Carbon balance of a primary tropical seasonal rain forest

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[1] The role of primary tropical rain forests in the global carbon cycle is under active debate. By combining long-term forest inventory data with physiological measurement data in a 1 ha permanent ecological research plot beneath an eddy covariance flux tower in a primary tropical seasonal rain forest, the ecosystem carbon balance was investigated and a detailed site-specific carbon budget was established. The studied ecosystem was a carbon sink as determined by both eddy covariance (1.19 Mg C ha^{-1} yr^{-1}) and biometric methods (3.59 Mg C ha^{-1} yr^{-1}). Biometric- and eddy covariance-based net ecosystem production showed no convergence in our investigation period. The large biomass increment, caused by the rapid annual growth rate of large trees, primarily accounted for the large ecosystem carbon sink derived from the biometric method. High leaf respiration in relation to carbon allocation and low ecosystem carbon use efficiency (0.34) were observed at our site.

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1. Introduction

[2] Understanding the distribution of the terrestrial carbon sink is the key to answering the "missing sink" question in global carbon cycle research [*Bolin*, 1977; *Woodwell et al.*, 1978]. It is also fundamental to understanding how ecosystems will respond to warming. Tropical forests occupy only 22% of the world's potential vegetation area [*Melillo et al.*, 1993], but they have been estimated to account for 59% of global carbon storage in forests [*Dixon et al.*, 1994] and 43% of the world's potential terrestrial net primary production [*Field et al.*, 1998]. Thus, the carbon balance of tropical forests could have a disproportionally large impact on the global carbon cycle. However, the role of tropical rain forests in the global carbon cycle remains under active debate.

[3] Primary old-growth forest is considered to be at a state of equilibrium, where carbon uptake equals carbon release and net ecosystem production is near zero [*Odum*, 1969; *Luyssaert et al.*, 2008]. Using a direct flux measurement method, eddy covariance, the first carbon flux measurement in tropical rain forest was carried out in Ducke of Amazon for 22 days in 1987. This campaign suggested the intact primary tropical rain forest was not in equilibrium but a net carbon sink [*Fan et al.*, 1990]. The sink hypothesis was supported by subsequent research in Jaru [*Grace et al.*, 1995a, 1995b, 1996], Cuineis [*Malhi et al.*, 1998], and results from the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) [*Carswell et al.*, 2002; *Hutyra et al.*, 2007]. However, this hypothesis has been challenged by two main questions. First, the underestimate of ecosystem respiration due to drainage flow and advection under calm night conditions [*Loescher et al.*, 2006] means that accurate measurement of the carbon balance is dependent on effective data processing [*Miller et al.*, 2004]. Second, most of the research covers brief periods. Interannual variation of ecosystem carbon balance was not fully investigated and remains unclear. A large-scale meteorological event, such as El Niño, can trigger a tropical rain forest shift from being a carbon sink into a carbon source, both of which are detected by direct field measurements [*Saleska et al.*, 2003; *Saigusa et al.*, 2008] and indirect ecosystem modeling [*Tian et al.*, 1998]. As an alternative way to investigate ecosystem carbon balance, the biometric-based method was carried out simultaneously and independently. Based on inventory data from 153 plots of tropical rain forests all over the world over a long period, a carbon sink of 0.71 megagrams of carbon per hectare per year (Mg C ha^{-1} yr^{-1}) was suggested [*Phillips et al.*, 1998]. This result, however, is still actively debated for its data accuracy and concept definition. On the one hand, tropical trees are often buttressed; this means that the measurement height is not strictly at breast height. Moreover, some rain forests at the floodplain are currently at the stage of primary succession [*Clark*, 2002; *Phillips et al.*, 2002]. On the other hand, biomass carbon accumulation is not conceptually the same as net ecosystem production, as initially presented by *Woodwell et al.* [1978], to indicate whether an ecosystem is a carbon sink or a carbon source [*Woodwell et al.*, 1978; *Randerson et al.*, 2002; *Chapin et al.*, 2006; *Lovett et al.*, 2006]. Necromass and soil organic matter should also be taken into

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account when assessing the carbon budget of a tropical forest. When taking the carbon balance of coarse woody debris (CWD) into account, an ecosystem that is accumulating carbon would then act as a carbon source [*Rice et al.*, 2004]. Researchers in southern China also showed that old-growth forest soil could accumulate carbon at a high rate [*Zhou et al.*, 2006]. On the regional scale, measurements of midday vertical atmospheric carbon dioxide distributions indicate that tropical land is a large carbon sink compared with earlier research [*Stephens et al.*, 2007]. If large regional carbon sinks existed, a large uptake by primary rain forest would be needed to surpass the land-use-induced carbon loss. Recently, the second largest area of tropical rain forest in the world, the Indo-Malaysian rain forest, was suggested to be a large carbon sink [*Kato and Tang*, 2008; *Kosugi et al.*, 2008; *Saigusa et al.*, 2008; *Hirata et al.*, 2008], supporting the regional carbon sinks. These findings demonstrate that much effort is needed to accurately assess the carbon balance with respect to techniques, and spatial and temporal variability.

[4] Using the eddy covariance technique, it is only possible to obtain a net carbon flux of the ecosystem-atmosphere interface [*Baldocchi et al.*, 1988, 2001]. Although the net ecosystem exchange (NEE) environment response-based flux partitioning can provide a rough estimate of gross primary production (GPP) and total ecosystem respiration (R_e) [*Grace et al.*, 1995b; *Reichstein et al.*, 2005], problems arise when further questions are asked. For example, which carbon pool components are responsible for the ecosystem carbon sink: biomass or soil? Carbon sequestration is a multiple biological process, which removes carbon from the atmosphere and stores it in terrestrial ecosystem pools, such as biomass, necromass, or soil [*Rice et al.*, 2004; *Zhou et al.*, 2006; *Ohtsuka et al.*, 2007]. An analysis of the contribution of different processes to net ecosystem production (NEP) should demonstrate where carbon is stored [*Barford et al.*, 2001]. Estimation not only of the total carbon sequestration but also of the contribution of every carbon pool is necessary to investigate the mechanism of carbon sequestration. Compared with the eddy covariance method, ecosystem carbon pool component analysis is an obvious advantage of the biometric method.

[5] As there were two practical methods to assess carbon balance, these two methods have been used together to investigate carbon balance, conferring the advantages of each individual method. Pioneering work, combining these two methods, has been done in temperate forests [*Law et al.*, 1999; *Granier et al.*, 2000; *Barford et al.*, 2001; *Curtis et al.*, 2002; *Ehman et al.*, 2002]. However, these results were generally not convergent and three issues have been raised: (1) the meteorological footprint from the eddy covariance method and the ecological inventory plot from the biometric-based method do not adequately overlap [*Schmid*, 1994, 1997; *Schmid and Lloyd*, 1999]; (2) the spatial and temporal variability induced a sampling problem and the gap-filling assumption in eddy covariance also had an important effect [*Ehman et al.*, 2002; *Schmid et al.*, 2003]; and (3) temporally offsets were involved. Photosynthetically assimilated carbon is stored, rather than being used for immediate growth [*Barford et al.*, 2001]. Convergences were observed in a Harvard (USA) forest after 8 years [*Barford et al.*, 2001], and in a Michigan (USA) forest during 1999–2003 [*Gough et al.*, 2008]. In tropical rain forests, the bio-

metric-based method and eddy covariance based method converged well in Para, Amazonian [*Saleska et al.*, 2003], but convergence was dependent on the *u** filter used in nighttime data processing [*Miller et al.*, 2004].

[6] Here, we present annual carbon balance and carbon budget estimates over 4 years (2003–2006) in a primary tropical rain forest located in southwestern Yunnan, China. Our study site is part of the ChinaFlux network and the Chinese Ecosystem Research Network (CERN) long-term carbon cycle research facilities [*Yu et al.*, 2006]. Our primary objectives were: (1) to investigate NEP of a primary tropical seasonal rain forest ecosystem, to determine the role of this primary tropical rain forest ecosystem in the global carbon cycle, i.e., a carbon sink or a carbon source; (2) to clarify which carbon pool component of the ecosystem (biomass, necromass, or soil organic matter) is the main contributor for ecosystem uptake or release of carbon; (3) to determine if there is biometric-based and micrometeorological-based net ecosystem production convergence in the ecosystem; and (4) to establish, in detail, an accurate and site-specific carbon budget for our research ecosystem.

2. Methods

2.1. Research Site

[7] Our study site (21°55′39″N, 101°15′55′″E, 750 m a.s.l.) is located in the Menglun Nature Reserve in Xishuangbanna, southwestern China (Figure 1). The site is approximately 800 km northeast of the Bay of Bengal and 600 km west of the Bay of Beibu [*Liu et al.*, 2007]. Xishuangbanna, located at the northern edge of tropical southwestern Asia, is a transitional area between the tropics and the subtropics. The climate is strongly seasonal with two air masses alternating during the year [*Zhang*, 1966]. Between May and October, the tropical southern monsoon from the Indian Ocean delivers most of the annual rainfall, whereas the dry and cold air of the southern edges of the subtropical jet streams dominates the climate between November and April [*Cao et al.*, 1996]. With a typical monsoon climate, there are three distinct seasons: humid hot rainy season (May–October), foggy cool dry season (November–February), and hot dry season (March–April).

[8] A permanent ecological research plot was set up in the Reserve in 1994, which belongs to the Xishuangbanna Forest Ecological Research Station, and is also part of the CERN. The soil is lateritic derived from siliceous rocks, such as granite and gneiss, with a pH from 4.5 to 5.5. A stream (about 1 m wide) winds through the site and the length of the valley is about 2 km. This is typical of tropical seasonal rain forest in this area [*Cao et al.*, 2006]. This forest differs from tropical Asian lowland rain forest in that some of its tree species are deciduous. The species richness is lower in Malaysian rain forests, higher than that those of Australian and African rain forests, and similar to the tropical forest on Barro Colorado Island, Panama [*Cao et al.*, 2006; *Zhu et al.*, 2006].

[9] Forty years of climate records from a weather station (560 m above sea level), 5 km southeast from the study site, show that the mean annual air temperature is 21.7°C, with a maximum monthly temperature of 25.7°C in June and a minimum of 15.9°C in January. The mean annual rainfall is 1487 mm, of which 1294 mm (87%) occurs in the rainy season, compared with 193 mm (13%) in the dry
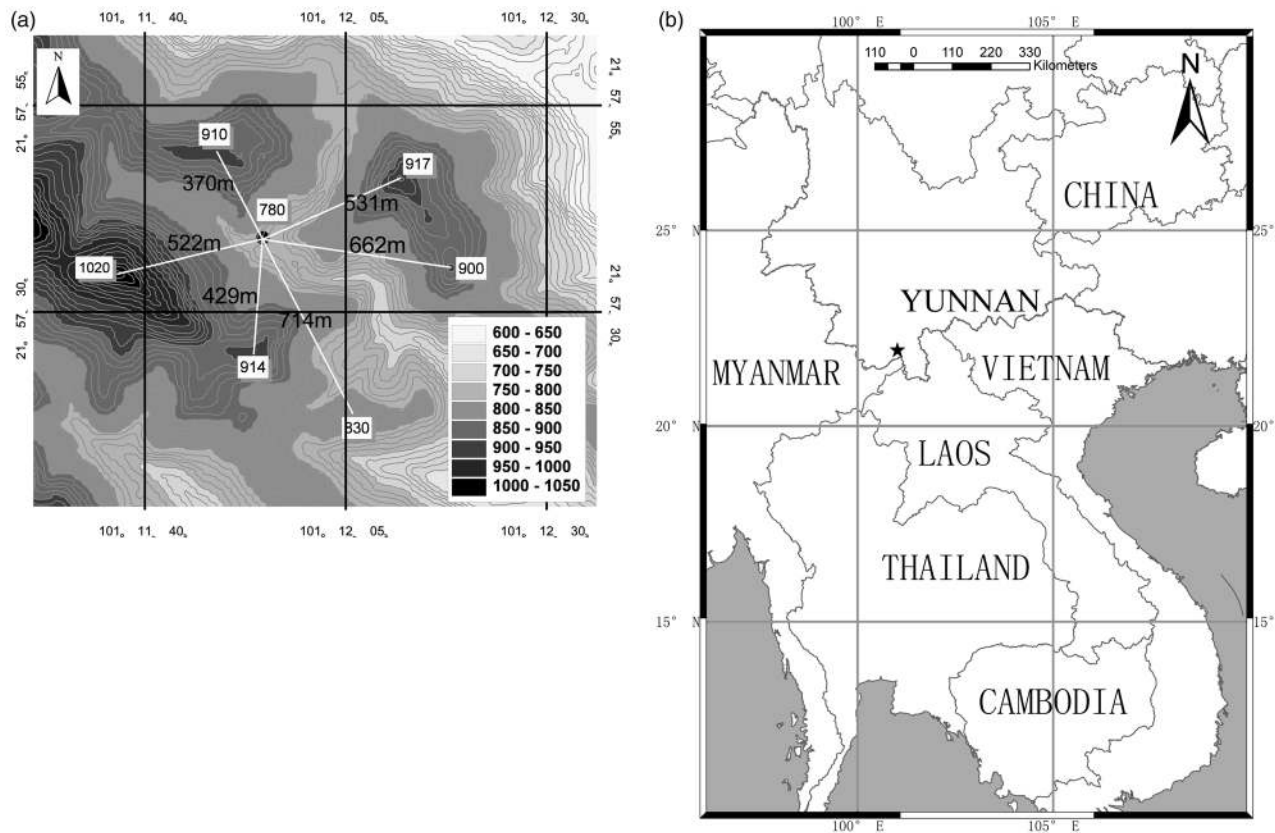
Figure 1. (a) Terrain of the permanent plot and flux tower (indicated by a black circle) and (b) geographical location of the study site (indicated by a star).

season. Class A pan evaporation varies between 1000 and 1200 mm yr^{-1}. The mean annual wind speed is 0.5 m s^{-1} [*Liu et al.*, 2005].

[10] The permanent ecological research plot is in the center of the Nature Reserve; it shows no sign of recent anthropogenic disturbance, other than hunting trails. With large logs, many epiphytes, uneven age distribution of plants, and emergent trees, this tropical seasonal rain forest can be considered primary, or "old-growth." The forest canopy is uneven and complex and can be divided into three layers (A, B and C). Dominating tree species in layer A are *Pometia tomentosa*, *Terminalia myriocarpa*, *Gironniera subaequalis* and *Garuga floribunda*, which can exceed 40 m high. Dominating tree species in layer B (16–30 m) are *Barringtonia fusicarpa*, *Gironniera subaequalis*, *Mitrephora maingayi*. Dominating tree species in layer C (lower than 16 m) are *Garcinia cowa*, *Knema erratica*, *Ardisia sinoaustralis* [*Cao et al.*, 1996].

2.2. Biometric Method and Eddy Covariance Method for Net Ecosystem Production Estimate

[11] The biometric method (BM)-based NEP method was developed based on research into plant physiology. Allometric relationships between morphological indexes, such as DBH and tree biomass, form the basis of BM-based NPP, and the corresponding NEP [*Kira et al.*, 1967; *Schulze*, 2006]. This work was advanced and enhanced by the IBP, and later by the International Geo-Biosphere Programme (IGBP). BM-based NEP is also conceptually equivalent to the sum of

the change in each carbon pool component [*Ohtsuka et al.*, 2007],

$$\mathrm{NEP(BM)} = \Delta C_B + \Delta C_N + \Delta C_{\mathrm{SOM}}. \qquad (1)$$

[12] EC-based NEP is an application of micrometeorology to carbon-cycle research [*Baldocchi et al.*, 1988; *Aubinet et al.*, 2000]. As the only way direct measure forest-atmosphere carbon exchange, it provides the immediate net flux of photosynthetic carbon uptake and respiratory release, without regard to plant growth, allocation, and other biological processes [*Baldocchi et al.*, 1988, 2001]. This method received many criticisms for underestimating nighttime respiration caused by drainage flow and advection under calm conditions [*Loescher et al.*, 2006].

2.3. Forest Inventory and Monitoring

[13] Forest inventory was carried out annually in the 1 ha permanent ecological research plot in the dry-hot subseason (March to April). At the beginning of the plot establishment, all trees with DBH (diameter at breast height) larger than 2 cm were identified to species, tagged, measured and mapped. The measurement height on the trunk of each tree was marked with red paint, ensuring comparable measurements of DBH afterward. Trees with significant buttresses were measured above buttress termination [*Cao et al.*, 1996]. Tree DBH was measured and the tree condition was also recorded, such as fallen, dead or pest attack. Site-specific allometric equations

Table 1. Biomass Equations for Different Organs Derived From Three Tropical Seasonal Rain Forests in Xishuangbanna, Southwestern China[a]

DBH Class	Sampling Numbers	Organs	A	B	R^2
2–5	46	stem	0.0733	2.5884	0.8960
		branches	0.0135	2.5158	0.7317
		leaf	0.0394	1.456	0.6675
		root	0.028	2.399	0.8266
5–20	55	stem	0.1086	2.3169	0.9453
		branches	0.0186	2.4685	0.8619
		leaf	0.0455	1.6636	0.7675
		root	0.0242	2.4205	0.9357
20–	22	stem	0.0401	2.6752	0.9663
		branches	0.0829	2.0395	0.9136
		leaf	0.0979	1.3584	0.7976
		root	0.0111	2.6801	0.9686

[a]Equation is expressed as $M_b = a \cdot (\mathrm{DBH})^b$, where M_b and DBH are biomass (kilograms) and diameter at breast height (centimeters), respectively.

(Table 1) and DBH were converted into tree biomass. These allometric equations were generated by destructive sampling of a total of 123 trees across all sizes; R^2 values all exceeded 0.66 [*Lv et al.*, 2007]. Stand biomass was treated as live tree biomass here, as the estimated nontree plant biomass was less than 5% of total stand biomass [*Feng et al.*, 1998; *Lv et al.*, 2007]. Track individual tree method was used to calculate annual biomass increment [*Clark et al.*, 2001a]. Before calculation, we excluded measurements outliers. Annual DBH increment outside the central of 99% of the frequency distribution was treated as an outlier. The uncertainty of annual DBH increment was estimated by bootstrap analysis (1000 repeated samples, with standard error obtained) [*Efron and Tibshirani*, 1986]. Trees were treated individually through time. Trees with no foliage and dry sapwood all around were recorded as dead. The dry mass of dead trees was estimated using the same equation for biomass, with leaf biomass excluded. Annual tree mortality in the plot was calculated as the sum of all dry mass of dead trees in that year. Biomass was converted to carbon density by a factor of 0.5.

[14] Aboveground litter was captured by 40 litter traps (area: 0.25 m^2) which were placed randomly within the permanent plot. Litter was collected weekly from the traps. All litter collections were sorted into leaves, branches, flowers, fruits, epiphytic materials and "mixed matter," then dried to a constant weight at 80°C. Components of litter were weighted separately [*Ren et al.*, 1998].

[15] Leaf area index was measured by a canopy analyzer (Model LAI-2000, Li-Cor, Lincoln, Nebraska, USA). We measured the background value (termed A value by LAI-2000) at the top of the tower (70 m). The LAI at different heights was measured where there was a platform on the tower. On each platform, fifteen points were sampled in different directions to eliminate the tower shadow effect. The LAI was measured monthly.

[16] To estimate standing coarse woody debris and standing litterfall carbon density, two additional experiments were carried out in 2005 [*Lv et al.*, 2006]. One was an inventory of coarse woody debris in three 1-ha plots near our permanent plot, with same tropical seasonal rain forest. Volumes of large logs were measured and converted to dry matter. For branches and small logs, parts of them were sampled to extrapolate to the stand. The other was establishing 5 quadrates with a size

of 1×1 m^2 in the permanent plot to measure standing aboveground litterfall. Collected litterfall were dried at 80°C to a constant mass and weighted [*Lv et al.*, 2006].

2.4. Soil Surface CO$_2$ Efflux and Soil Carbon Density Measurement

[17] Static chambers complied with a gas chromatography (4890D GC, Agilent Co. Produced) was used to measure soil CO$_2$ efflux in the permanent plot [*Sha et al.*, 2005]. Two treatments were applied with six replicates. In treatment A, total soil CO$_2$ efflux including soil organic matter respiration, litterfall respiration, coarse root respiration, and fine root respiration was measured. In treatment B, litterfall was removed before measurement. Sampling was done on every Monday morning between 0900 to 1100 local time from October 2002 until December 2007. The difference between treatment A and treatment B was treated as the aboveground litter respiration. Since aboveground litter was either converted into soil organic matter or efflux as CO$_2$ into the air, annual transfer of litter into soil organic matter was calculated as the difference between annual aboveground litter production and aboveground litter respiration.

[18] Sequential soil coring was used to measure biomass of live and dead fine roots and fine-root production [*McClaugherty et al.*, 1982]. Three plots (10 × 10 m) were selected for root coring. Ten points were sampled in each plot at monthly intervals. The corer was 8 cm in diameter. Cores were kept at 5°C until processing. Soil samples were sieved through 2 mm and intact fine roots were sorted into live and dead by visual inspection under a microscope. Both fresh weight and 80°C dried weight was recorded. Belowground litter carbon density was calculated from biomass of dead fine roots. A standard method of nylon litter bags was used to measure decomposition and percentage of dry mass loss of fine roots. The dried fine roots were cut to 5 cm length and put into nylon bags. A total of 180 bags each time were labeled with tags and replaced into soil to determine fine root decomposition rates [*Fang and Sha*, 2005]. Belowground litter production (L_{BG}) was estimated as the difference between maximum and minimum measured fine-root biomass [*McClaugherty et al.*, 1982].

[19] Respiration of fine and coarse roots was calculated separately. Fine root respiration was estimated as 39% of total soil surface CO$_2$ efflux [*Lu*, 2009]. The trenching method was used to separate root respiration. Soil surface CO$_2$ flux was measured by an open-flow gas exchange system formed by a self-made chamber and an infrared gas analyzer (Li-840, Li-Cor, Lincoln, Nebraska, USA).

[20] We have not conducted coarse root respiration measurement at our site. The coarse root respiration estimated here was based on an assumption that it can be treated as woody organs. Each year, based on the inventoried DBH data and allometric equations, the biomass ratio between coarse root and woody organs can be estimated. We assumed respiration per unit coarse root biomass was same as per unit of woody-organs biomass [*Saleska et al.*, 2003]. Thus, coarse root respiration was calculated from woody respiration and its biomass ratio.

[21] Respiration of coarse woody debris has seldom been constrained in forest ecosystem carbon balance research. This issue should not be neglected as in boreal or temperate forests, because high turnover rates have been commonly observed in

tropical forests. However, there was no data available for this important issue in our site. So, we adapted a empirical parameter (R_{CWD} = k × (total CWD carbon density)) which was free of decay class and other environmental factors to calculate this flux [*Rice et al.*, 2004]. There were two considerations for choosing the empirical parameter. First, it should have upper and lower bounds. Upper bound is k = $0.17 \, yr^{-1}$, from a study of CWD mass loss over 10–15 years in a tropical forest near Manaus [*Chambers et al.*, 2000]. Lower bound is k = $0.0825 \, yr^{-1}$, based on an average across non-pine temperate forests (oak-hickory and bottomland hardwoods) in the southern United States [*Turner et al.*, 1995]. Second, we expected that the CWD carbon pool was in steady state because there was no strong mortality event observed in the past 10 years at our site. This suggests that input should nearly equal output of CWD. The annual CWD input was treated as annual tree mortality. Based on the above two considerations, k = 0.13 was accepted and applied to our data set.

[22] Five soil profiles (1 m depth) were extracted in the permanent plot to collect soil samples at 20 cm depth interval. Bulk density was determined by drying at 80°C and organic matter content was measured by $K_2Cr_2O_7$ oxidation. Based on bulk density and organic matter of each layer (total 5 layers), total organic matter in the top 1 m of each profile was estimated. Soil organic carbon density was calculated as soil organic matter density multiplied by a conversion factor of 0.5 [*Lv et al.*, 2006].

2.5. Leaf and Wood Respiration

[23] An infrared gas analyzer Li-820 (Li-Cor, Lincoln, Nebraska, USA) connected with a self-made chamber was used to measure in situ stem respiration. The top ten species by important value were chosen in this study [*Yan et al.*, 2008]. Five trees were selected for each species. The measurement height was at 1.3 m. North and south faces were measured separately. The chamber was attached to the bole surface. Plasticene was used to prevent chamber leaks. After 5 to 6 min, the CO_2 concentration in the chamber was increasing steadily and linearly. Concentration was logged for 2 min. The slope of the linear increase of CO_2 concentration was calculated as efflux rate. Holes were drilled in the boles and temperature sensors were installed to obtain bole temperatures. The stem CO_2 efflux measurements were carried out in January, April, June and October to represent the fog-cool subseason, dry-hot subseason, early rainy subseason, and late rainy subseason, respectively. To extrapolate half-hourly wood respiration to a whole year, a regression relationship between measured CO_2 efflux and bole temperature was developed. To obtain woody respiration of the whole stand, the sapwood volume was used as an upscaling index. We first relate sapwood area to DBH, based on site-specific allometric equations. The DBH sapwood area allometry was measured in our site. At breast height, a hole was drilled and dye was injected. In sunny days, after several hours, a core was taken above the dye injection point and the sapwood width was measured. Forty trees were sampled, of several species. We converted stem respiration from a surface area to a sapwood volume based respiration as follows:

$$E_V = \frac{S}{V} E_S, \qquad (2)$$

where E_v is CO_2 efflux per unit of sapwood volume (μmol $m^{-3} \, s^{-1}$), E_s is CO_2 efflux per unit stem surface area (μmol $m^{-2} \, s^{-1}$), S and V are stem surface area (m^2) and sapwood volume (m^3), respectively.

[24] A portable photosynthesis system Li-6400 (Li-Cor, Lincoln, Nebraska, USA) was used to measure leaf respiration. The forest canopy was tall, so we measured in situ leaf respiration of dominant trees from the meteorological tower. Three large trees were accessible for sampling from the tower. They are two *Pometia tomentosa* Binn. trees and one *Gironniera subaequalis* Planch. tree. We divided each large tree canopy into three layers by visual estimation. Three leaves were measured for each layer. Three leaves of under canopy saplings (*Pometia tomentosa* Binn.) were also measured. The measurement frequency was same as for stem respiration. The Li-6400 was connected with a LED light source (closed), creating a dark chamber. The in-chamber leaf temperature was controlled with a predesigned temperature gradient (16.0, 17.0, 18.0, 19.0, 20.0, 21.0, 22.0, 23.0, 24.0, 25.0, 26.0, 27.0 in °C). Every time before logging data, the system was "matched." The canopy analyzer (LAI-2000) based leaf area index/density was used for scaling from leaf to the canopy level as follows [*Xu*, 2006]:

$$R_{leaf} = \sum_i \alpha_i \exp(\beta_i T) \cdot LAD_i, \qquad (3)$$

Where α_i and β_i are temperature-respiration fitted parameters at the i layer. LAD_i is the leaf area density at the ith layer.

2.6. Eddy Covariance Flux Measurement

2.6.1. Instrumentation

[25] The eddy covariance equipment was mounting at the height of 48.8 m (which is near 1.5 times of canopy height) on a 70 m tower in the center of the permanent plot. Eddy covariance system included a 3-D sonic anemometer (model CSAT-3, Campbell Scientific Inc., Logan, UT, USA) and an infrared open-path gas analyzer (model LI-7500, Li-Cor Inc., Lincoln, NE, USA). Data was retrieved by a control system (model CR5000, Campbell Scientific Inc., Logan, UT, USA) at a frequency of 10 Hz.

2.6.2. Calculating NEE

[26] Net ecosystem carbon exchange (NEE) between the forest ecosystem and the atmosphere consists of two components: a turbulent eddy flux transported across the plane of instrumentation above the forest (F_c), and exchange below the instrumentation height, which was manifested as a change in the mean concentration of CO_2 in the forest air column (F_s) [*Hollinger et al.*, 1994]. F_c was calculated as the mean covariance between fluctuations in vertical wind velocity (w) and the density of CO_2 (c) [*Baldocchi et al.*, 1988],

$$F_c = \rho \overline{w'c'}, \qquad (4)$$

where ρ is air density, primes denote deviations from the mean, and the overbar signifies a time average (here 30 min was the averaging period). F_s is calculated as

$$\delta F s = \frac{\delta c}{\delta t} \cdot z_r, \qquad (5)$$

where δc is the discrete dynamic of CO_2 concentration (mg $s^{-2}\,s^{-1}$), δt is the time interval (30 min), and z_r is the reference height (48.8 m). NEE was calculated as

$$NEE = F_c + F_s. \qquad (6)$$

[27] By convention, negative values of NEE indicate CO_2 flux from air into the forest, and vice versa.

2.7. Quality Assessment and Control (QA/QC) of NEP Estimation by EC and BM Method

[28] We investigated the uncertainties of BM-based NEP assessment. First, site-specific allometric equations were required [*Clark et al.*, 2001a]. In our research, we sampled 123 trees from three 1 ha plots of primary tropical seasonal rain forest near our sites in this region to derive site-specific equations. Tree-height measurement is difficult and imprecise due to structural complexity of the canopy [*Brown et al.*, 1989]. Choosing accurately measured DBH as the single independent variable, a power law allometric equation was developed, fulfilling our first criterion. Second, all litter was collected during the investigation interval (1 year) and only litter produced in that year was captured [*Clark et al.*, 2001a]. We collected aboveground litter weekly to avoid significant losses due to decomposition. Specifically, due to strong seasonality of rainfall, these comprised most of the canopy tree defoliation in the dry season. This means that leaf longevity was generally less than 1 year. In the 1 ha plot, 40 litter traps were randomly allocated to count for spatial heterogeneity. The litter traps collect litter fallen in a particular year, but not necessarily the leaves produced in that year. Probably from the previous years, or even earlier in the case of evergreen trees. Similar limitations apply to woody biomass increment. Therefore, a time lag exists between actual NPP and estimated NPP. Third, ecosystems underground may contribute to some of the uncertainty in BM-based NEP assessment [*Fang and Wang*, 2007]. For example, separating autotrophic and heterotrophic respiration contributions to soil efflux is important and difficult work in forest ecosystems [*Hanson et al.*, 2000]. We applied trench method in our research [*Lu*, 2009]. The sampling depth of only 1 m may underestimate fine root respiration if deep roots are common. Fourth, in NPP estimation, only biomass increment and litter production were taken into account. Processes such as aboveground losses to consumers, volatile and leached organics, root losses to herbivores, root exudates, and carbohydrate export to symbionts were not taken into account. Omission of these components often causes underestimation of NPP [*Clark et al.*, 2001a].

[29] Nine steps of QA/QC were carried out to obtain defensible annual EC-based NEE (-NEP).

[30] 1. Physically impossible values were excluded before calculating averages, variances, and covariance. The upper limit and lower limit for physical exclusion was set as by the TK2 software (Department of Micrometeorology, University of Bayreuth, Germany).

[31] 2. The energy balance closure for an ecosystem can be written as

$$LE + H = R_n - G - S - Q, \qquad (7)$$

where LE is latent heat, H is sensible heat, R_n is net radiation, G is soil heat flux, S is canopy heat storage, and Q is the sum of all additional energy sources and sinks, they are all in units of energy. As S and Q have usually been neglected, LE+H and R_n-G were plotted, and we expected the slope of this regression line to be near one and the line should intercept the origin. R_n and G were measured directly by net radiometer and two soil heat flux plates, respectively; LE and H were measured by the eddy covariance system (CSAT-3, and Li-7500). The result in our site shows that LE+H represent near 75% of the R_n-G in the dry-hot subseason of 2005.

[32] 3. According to the Kolmogorov'a law, the spectral density can be plotted as a function of frequency,

$$nS(n) = \alpha\varepsilon^{2/3}n^{-2/3}, \qquad (8)$$

where α is the Kolmogorov constant and ε is the dissipation rate. Results show that power spectra and cospectra obey the $-2/3$ and $-4/3$ power law at our site.

[33] 4. Monin-Obukhov similarity theory point out that the dimensionless variance can be explained as a function of stability index ($-(z-d)/L$) with exponent of 1/3, which also called flux variance similarity [*Foken and Wichura*, 1996]. The so-called flux-variance similarity are basic characteristics of atmospheric turbulent [*Kaimal and Finnigan*, 1994; *Stull*, 1988]. In our site, flux covariance similarity obeys the $-1/3$ rule with high correlation coefficients.

[34] 5. We estimated the dimensions of flux source area or "footprint" with the statistical source area model of *Schmid* [1994]. Three input variables were needed, z_m/z_o, z_m/L, and S_v/u^*. The z_m was calculated from roughness length (z_o) and zero-plane displacement (d), L is the Monin-Obukhov length, S_v is variance of side-way wind deviation. We must point out that the footprint analysis shows that in our site, the eddy flux was not only from tropical seasonal rain forest, but also from a nearby evergreen broadleaf forest, occurred at higher elevation.

[35] 6. It is necessary for us to choose an effective averaging time period (T) in order to obtain the turbulent fluctuation,

$$w'(t) = w(t) - \overline{w} \qquad (9)$$

$$\overline{w(t)} = \overline{w} = \frac{1}{T}\int_0^T w(t)dt, \qquad (10)$$

where $w(t)$ is a time series, overbar means averaging, and primes means fluctuations. In our study, a 30 min interval was chosen and the effectiveness of this time interval was tested [*Sun et al.*, 2005].

[36] 7. In this study, three-dimensional rotation of the coordinates was applied to the wind components to remove the effect of instrument tilt and irregularity on the airflow [*Tanner and Thurtell*, 1969]. The flux data were corrected for the variation of air density caused by transfer of heat and water vapor [*Webb et al.*, 1980].

[37] 8. Gap-filling was a necessary step to obtain the annual carbon exchange. The most widely used methods for gap-filling were mean diurnal variation (MDV) and nonlinear
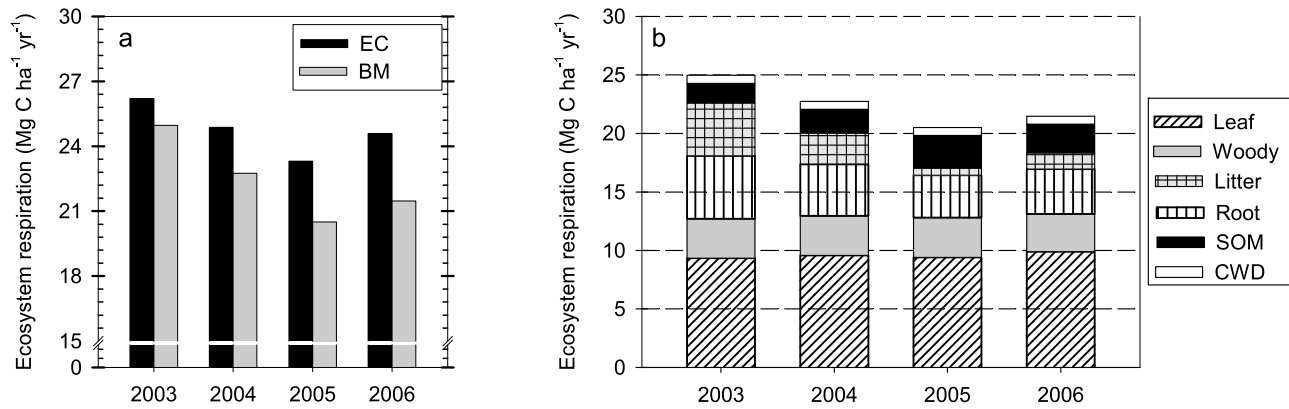
Figure 2. (a) Ecosystem respiration and (b) its components. EC and BM represent eddy covariance and biometric method derived ecosystem respiration; Leaf, Woody, Litter, Root, SOM, and CWD represent respiration carbon dioxide efflux from leaf, wood, fine litter, root, soil organic matter, and coarse woody debris, respectively.

regression (NLR) [*Falge et al.*, 2001]. The NLR method was used for gap-filling in our site.

[38] 9. The underestimation of NEE at nighttime is mainly due to insufficient turbulent exchange. Friction velocity ($u*$) is a good indicator of turbulent intensity. So we expected the NEE at nighttime would increase with $u*$, and would be saturated at a certain point ($u*$ threshold). Nighttime NEE under conditions with $u*$ larger than $u*$ threshold should have no underestimation. The $u*$ and nighttime NEE were plotted and the threshold $u*$ was selected based on this plot. In our site, a threshold $u*$ of 0.2 m s^{-1} was selected.

2.8. Ecosystem Production

[39] The equations to calculate ecosystem production based on biometric method are as follows [*Schulze et al.*, 2006; *Fang et al.*, 2007]:

$$GPP = B_{in} + L + R_a, \qquad (11)$$

$$NPP = B_{in} + L, \qquad (12)$$

$$NEP = B_{in} + L - R_h, \qquad (13)$$

where GPP is gross primary production, B_{in} is biomass increment, L is total ecosystem litterfall production, R_a is ecosystem autotrophic respiration, and R_h is ecosystem heterotrophic respiration.

[40] To estimate the gross ecosystem carbon exchange (GEE(-GPP)), we estimated the daytime ecosystem respiration (RE$_{day}$) based on the relationship between nighttime ecosystem respiration (RE$_{night}$) and soil temperature [*Reichstein et al.*, 2005; *Lloyd and Taylor*, 1994]. Total ecosystem respiration (RE) was defined as

$$RE = RE_{night} + RE_{day} \qquad (14)$$

[41] GEE were calculated according to the equation:

$$GEE = NEE - RE. \qquad (15)$$

[42] The EC-based NEE and GEE was equal to BM-based NEP and GPP but with an opposite sign.

3. Results

3.1. Ecosystem Respiration

[43] Our estimate of ecosystem respiration from biometric methods was less than our estimate from eddy covariance method (Figure 2a). Significant interannual variation of R_e was observed by both methods. The highest R_e in 2003 was 26.20 Mg C ha^{-1} yr^{-1} and 24.96 Mg C ha^{-1} yr^{-1} using EC and BM methods, while the lowest R_e in 2005 was 23.79 Mg C ha^{-1} yr^{-1} and 20.50 Mg C ha^{-1} yr^{-1} using EC and BM methods. The weight and dynamics of each ecosystem respiration component is shown (Figure 2b). Autotrophic respiration (R_a) was larger than heterotrophic respiration (R_h). Leaf respiration (R_{leaf}) was largest among all autotrophic respiration components with a 4 year average of 9.55 Mg C ha^{-1} yr^{-1}. The total aboveground autotrophic respiration (12.89 Mg C ha^{-1} yr^{-1}) was higher than total belowground autotrophic respiration (4.32 Mg C ha^{-1} yr^{-1}). Litter respiration (R_L) was the most variable component in heterotrophic respiration. Significant inter-annual variation of R_L was also the main contributor to interannual variation of R_h.

3.2. Ecosystem Production

[44] Ecosystem GPP in our site was investigated using EC and BM methods simultaneously (Figure 3a). The EC-based GPP (4 year mean value) was slightly lower than BM-based GPP. The highest GPP in 2003 was 27.48 Mg C ha^{-1} yr^{-1} and 27.42 Mg C ha^{-1} yr^{-1} using EC and BM methods, while the lowest R_e in 2005 was 23.97 Mg C ha^{-1} yr^{-1} and 24.79 Mg C ha^{-1} yr^{-1} using EC and BM methods, respectively. NPP and its components (ΔB and L) in our site are shown in Figure 3b. A nearly constant NPP was obtained by the sum of large varied biomass increments and litter production. For a primary forest, this is a "surprising result" to some extent [*Jarvis et al.*, 2001]. However, this result was confirmed and explained by further information from our site. NEP, both directly measured by the EC system and indirectly inferred from NPP and R_h, is shown in Figure 4. BM-based sink
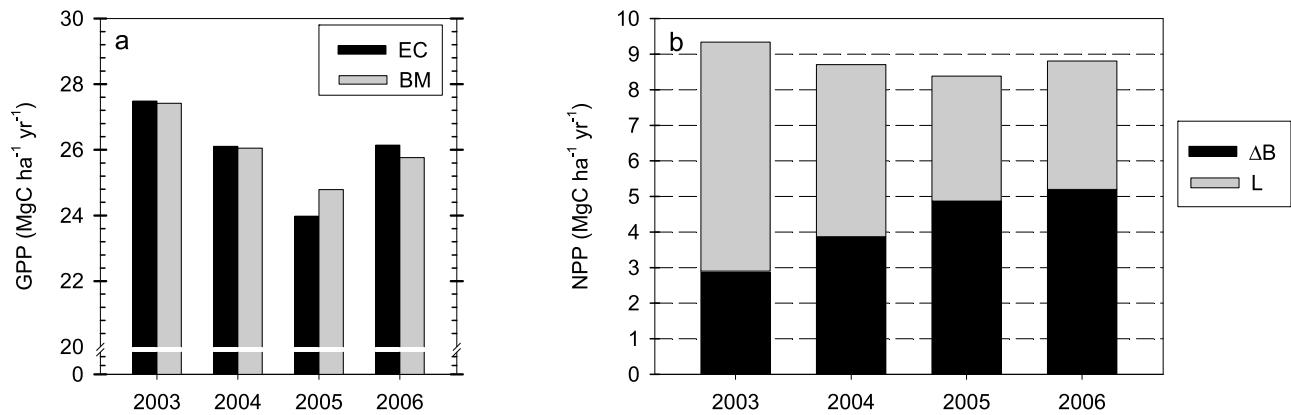
Figure 3. (a) Gross primary production (GPP) and (b) net primary production (NPP) components. EC and BM represent eddy covariance and biometric method derived GPP; ΔB and L are biomass increment and litter production, and NPP is the sum of ΔB and L.

strength NEP was larger than EC-based NEP. The NEP detected by BM and EC methods shows no convergence (neither in magnitude nor temporal trend) during our investigation. The smallest sink observed by EC in 2005 was a large sink as estimated by BM. NEP was a slightly difference between the large photosynthetic carbon uptake and respiratory carbon release in primary tropical rain forests. Although we observed similar temporal trends in GPP and R_e by EC and BM methods, the sensible difference (NEP) did not following the same trend through time.

3.3. Ecosystem Carbon Budget

[45] The biometric-based ecosystem carbon budget of our site is shown in Figure 5. Carbon density of biomass, necromass, and soil organic matter were 147.47 Mg C ha^{-1} yr^{-1}, 10.53 Mg C ha^{-1} yr^{-1} and 81.85 Mg C ha^{-1} yr^{-1}, respectively. Flux was defined as the transfer rate of carbon between carbon pools. The total ecosystem-atmosphere exchange, also termed GPP, was 26.01 Mg C ha^{-1} yr^{-1}. Of the GPP, approximately 66% was respired through R_{leaf} (9.55 Mg C ha^{-1} yr^{-1}), (R_{woody}) (3.34 Mg C ha^{-1} yr^{-1}), and root respiration (R_{root}) (4.31 Mg C ha^{-1} yr^{-1}); the remaining GPP is termed NPP (8.80 Mg C ha^{-1} yr^{-1}). This carbon is fixed into plant structure biomass, before eventually being respired, in the form of litter (R_L) (2.30 Mg C ha^{-1} yr^{-1}), CWD (R_{CWD}) (0.68 Mg C ha^{-1} yr^{-1}), and soil organic matter (R_{SOM}) (2.24 Mg C ha^{-1} yr^{-1}). The internal transformation between carbon pool components includes aboveground litter production (L_{AG}) (3.92 Mg C ha^{-1} yr^{-1}), belowground litter production (L_{BG}) (0.67 Mg C ha^{-1} yr^{-1}), annual tree mortality (0.72 Mg C ha^{-1} yr^{-1}) and from litter to soil organic matter (T_s) (1.62 Mg C ha^{-1} yr^{-1}).

4. Discussion

4.1. Primary Tropical Rain Forest: A Carbon Sink or a Carbon Source?

[46] Four-year EC and BM data indicated that our studied forest was a carbon sink of 1.19 Mg C ha^{-1} yr^{-1} and 3.59 Mg C ha^{-1} yr^{-1}, respectively. *Luyssaert et al.* [2007] reported an average NEP value of 4.03 Mg C ha^{-1} yr^{-1}, based on compilation of 29 tropical humid evergreen forest sites. The observation of that this primary tropical forest is a carbon sink

supports many other recent studies which indicate old-growth tropical forest can continue to accumulate carbon, contrary to the longstanding view that they are carbon neutral [*Luyssaert et al.*, 2008].

[47] In contrast with the active debate on the tropical terrestrial carbon sink, the northern hemisphere high-latitude carbon sink has been confirmed by direct flux measurements [*Wofsy et al.*, 1993; *Goulden et al.*, 1996; *Barford et al.*, 2001], inventory-based carbon budgets [*Kauppi et al.*, 1992; *Dixon et al.*, 1994; *Fang et al.*, 2001], atmospheric component measurements and carbon dioxide concentration inversion [*Ciais et al.*, 1995; *Keeling et al.*, 1996; *Battle et al.*, 2000], and ecosystem modeling [*Tans et al.*, 1990]. Global warming [*Schimel*, 1995], elevation of atmospheric carbon dioxide [*Fan et al.*, 1998; *Körner et al.*, 2005], and nitrogen deposition [*Holland et al.*, 1997; *Nadelhoffer et al.*, 1999; *Magnani et al.*, 2007; *Janssens and Luyssaert*, 2009], were
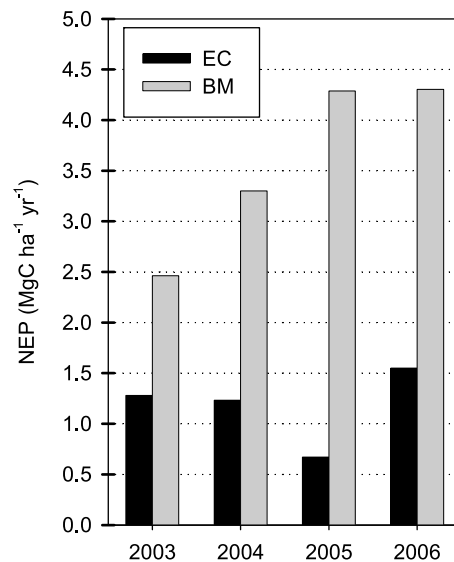

Figure 4. Comparison between eddy covariance based annual net ecosystem production (NEP) (black bar) and biometric-based NEP (gray bar) for the period 2003 through 2006.
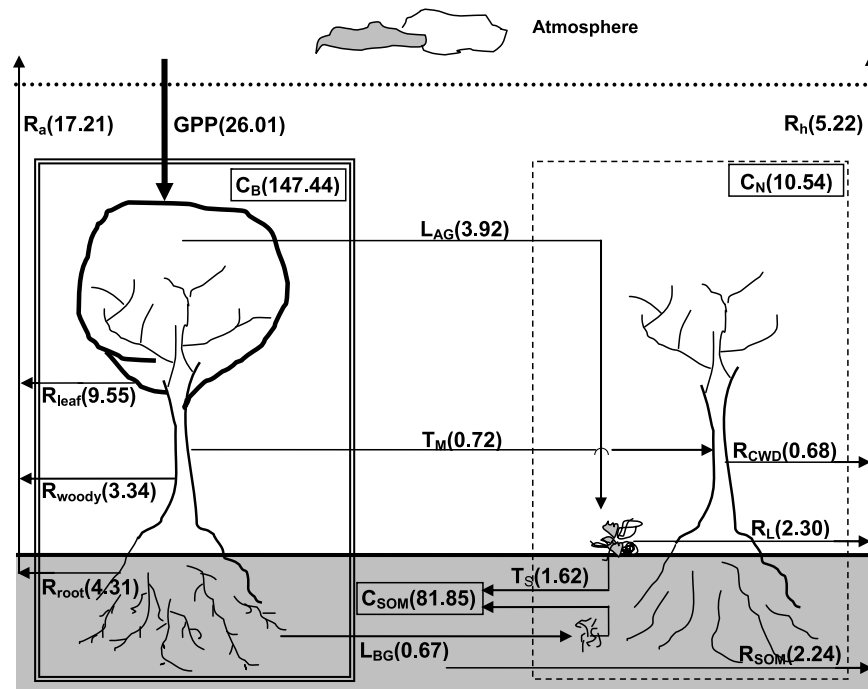
Figure 5. Site-specific carbon budget. Squares indicate carbon pools (Mg C ha^{-1}). C_B, C_{SOM}, and C_N are the biomass, soil organic matter, and necromass carbon pools, respectively. Arrows indicate carbon fluxes (Mg C ha^{-1} yr^{-1}). GPP is gross primary production, L_{AG} is aboveground fine litter production, L_{BG} is belowground fine litter production, T_M is annual tree mortality, and T_S is transfer of carbon from litter to soil. R_a, R_h, R_{leaf}, R_{woody}, R_{root}, R_L, R_{SOM}, and R_{CWD} are total ecosystem autotrophic respiration, total ecosystem heterotrophic respiration, leaf respiration, wood respiration, root respiration, fine litter respiration, soil organic matter respiration, and coarse woody debris respiration, respectively. The numbers in parentheses are the site-specific estimates of pools and fluxes.

treated as the three primary factors that shape the terrestrial carbon sink. The difference between tropical and high-latitude regions is that tropical regions are not nitrogen limited, as phosphorus leaches quickly due to a high turnover rate, while temperate regions are nitrogen limited [*Aber et al.*, 1998]. The carbon sink in primary tropical rain forests needs further investigation.

4.2. Convergence of Meteorological-Based NEE and BM-Based NEP

[48] BM- and EC-based NEP were not convergent at our study during 2003–2006 (Figure 4). Four reasons may account for this. First, the advection flux cannot be neglected in NEP estimation at this site. Advection experiments in relatively homogenous terrain and forest cover indicate that nighttime advection has a pronounced effect on carbon balance as estimated by meteorological methods [*Mammarella et al.*, 2007]. At the Tumbarumba station, horizontal and vertical advection were significant under stable atmospheric conditions [*Leuning et al.*, 2008]. Located in a calm zone with complex terrain, the advection flux may play a large role in NEP estimation in our site. Second, the traditional fixed friction velocity ($u*$) threshold (0.2 m s^{-1}) applied in this study to avoid nighttime underestimation of ecosystem respiration was invalid [*Valentini et al.*, 2000]. At our site, a threshold $u*$ of 0.2 m s^{-1} removed most of the nighttime data and the remaining small fraction of nighttime data were extrapolated (Figure 6a). We make a comparison between

NEP estimated without $u*$ threshold and the maximum possible $u*$ threshold of 0.2 m s^{-1} (Figure 6b). NEP estimated without a $u*$ filter was in the same range of BM-based NEP estimates. Third, the eddy footprint and inventory plot were not identical. Tropical seasonal rain forest only exists at the valley bottom near the stream [*Zhu*, 2006]. With rising elevation, tropical seasonal rain forest was replaced by subtropical evergreen broadleaf forest [*Wu*, 1980]. Using the Flux Source Area Model (FSAM) [*Schmid*, 2002], the source area of our flux tower under unstable conditions was estimated. The source area is smallest under unstable conditions. Even under these conditions, the source area of eddy flux is larger than our inventory plot. It is therefore unavoidable that our eddy flux data are influenced by the nearby subtropical evergreen broadleaf forest. Fourth, EC-based NEE is a measure of immediate carbon exchange, while BM-based NEP was estimated from tree growth. There is a time lag between photosynthetic carbon uptake and tree growth, as photosynthetically assimilated carbon is incorporated into carbohydrate compounds rather than being used immediately for tree growth. For example, the response of stomata to soil moisture could be detected by eddy flux, but defoliation caused by a water deficit may take much longer. The lag effect should be reduced after 4 years in this undisturbed forest ecosystem. The lag effect was diminished and BM-based NEP converged with EC-based NEE after 8 years in a temperate forest [*Barford et al.*, 2001]. However, the observed data showed that our site experienced a severe
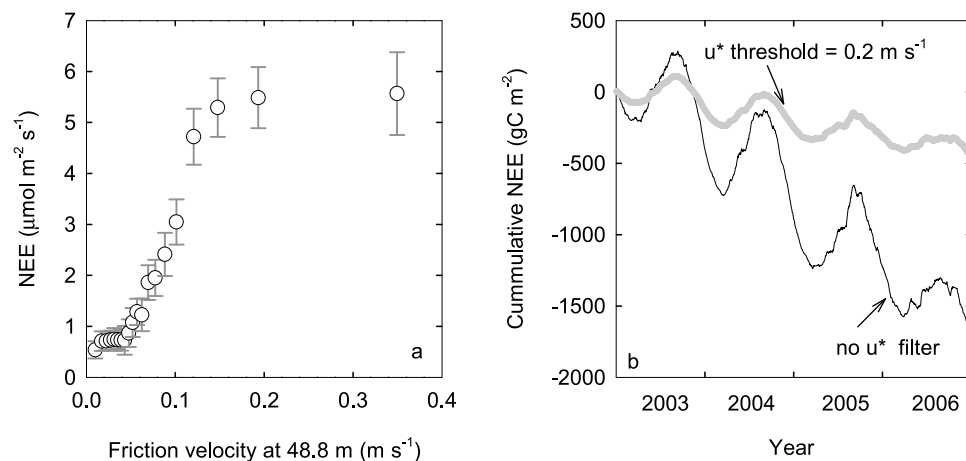
Figure 6. Effect of u^* filtering on net ecosystem carbon exchange. (a) The relationship between nighttime net ecosystem carbon exchange (NEE) and friction velocity (u^*) to determine u^* threshold in 2005. All data (n = 7624) were first sorted ascending according to u^* and then divided into 20 segments; u^* was the median of each segment, and NEE is the average value (error bars indicate standard error) of each segment. (b) Cumulative NEE under different u^* filtering. Grey line indicates the threshold of 0.2 m s^{-1} was used, and black line refers to no u^* filtering.

rainfall shortage (Figure 7a) and that drought may have contributed to dramatic interannual variation of aboveground litterfall (Figure 7b) during the investigation [*Bonal et al.*, 2008]. This disturbance will affect convergence of these two methods.

4.3. Contribution of Each Carbon Pool Component to the NEP

[49] The carbon input, output, and net budget of each carbon pool component in our site is shown in Figure 8. Biomass accumulates carbon at an average rate of 3.49 Mg C ha^{-1} yr^{-1} (Figure 8a), which was mainly contributed by the biomass increment. The 4 year biomass increment obtained in this study (4.21 Mg C ha^{-1} yr^{-1}) was smaller than that reported before for this permanent plot (5.85 Mg C ha^{-1} yr^{-1}) [*Zheng et al.*, 1999; 2000], in Hainan Island, China (4.80 Mg C ha^{-1} yr^{-1}) [*Li et al.*, 1998], and in Porce, Colombia (6.19 Mg C ha^{-1} yr^{-1}) [*Sierra et al.*, 2007], but larger than that in Khao Chong, Thailand (1.64 Mg C ha^{-1} yr^{-1}) [*Kira and Shidei*, 1967], Pasoh, Malaysia (1.35 Mg C ha^{-1} yr^{-1}) [*Kira et al.*, 1967], and Tapajós, Brazil (3.18 Mg C ha^{-1} yr^{-1}) [*Rice et al.*, 2004]. It was also slightly higher than the average value reported for all tropical forests over the world [*Clark et al.*, 2001b]. To determine further information on the cause of this large biomass increment, we analyzed each DBH class contribution to the total biomass increment. A histogram of the distribution of DBH classes is presented in Figure 9a. Most of the trees (68.24%) in our site had a DBH smaller than 5 cm. The number of trees in each DBH class decreased with increasing DBH. This is a typical for natural forests [*De Liocourt*, 1898], similar to the tropical Dipterocarpaceae forest in Sebulu, Indonesia [*Sukristijono et al.*, 1990], but different from that found in an 18 year old cypress plantation in Nagoya, Japan [*Akio and Hozumi*, 1983]. The DBH increment was divided into 36 classes according to the relative frequency of DBH. The finding that DBH increment increased with increasing DBH fitted well with a two-

parameter exponential equation (Figure 9b). It was surprising that large trees had such a fast growth rate in this old-growth tropical seasonal rain forest, as the traditional view is that large old-growth forest trees have slow or no growth. Actively growing old large trees were also observed in Europe due to silvicultural treatment [*Perrin*, 1954] and uneven-aged stand structure [*Susmel*, 1980]. Two implications can be derived from the above analysis. First, the low growth rate of small trees may be induced by their low light resources in this community [*Dou et al.*, 2005]. Second, this stand was not as old as we had expected. Analysis and comparison of community properties with other rain forests around the world showed that stem density (DBH ≥ 10 cm) in our site was dramatically lower, with 386 trees ha^{-1}, than in the same type of primary tropical rain forest in Tapajós, Brazil, 470 trees ha^{-1} (DBH ≥ 10 cm) [*Rice et al.*, 2004]; Sarawak, Malaysia, 778 trees ha^{-1} [*Proctor et al.*, 1983]; Pasoh, Malaysia, 530 trees ha^{-1}; Queensland, Australia, 975 trees ha^{-1}; Mishana, Peru, 841 trees ha^{-1}; and San Carlos, Venezuela, 744 trees ha^{-1} [*Phillips et al.*, 1994]. The relatively low density of tree stems may enhance the resource availability and reduce inner-species and interspecies competition for each individual. Therefore, low stem density trees will have fast growth rates. Lower stem density (284 trees ha^{-1}, DBH ≥ 10 cm), coinciding with higher biomass increment (4.80 Mg C ha^{-1} yr^{-1}), was also observed in a tropical mountain rain forest, Hainan Island, China [*Li et al.*, 1997, 1998]. Biomass increment was also categorized into 36 classes and a strong logistic relationship exists between DBH and biomass increment (Figure 9c). Trees with DBH ≥ 10 cm account for 86.70% of the biomass increment, although they only constitute 13.84% of individuals. Large trees (DBH ≥ 10) are the main contributors to biomass increment and play an important role in ecosystem carbon balance [*Clark and Clark*, 1996].

[50] Both C_N and C_{SOM} represent small net carbon accumulation rates near to zero (Figures 8b and 8c). The net
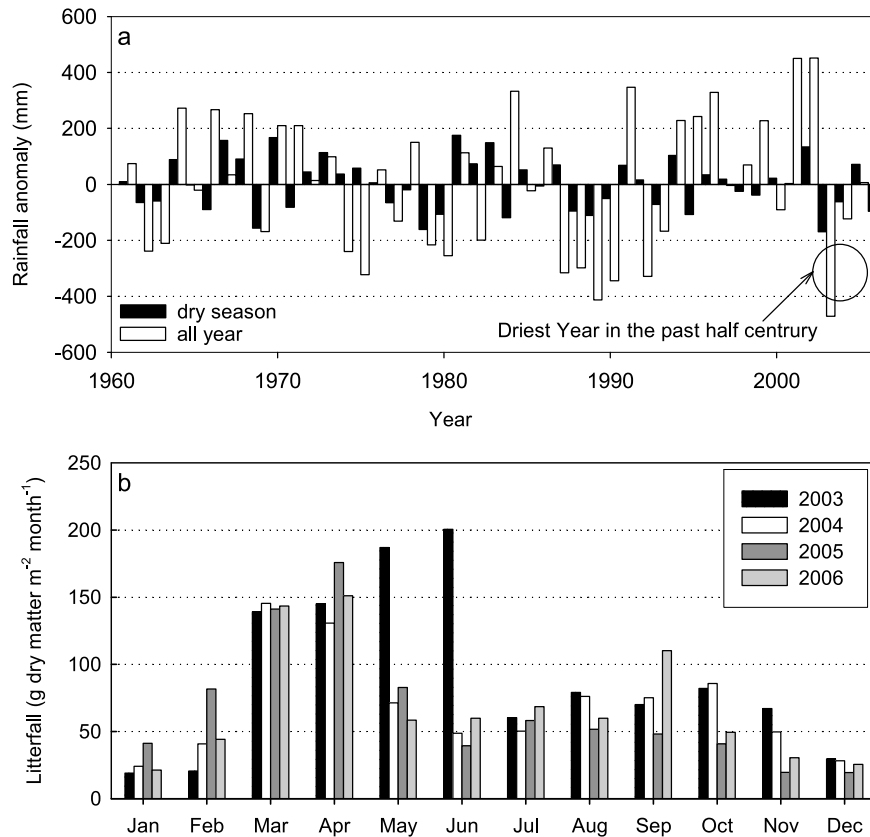
Figure 7. (a) Rainfall anomaly in recent years (1960–2006) and (b) monthly variation of aboveground litterfall production in our studied site. Rainfall data was collected from an ecological station 5 km from our permanent plot. The black bar shows dry season only; the white bar indicates rainfall anomaly in a year. In 2003, the lowest rainfall in the past 46 years was observed.

carbon balance result for C_N was consistent with the necromass carbon density inventory, and both indicate that tree mortality was not obviously enhanced during the investigation period. Disturbance-enhanced tree mortality and carbon losses were not observed in this study, compared with studies in the Amazon [*Saleska et al.*, 2003; *Rice et al.*, 2004] and Columbia [*Sierra et al.*, 2007]. Soil organic matter did accumulate carbon in our site, but at a very small rate, far less than that observed in a subtropical evergreen broadleaf forest (0.61 Mg C ha^{-1} yr^{-1}) in southern China [*Zhou et al.*, 2006].

4.4. Carbon Allocation and Carbon Using Efficiency

[51] As we can accurately measure and model GPP and the annual NPP, allocation of carbon to belowground plant structures is one of the most important, yet least well quantified, fluxes of carbon in terrestrial ecosystems. *Raich and Nadelhoffer* [1989] suggested that total belowground carbon allocation (TBCA) could be estimated from the difference between annual rates of soil carbon efflux (F_{soil}) and L_{AG}. For the near steady state, based on the conservation of mass, TBCA can be expressed as

$$\text{TBCA} = F_{soil} - L_{AG}. \qquad (16)$$

[52] In a literature review of mature forests worldwide, the same authors give an empirical equation between F_{soil} and L_{AG} to estimate TBCA,

$$F_{soil} = 2.92L_{AG} + 130, \qquad (17)$$

where both expressed as grams of carbon per square meter per year. *Davidson et al.* [2002] confirmed this method and provided another empirical equation,

$$F_{soil} = 2.80L_{AG} + 287. \qquad (18)$$

[53] Using the 4 year data from our site, we derived an empirical site-specific equation (Figure 10a),

$$F_{soil} = 1.72L_{AG} + 214. \qquad (19)$$

[54] There are two implications on Figure 10a and equation (19). First, the measurement of L_{AG} and F_{soil} were independent, therefore close linear relationship between annual L_{AG} and F_{soil} support our methodology. Second, the equation (19) was only tested and derived during our study, including drought (Figure 7a). The use of a general equation with fixed parameters was not supported by our findings. During our investigation interval, equation (19) suggests that
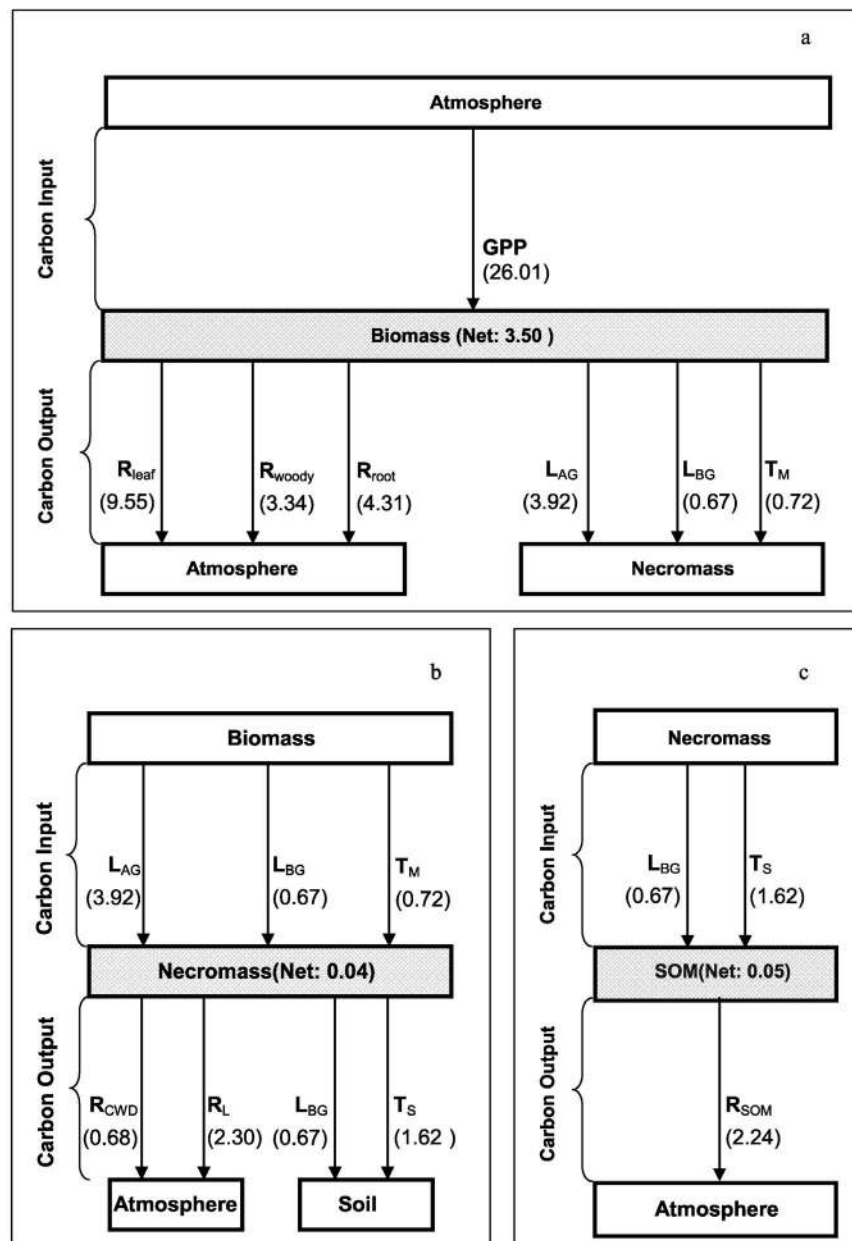
Figure 8. Carbon budget of each carbon pool component: (a) biomass carbon pool, (b) necromass carbon pool, and (c) soil organic matter carbon pool Arrows represent carbon flux (Mg C ha^{-1} yr^{-1}) with values in parentheses. The carbon input minus carbon output is the net carbon accumulation of each component.

the F_{soil} value is roughly twice L_{AG}, which further implies that TBCA roughly equals L_{AG} in our studied site. This was inconsistent with the above equations, which suggested F_{soil} equals L_{AG} [*Raich and Nadelhoffer*, 1989; *Davidson et al.*, 2002]. The *Raich and Nadelhoffer* [1989] and *Davidson et al.* [2002] methods are appropriate for steady state conditions.

[55] Annual carbon balance was divided into five components and we estimated GPP as the sum of those five. Figure 10b shows the carbon allocation pattern of our site during the investigation period. Compared with the carbon allocation pattern, based on review of 29 studies [*Litton et al.*, 2007], the site-specific carbon allocation pattern here was out of that range. Leaf respiration was the largest component in

GPP and appeared the most disproportionate in the ecosystem carbon allocation pattern. Estimation of stand-level leaf respiration was difficult for several reasons. The first issue was the effect of light on leaf respiration when measurements were carried out during daytime. There is growing evidence that leaf respiration values are lower in the light than in the dark due to light inhibition [*Graham*, 1980; *Atkin et al.*, 1998; *Chambers et al.*, 2004]. This will lead to underestimation of leaf respiration if measurements were carried out in the daytime [*Chambers et al.*, 2004; *Malhi et al.*, 2009]. However, the postillumination carbon dioxide burst and light-enhanced dark respiration will potentially rectify this underestimation [*Atkin et al.*, 2000; *Chambers et al.*, 2004]. In our site, we make a comparison between the leaf respiration
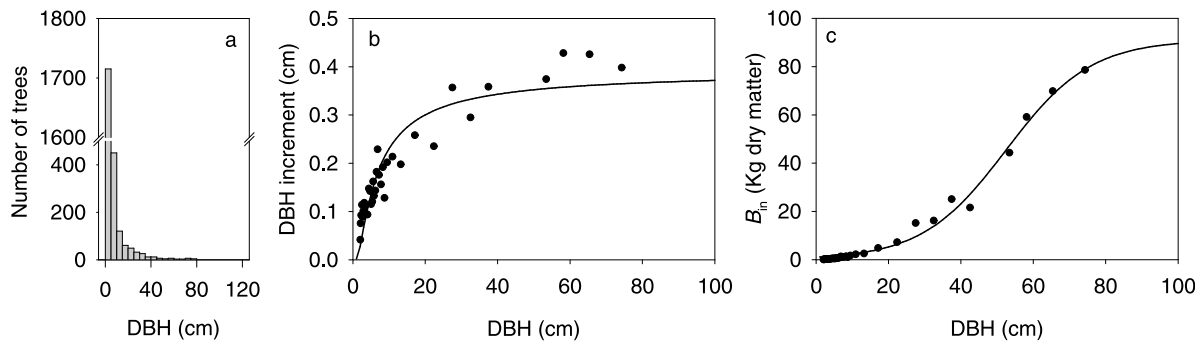
Figure 9. Contribution of each DBH class to ecosystem biomass increment. (a) The frequency distribution of DBH. (b) The relationship between DBH and DBH increment fitted by a exponential equation: $y = 0.39181 \cdot \exp(\frac{-5.3268}{x})$, $r^2 = 0.86566$. (c) The relationship between DBH and biomass increment fitted by the logistic equation: $y = \frac{91.076}{1 + 90.690 \cdot \exp(-0.00094579 \cdot 91.076 \cdot x)}$, $r^2 = 0.99101$.

rate measured during the daytime and the photosynthesis-light-response curve derived from the dark respiration rate [*Song et al.*, 2006, 2008]. The result shows that underestimation of leaf respiration under light conditions is negligible and correction for underestimation [*Lloyd et al.*, 2009] is not necessary. The second issue is spatial heterogeneity of leaf respiration. Leaf position (such as height, sun/shade, exposure) and leaf traits (such as nitrogen content, specific leaf area) can affect leaf respiration significantly. *Yoda* [1983] reported that leaf samples taken from different height levels showed different respiration rates even when they were from the same trees. Leaf respiration tended to relate to leaf nitrogen content as measured in two tropical rain forests [*Meir*, 1996]. It is difficult to take the entire spectrum of leaf economics into account when scaling leaf respiration. We

assume that leaf functional traits are related to tree height [*Yoda*, 1983], and therefore, only tree height was taken into account for spatial upscaling here. The third issue is the chosen scaling index. *Fang et al.* [2007] reported stand-level leaf respiration based on the assumption that the respiration flux proportional to leaf weight. The allometric-derived leaf biomass was used in upscaling; however, some uncertainties remained about this scaling scheme. Most research in this area measures leaf respiration per leaf area with an infrared gas analyzer [*Meir*, 1996; *Chambers et al.*, 2004; *Cavaleri et al.*, 2008] and the most common index for spatial upscaling is leaf area index (LAI). For broad-leaf evergreen forests, the canopy analyzer (LAI-2000, Li-Cor, Lincoln, Nebraska, USA) will give quite good estimates. Therefore, we used LAI-2000 measured LAI for upscaling in our site. In fact, our
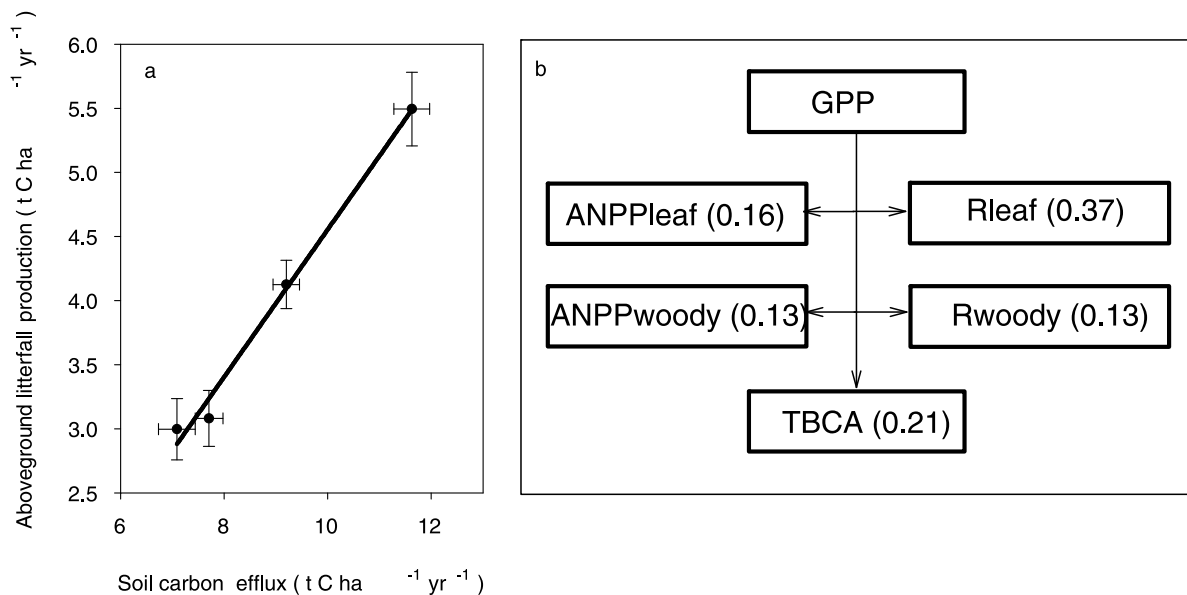

Figure 10. Ecosystem carbon allocation. (a) The linear relationship between soil carbon efflux (F_{soil}) and aboveground litter production (L_{AG}) and estimation of total belowground carbon allocation. (b) Simplified diagram depicting the major components of the carbon budget in the Xishuangbanna tropical seasonal rain forest ecosystem during 2003–2006 and the partitioning of GPP into carbon fluxes: leaf ($ANPP_{leaf}$) and wood ($ANPP_{woody}$) aboveground net primary production and leaf (R_{leaf}) and wood (R_{woody}) autotrophic respiration and total belowground carbon allocation (TBCA). Values in parentheses are percentages of GPP.

carbon allocation pattern is comparable and may be typical for tropical rain forests, which differ from temperate forests. Leaf respiration usually occupies 40–60% of total R_a [*Tadaki*, 1965; *Yoda et al.*, 1965; *Kira et al.*, 1967; *Yoda*, 1967], and values as high as 89% have been reported in tropical forests [*Müller and Nielsen*, 1965]. In an old-growth tropical rain forest with 30 Mg C ha^{-1} yr^{-1} GPP, R_{leaf} was estimated as 9.8 Mg C ha^{-1} yr^{-1} [*Chambers et al.*, 2004]. The pioneering work of *Yoda* [1967; 1983] in Southeast Asia suggested leaf respiration rates of 19.0 Mg C ha^{-1} yr^{-1} and 30.1 Mg C ha^{-1} yr^{-1} in Pasoh, Malaysia and Khao Chong, Thailand, respectively [*Yoda*, 1967; *Yoda*, 1983]. Leaf respiration was estimated to be 37% of the total ecosystem respiration in old-growth tropical rain forest in Costa Rica [*Cavaleri*, 2007].

[56] Carbon use efficiency (CUE) is defined as the ratio of NPP to total carbon fixation [*Chambers et al.*, 2004]. It is an index describing the capacity of forests to transfer carbon from the atmosphere to biomass [*Gifford*, 2003; *Chambers et al.*, 2004] and includes important parameters to compare carbon cycle variability among ecosystems [*Ryan et al.*, 1997; *Amthor*, 2000]. Based on data from seven temperate forests, a CUE of 0.47 was suggested [*Waring et al.*, 1998], and more recently, a CUE of 0.53 has been proposed [*DeLucia et al.*, 2007]. Using NPP and R_a values, we calculated CUE for leaf, woody tissue, and root as 0.33, 0.47, and 0.30, respectively. Total ecosystem CUE derived by BM and EC in our studied site was very close to that of *DeLucia et al.* [2007], and significantly lower than the widely suggested CUE of 0.47. Thus, it seems that tropical rain forests differ from the presumably constant CUE of temperate forests. Though tropical rain forests have a high capacity to assimilate carbon dioxide from the atmosphere, only a small part of this carbon is integrated into new tissue. *Chambers et al.* [2004] give two explanations for the low CUE in tropical rain forests. The respiratory demands per unit of photosynthate are simply greater in tropical rain forests [*Woodwell*, 1983], and carbon fixed by photosynthesis is respired through alternative pathways and other futile cycles as wastage respiration in nutrient-deficit tropical rain forests [*Lambers*, 1982; 1997]. *Malhi et al.* [2009] attribute the low CUE observed at tropical sites to a reflection of their old-growth status or low soil fertility, rather than their tropical climate, implying that high temperature does not drive an increase in autotrophic respiration relative to photosynthesis. The mechanisms leading to the low CUE detected in tropical rain forests require further investigation.

5. Conclusions

[57] We conducted BM- and EC-based flux measurements over 4 years (2003–2006) in a permanent ecological research plot of a primary tropical seasonal forest in southwestern China and made the following conclusions.

[58] 1. A site-specific detailed ecosystem carbon budget was established. NPP was 8.80 Mg C ha^{-1} yr^{-1}, which include biomass increment (4.21 Mg C ha^{-1} yr^{-1}) and litter production (4.59 Mg C ha^{-1} yr^{-1}). GPP derived from the BM method was 26.01 Mg C ha^{-1} yr^{-1} and ecosystem autotrophic respiration was estimated as 17.21 Mg C ha^{-1} yr^{-1}, including leaf respiration (9.55 Mg C ha^{-1} yr^{-1}), woody respiration (3.34 Mg C ha^{-1} yr^{-1}), and root respiration (4.31 Mg C ha^{-1} yr^{-1}). NEP derived from the BM method was 3.59 Mg C ha^{-1} yr^{-1} and heterotrophic respiration was estimated as 5.21 Mg C ha^{-1} yr^{-1}, including fine litter respiration (2.30 Mg C ha^{-1} yr^{-1}), soil organic matter respiration (2.24 Mg C ha^{-1} yr^{-1}), and CWD respiration (0.68 Mg C ha^{-1} yr^{-1}).

[59] 2. The studied primary tropical seasonal rain forest was a carbon sink, as evidenced by both the EC (1.19 Mg C ha^{-1} yr^{-1}) and BM method (3.59 Mg C ha^{-1} yr^{-1}).

[60] 3. The BM- and EC-based GPP were 26.01 and 25.94 Mg C ha^{-1} yr^{-1}, respectively. The BM− and EC-based ecosystem respiration were 22.42 and 24.75 Mg C ha^{-1} yr^{-1}, respectively. NEP, which shows the slightest difference between GPP and ecosystem respiration, showed no convergence by the EC and BM methods during our investigation period. In addition to the substantial methodological differences between these two methods, four factors were addressed to explain the mismatch of EC and BM estimates.

[61] 4. The contributions of changing necromass and soil organic carbon pools to NEP were negligible. The large biomass increment of 4.21 Mg C ha^{-1} yr^{-1} caused by the relatively fast growth rate of large trees (DBH ≥ 10 cm) primarily accounted for the large ecosystem carbon sink indicated by the BM method.

[62] 5. Leaf respiration was the largest component in GPP and the most disproportionate in the ecosystem carbon allocation pattern in our study. This allocation pattern was similar to that reported in other studies of primary tropical rain forest. Low CUE (0.34), a distinctive property of primary tropical rain forests was observed in our site.

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