harvest all plants with dbh < 2 cm but height > 1 m and ten 2 m × 2 m subplots to harvest all plants with height < 1 m. All plant materials were completely harvested from these subplots and transported to the laboratory for subsequent dry weight determination. Plant samples were divided into four fractions, namely, leaves, branches, stems and roots. Dry samples were weighed and ground for elemental analysis.

Height and diameter of all dead trees were measured in each plot and the mass of dead trees was the product of volume of trunk and specific gravity of large dead wood. Large fractions of downed wood were surveyed in the whole plot and fine fractions were measured in nine 5 m × 5 m subplots systematically distributed in each plot. Woody debris was weighed in the field and a sample of about 10% of the fresh weight in the subplots was used to estimate dry weights in the laboratory. In the case of large downed trees, bole volume was estimated by measuring length and diameter, and three cross-sections (from top, middle and bottom of the wood) were sampled to estimate the wood density.

Litter was collected in nine 1 m × 1 m quadrats distributed evenly in each plot. Here, litter was defined as detached and dead leaves, twigs (diameter < 2 cm), fruits, flowers and barks. Samples were oven dried at 70 °C and weighed.

Mineral soil samples were taken with a cylindrical soil sampler at 16 sites dispersed

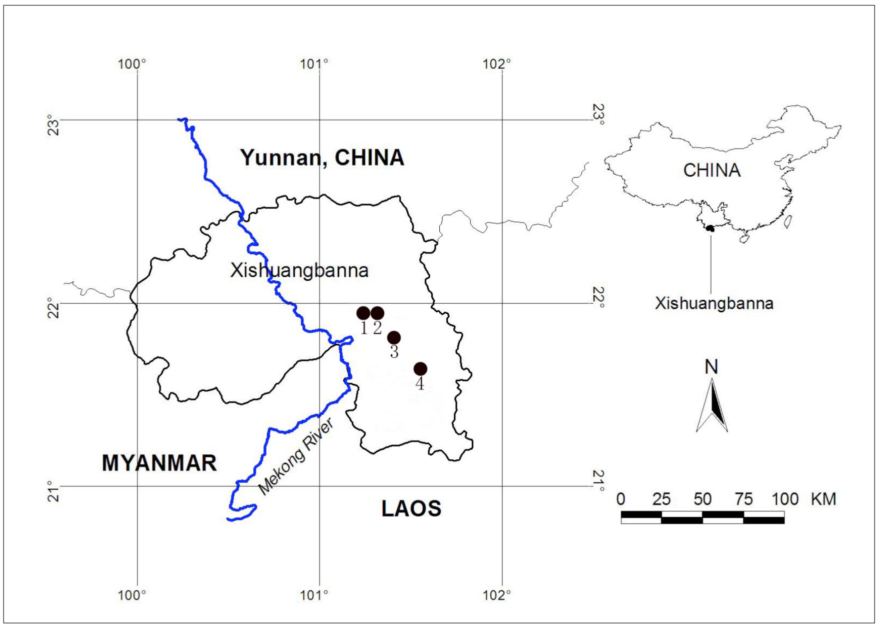

Figure 1 Map showing the locations of four plots in tropical forests over limestone in Xishuangbanna, SW China

in each plot. At each sampling site, three to five points were collected and mixed to a final sample. In cases where the bedrock was exposed and mineral soil lacking, no samples were taken. This was the case in 5 of the 16 sampling sites in plot 1, 7 in plot 2, 3 in plot 3, and 10 in plot 4. In the calculation of the total soil organic C stock in each plot, the total stock was reduced proportionally. Soil samples were taken at each 10 cm depth to the rock stratum. The deepest soil profile was 1 m. Soil bulk density at each site was quantified using the stone-free dry weights and the sampling tube volumes corrected for the stone volumes.

Chemical analysis

For all plant and soil materials, oven-dried samples were ground into fine, homogeneous powder in a ball mill grinder. When only a part of a sample disc of large diameter stems (dbh > 10 cm) was ground, care was taken to ensure subsamples were the same proportion of heartwood and sapwood as the whole sample disc. Total organic C content was determined using H_2SO_4–$K_2Cr_2O_7$ oxidation method. Using this method, the measured values of organic C were not affected by carbonate C (Sun et al. 2007). However, this method underestimated organic C content due to incomplete oxidation.

Statistical analysis

Two-way ANOVA was used to compare the effects of species and plant parts on tissue C concentration. Paired t-tests were used to compare the differences in C storage between woody lianas, shrub layer and herb layer in the tropical limestone forests. Statistical significance was defined as $p < 0.05$. All analyses were performed with SPSS 13.0.

RESULTS

Tree stem density ranged from 189 to 389 stems per plot and total basal area ranged from 7.6 to 10.1 m^2 per plot (results not shown). There were 100 tree species (dbh ≥ 5 cm) identified across the four plots. However, five species (*Cleistanthus sumatranus*, *Lasiococca comberi*, *Celtis wightii*, *Cleidion brevipetiolatum* and *Sumbaviopsis albicans*) with the highest importance value index (IVI) accounted for 70% of total stem density and 80% of total basal area.

Plant tissue C content varied greatly among species and plant parts with C contents in leaves and branches generally being lower than those of stems and roots (Table 2). Leaf C content ranged from 33 to 45%, branch C content varied from 40 to 47%, stem C varied from 43 to 48% and root C varied from 44 to 48% (Figure 2). Mean

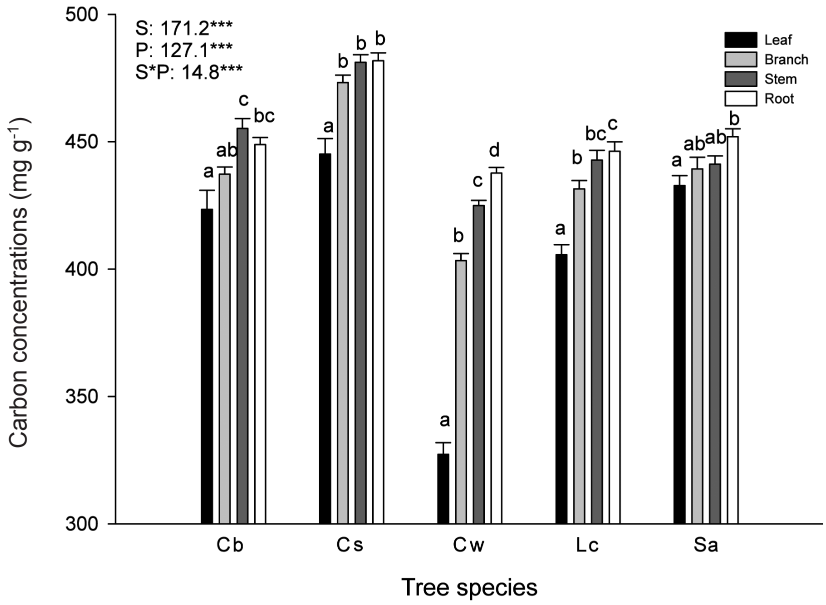

Figure 2 Plant tissue C concentrations (mean ± SE) in different parts of the five dominant tree species in tropical forests over limestone in Xishuangbanna, SW China. Cb = *Cleidion brevipetiolatum*, Cs = *Cleistanthus sumatranus*, Cw = *Celtis wightii*, Lc = *Lasiococca comberi*, Sa = *Sumbaviopsis albicans*; different letters on bars indicate significant differences ($p \leq 0.05$) of C concentration between different plant parts for the same species; S = species identity, P = part; *** = $p < 0.001$

C contents for leaves, branches, stems and roots of trees were 41, 44, 45 and 46% respectively. Species-specific C content was used to estimate C storage of the five dominant tree species and mean values were used to estimate C storage in different plant parts of other tree species.

Mean ecosystem C stock in tropical limestone forests was 214 ± 28 t C ha^{-1} with the tree layer being the largest carbon pool (155 ± 28 t C ha^{-1}), comprising 73% of the total ecosystem C stock of the forest (Table 2). Roots contributed 20% of the C stored in the tree layer. The tree layer C stock varied by a factor of two between the four plots which also exhibited contrasting dbh class distribution patterns (Figure 3). While small and middle dbh classes contributed the most to C stock in plots 1, 2 and 4, large dbh classes made the most important contribution in plot 3.

Carbon stock in both shrub and herb layers was < 1 t C ha^{-1}, accounting for 0.2 and 0.1% respectively of the total C stock in this ecosystem (Table 2). On average, > 3 t C ha^{-1} were stored in woody lianas. Averaged across the four plots, C stock in woody debris was 2.5 ± 0.7 t C ha^{-1}, ranging from 1.4 to 4.4 t C ha^{-1}. The highest C stock of woody debris was observed in plot

Table 2 Carbon density (t C ha^{-1}) in different components of tropical forests over limestone in Xishuangbanna, SW China

Component	Plot 1	Plot 2	Plot 3	Plot 4	Mean ± SE
Tree layer					
Leaf	2.32	2.19	2.59	2.16	2.32 ± 0.10
Branch	20.23	19.89	24.45	21.07	21.41 ± 1.04
Stem	69.92	74.82	144.05	111.13	99.98 ± 17.33
Root	20.77	23.57	47.23	35.31	31.72 ± 6.05
Subtotal	113.25	120.46	218.32	169.66	155.42 ± 24.43
Shrub layer					
Leaf	0.08	0.06	0.05	0.05	0.06 ± 0.01
Branch	0.10	0.07	0.06	0.06	0.07 ± 0.01
Stem	0.44	0.24	0.23	0.18	0.27 ± 0.06
Root	0.14	0.09	0.13	0.09	0.11 ± 0.01
Subtotal	0.76	0.45	0.46	0.38	0.52 ± 0.08
Herb layer					
Aboveground	0.14	0.11	0.25	0.08	0.14 ± 0.04
Belowground	0.06	0.05	0.24	0.03	0.09 ± 0.05
Subtotal	0.19	0.15	0.48	0.12	0.23 ± 0.08
Woody lianas	3.10	3.78	2.41	3.11	3.10 ± 0.28
Woody debris					
Standing dead tree	1.75	1.66	0.86	0.29	1.14 ± 0.35
Fallen branch	0.30	0.57	0.50	0.31	0.42 ± 0.07
Fallen dead tree	-	-	-	3.82	0.96 ± 0.96
Subtotal	2.05	2.23	1.36	4.42	2.51 ± 0.66
Fine litter					
Leaf	1.25	1.07	0.50	0.80	0.90 ± 0.16
Twig	0.79	0.98	0.55	0.36	0.67 ± 0.14
Flower and fruit	0.01	0.09	0.01	0.01	0.03 ± 0.02
Other	0.07	0.06	0.03	0.06	0.05 ± 0.01
Subtotal	2.12	2.20	1.08	1.23	1.66 ± 0.29
Soil	59.96	41.12	72.03	26.97	50.02 ± 9.97
Total	181.42	173.42	294.32	205.89	213.76 ± 27.73

4, mainly due to the large stock of fallen dead trees. There was no fallen dead tree in other plots. On average, C stock in the litter layer was 1.7 ± 0.3 t C ha^{-1}, ranging from 1.1 to 2.2 t C ha^{-1} in individual plots. Soil organic C to 1 m depth was 50.0 ± 10.0 t C ha^{-1}, comprising 23% of the ecosystem total C stock. Estimated soil organic C at 40 cm represented 72–84% of the soil organic C to 1 m (Figure 4).

DISCUSSION

A generic conversion factor of 50% has been widely used to estimate C stocks in plant biomass (Clark et al. 2001, Chave et al. 2008). However, using such a generic conversion factor may induce a bias in forest C stock estimation (Zhang et al. 2009). The error associated with C storage estimation may be reduced by up to 10% when

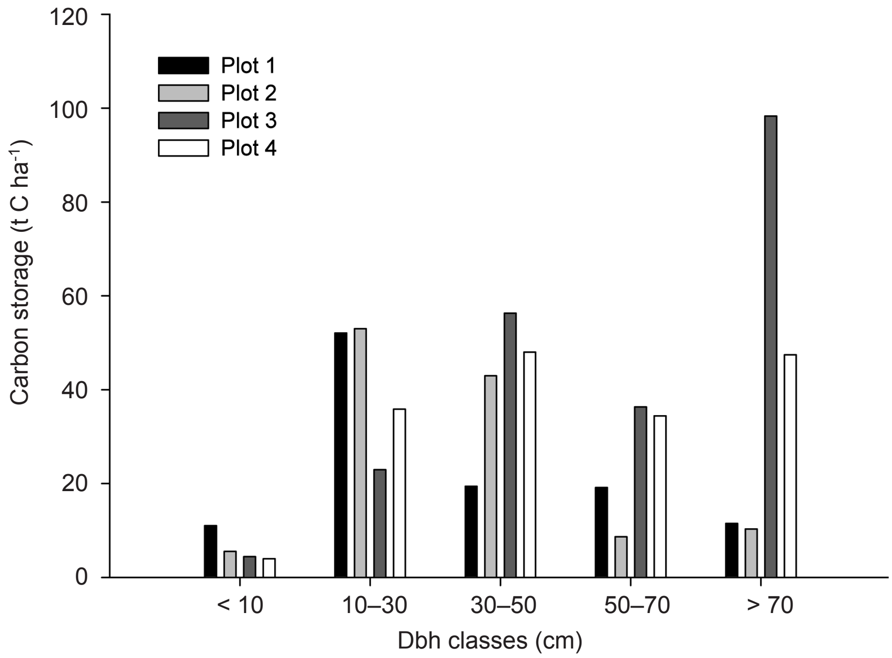

Figure 3 Carbon storage in different dbh classes of trees in tropical forests over limestone in Xishuangbanna, SW China

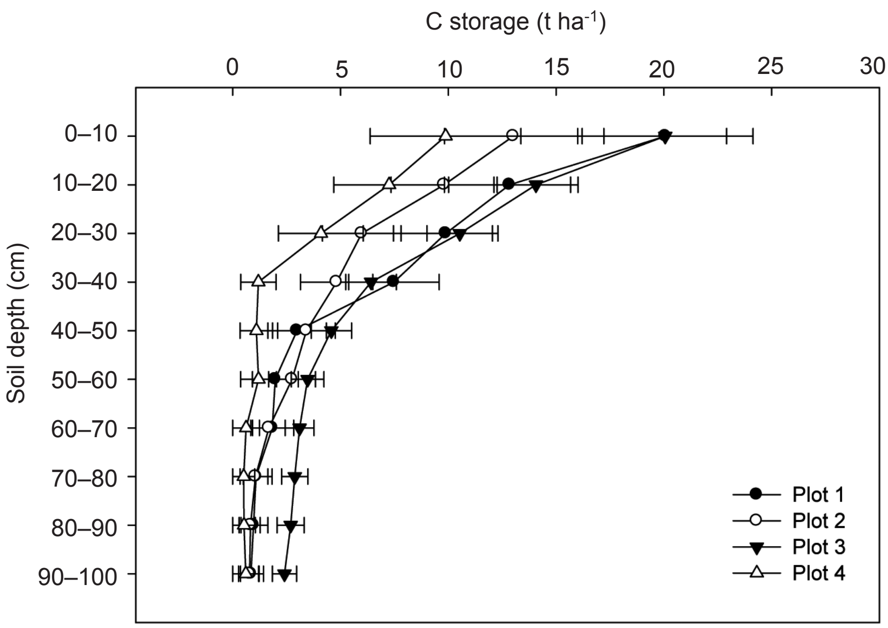

Figure 4 General patterns of C storage in soils of four plots in tropical forests over limestone in Xishuangbanna, SW China

interspecific variation in C concentration is being fully considered (Elias & Potvin 2003). In this study, we estimated the C stock in plant biomass of tropical limestone forest based on actual C concentrations in plant tissues of five dominant tree species. We found that C concentrations varied with species identity and parts. In most cases, measured C concentrations were less than the typical conversion factor of 50%. Mean C contents in branches, stems and roots of the dominant species were 44, 45 and 46% respectively. Given that woody tissues account for the majority of biomass C stock in forest ecosystems, we suggest that 45% could be an appropriate conversion factor for tree biomass C estimation in the tropical limestone forests in this area.

This study is one of the few studies focusing on C stock of tropical forests over limestone. Carbon stocks of vegetation and soil in tropical forests vary greatly by topography, climate and geologic substrate (Vieira et al. 2004, Laumonier et al. 2010). It has been estimated that biomass C stocks of tropical forests in Asia range from < 50 to > 360 t C ha^{-1} with most forests having 100–200 t C ha^{-1} (Lasco 2002). We found that C stock in tree biomass of tropical forests over limestone in Xishuangbanna was 155 t C ha^{-1}, with 80% stored in the aboveground biomass. The aboveground C stock in tropical forests over limestone in this area was lower than that of tropical forest over limestone in Sarawak (about 170 t C ha^{-1}) (Proctor et al. 1983). We suspected that lower precipitation and annual mean temperature might account for the lower C pool of living tree biomass in the tropical forests over limestone in Xishuangbanna. Compared with the tropical seasonal rainforests in Xishuangbanna which occur on non-limestone soils and receive more scientific attention, carbon stock in tree biomass of tropical forests over limestone is also much lower (198 vs. 155 t C ha^{-1}) (Lü et al. 2010). We attributed this difference to the limited soil volume in forest over limestone and hence limited water retention capacity and nutrient absorption. The limestone soils were very shallow (average depth 33 cm) and occurred as matrix between hard, sharply-angled limestone rocks.

The distribution of tree biomass C by dbh class showed a contrasting pattern across the four plots in this study. Large trees (dbh > 70 cm) comprised 45% of the C stock in plot 3, whereas they contributed 10% each in plots 1 and 2. Averaged across these plots, large trees contributed 23% of the tree layer C stock. In contrast, large trees accounted on average for more than 45% of the C stock in the tropical seasonal rainforest in Xishuangbanna (Lü et al. 2010). As the tree biomass C stocks in tropical seasonal rainforest were 20% higher than in tropical forest over limestone in Xishuangbanna, our results indicated that large trees had strong influence on tree biomass C stock. In the neotropical area, it was found that the contribution of large trees to biomass C stock ranged from less than 10% in very dry forests to more than 35% in moist forests (Delaney et al. 1997). Given the important role they play in C storage and other ecosystem functioning, the heterogeneous distribution of large trees in different forests should be given more attention.

In this study, roots accounted for more than 20% of the C stored in tree biomass. In another study, similar result was obtained in the tropical seasonal rainforests in Xishuangbanna (Lü et al. 2010), indicating that the contribution of belowground biomass to C storage would not vary greatly in different tropical forest vegetation types in this area. In contrast, another study reported that 50% of total tree biomass occurred belowground in a tropical dry forest over limestone in Puerto Rico (Murphy & Lugo 1986). However, in a study based on data from 33 moist and wet tropical forests, belowground biomass took up 16% of total biomass (Brown & Lugo 1982). On the other hand, the C density of roots in the present study, amounting to 32 t C ha^{-1}, was relatively high compared with mean root biomass of 49 t ha^{-1} reported for tropical rainforests in a global-scale meta-analysis (Jackson et al. 1996). These comparisons indicated that a higher proportion of biomass, and consequently more C, is stored in roots in tropical dry forests than in tropical moist or wet forests.

While aboveground biomass of living trees is the most commonly studied compartment, coarse woody debris can also be a major contributor to C stocks in tropical forests. The stocks of coarse woody debris in tropical forests vary widely from as low as 0 to as high as 60 t ha^{-1} (Baker et al. 2007). Compared with many other tropical forests in South-East Asia (Lasco et al. 2004, Yang et al. 2010), coarse woody debris stocks are low in the tropical forests over limestone in Xishuangbanna. Low coarse woody debris estimates may be the result of low rates of input and/or high rates of decomposition. In the study area, dry and nutrient-poor soils may explain the relative absence of trees with dbh > 10 cm and thus the low input of coarse woody debris. Additionally, low coarse woody debris stocks indicate that the forests have not experienced a recent, large-scale disturbance event. Direct measurements of decomposition rates of coarse woody debris would further improve our understanding of carbon cycling in tropical forests over limestone.

Litter constitutes an important flux of soil organic C. The C stocks in the litter of tropical forests over limestone in Xishuangbanna ranged from 1.08 to 2.22 t C ha^{-1}, which were similar to those reported for tropical seasonal rainforests in the same area (1.4 t C ha^{-1}) (Lü et al. 2010) and tropical secondary forest at the Makiling Forest Reserve in the Philippines (1.9 t C ha^{-1}) (Lasco et al. 2004). However, these values were much lower than the range (2.6–3.8 t C ha^{-1}) reported for other tropical forests (Brown & Lugo 1982). The relatively low quantities of C stored in litter stock in tropical forests in Xishuangbanna may be due to the high decomposition rate as reported in a 10-year study by Tang et al. (2010).

Mineral soil is the second largest C pool in the study area, comprising more than 20% of the total ecosystem C storage. These values are much lower than those of forests over limestone in Malaysia (Proctor et al. 1983). Carbon stock of the top 10-cm soil in tropical forests over limestone in Xishuangbanna was 10–20 t C ha^{-1}, whereas the corresponding value was 82 t C ha^{-1} in forests over limestone in Sarawak, Malaysia (Proctor et al. 1983). The higher C stock in forests over limestone in the latter can be attributed to the high concentrations of organic C. The fraction of organic C in 0–10 cm layer of soils in Sarawak was 42% (Proctor et al. 1983) but it was 3% in Xishuangbanna. The soil C pool (to a depth of 1m) in tropical forests over limestone in Xishuangbanna (50 t C ha^{-1}) was much lower than that of tropical seasonal rainforests (91 t C ha^{-1}) in the same area (Lü et al. 2010), which might be accounted for by the shallower soil depth in forests over limestone. Soil C densities in forests of tropical Asia ranged from 50 to 120 t C ha^{-1} (Palm et al. 1986). Our results clearly indicated that soil C storage of tropical forests over limestone in Xishuangbanna was in the lower end of tropical forest ecosystems in tropical Asia.

In the present study, we showed that in forests over limestone in Xishuangbanna, plant biomass contained 80% of the total C pool while soil contained 20%. Compared with tropical forests in other areas and on non-limestone substrate, a higher percentage of C stock was accounted for by plant biomass in tropical forests over limestone in Xishuangbanna. For example, based on 23 long-term permanent forest plots in five life zones of Venezuela, Delaney et al. (1997) found that soil contained as much or more C than plant biomass. However, none of their plots contained tropical forest over limestone. Similarly, soil comprised more than 40% of the ecosystem C stocks in a secondary tropical forest in Philippines (Lasco et al. 2004) and in afromontane rainforests in Tanzania (Munishi & Shear 2004). A high percentage of the C stock in plant biomass and a low percentage in soil implied that C stock in tropical forests over limestone was more vulnerable to the destruction of vegetation than in other tropical forests. This is of particular concern in South-East Asia where limestone quarrying rates exceeded those in other tropical areas (Clements et al. 2006). Previous studies also stressed the importance of limestone karsts in biodiversity conservation (Clements et al. 2006) and results from the present study showed that tropical limestone forests contained a large reservoir of atmospheric CO_2. Consequently, we concluded that tropical forests over limestone deserved more attention regarding their role in C sequestration.

ACKNOWLEDGEMENTS

We thank Y Lu and DF Chen for their help in the field. This study was supported by the Field Station Foundation of Chinese Academy of Sciences (CAS) and 'Light of Western China' of CAS.

REFERENCES

Baker TR, Coronado ENH, Phillips OL, Martin J, Van Der Heijden GMF, Garcia, M & Espejo JS. 2007. Low stocks of coarse woody debris in a southwest Amazonian forest. *Oecologia* 152: 495–504.

Brown S, Gillespie AJR & Lugo AE. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science* 35: 881–902.

Brown S & Lugo AE. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14: 161–187.

Cao M, Zou XM, Warren M & Zhu H. 2006. Tropical forests of Xishuangbanna, China. *Biotropica* 38: 306–309.

Chambers JQ, Dos Santos J, Ribeiro RJ & Higuchi N. 2001. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecology and Management* 152: 73–84.

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Folster H, Fromard F, Higuchi N, Kira T, Lescure JP, Nelson BW, Ogawa H, Puig H, Riera B & Yamakura T. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99.

Chave J, Olivier J, Bongers F, Chatelet P, Forget PM, Van Der Meer P, Norden N, Riera B & Charles-Dominique P. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology* 24: 355–366.

Chave J, Riera B & Dubois MA. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology* 17: 79–96.

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR & Ni J. 2001. Measuring net primary production in forests: concepts and field methods. *Ecological Applications* 11: 356–370.

Clements R, Sodhi NS, Schilthuizen M & Ng PKL. 2006. Limestone karsts of southeast Asia: imperiled arks of biodiversity. *Bioscience* 56: 733–742.

Day MJ & Urich PB. 2000. An assessment of protected karst landscape in Southeast Asia. *Cave Karst Science* 27: 61–70.

Delaney M, Brown S, Lugo AE, Torreslezama A & Quintero NB. 1997. The distribution of organic carbon in major components of forests located in five life zones of Venezuela. *Journal of Tropical Ecology* 13: 697–708.

Elias M & Potvin C. 2003. Assessing inter- and intra-specific variation in trunk carbon concentration for 32 neotropical tree species. *Canadian Journal of Forest Research* 33: 1039–1045.

Houghton RA. 2005. Aboveground forest biomass and the global carbon balance. *Global Change Biology* 11: 945–958.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE & Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108: 389–411.

Lasco R.D. 2002. Forest carbon budgets in Southeast Asia following harvesting and land cover change. *Science in China: Series C* 45: 55–64.

Lasco RD, Guillermo IQ, Cruz RVO, Bantayan NC & Pulhin FB. 2004. Carbon stocks assessment of a secondary forest in Mount Makiling Forest Reserve, Philippines. *Journal of Tropical Forest Science* 16: 35–45.

Laumonier Y, Edin A, Kanninen M & Munandar AW. 2010. Landscape-scale variation in the structure and biomass of the hill dipterocarp forest of Sumatra: implications for carbon stock assessments. *Forest Ecology and Management* 259: 505–513.

Lü XT, Yin JX, Jepsen MR & Tang JW. 2010. Ecosystem carbon storage and partitioning in a tropical seasonal forest in Southwestern China. *Forest Ecology and Management* 260: 1798–1803.

Munishi PKT & Shear TH. 2004. Carbon storage in afromontane rain forests of the Eastern Arc Mountains of Tanzania: their net contribution to atmospheric carbon. *Journal of Tropical Forest Science* 16: 78–93.

Murphy PG & Lugo AE. 1986. Structure and biomass of a subtropical dry forest in Puerto-Rico. *Biotropica* 18: 89–96.

Palm CA, Houghton RA & Melillo JM. 1986. Atmospheric carbon dioxide from deforestation in Southeast Asia. *Biotropica* 18: 177–188.

Proctor J, Anderson JM, Chai P & Vallack HW. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *Journal of Ecology* 71: 237–260.

Qi JF & Tang JW. 2008. Biomass and its allocation pattern of monsoon rain forest over limestone in Xishuangbanna of Southwest China. *Chinese Journal of Ecology* 27: 167–177.

Sierra CA, Del Valle JI, Orrego SA, Moreno FH, Harmon ME, Zapata M, Colorado GJ, Herrera MA, Lara W, Restrepo DE, Berrouet LM, Loaiza LM & Benjumea JF. 2007. Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. *Forest Ecology and Management* 243: 299–309.

Sun B, Shi JP & Yang LZ. 2007. *Protocols for Standard Soil Observation and Measurement in Terrestrial Ecosystems.* China Environmental Science Press, Beijing.

Tang JW, Cao M, Zhang JH & Li MH. 2010. Litterfall production, decomposition and nutrient use efficiency varies with tropical forest types in Xishuangbanna, SW China: a 10-year study. *Plant and Soil* 335: 271–288.

Vieira S, De Camargo PB, Selhorst D, Da Silava R, Hutyra L, Chambers JQ, Brown IF, Higuchi N, Dos Santos J, Wofsy SC, Trumbore SE & Martinelli LA. 2004. Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* 140: 468–479.

Yang FF, Li YL, Zhou GY, Wenigmann KO, Zhang DQ, Wenigmann M, Liu SZ & Zhang QM. 2010. Dynamics of coarse woody debris and decomposition rates in an old-growth forest in lower tropical China. *Forest Ecology and Management* 259: 1666–1672.

Zhang QZ, Wang CK, Wang XC & Quan XK. 2009. Carbon concentration variability of 10 Chinese temperate tree species. *Forest Ecology and Management* 258: 722–727.

Zheng Z, Feng ZL, Cao M, Li ZF & Zhang JH. 2006 Forest structure and biomass of a tropical seasonal rain forest in Xishuangbanna, Southwest China. *Biotropica* 38: 318–327.