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Respiration controls the unexpected seasonal pattern of carbon flux in an Asian tropical rain forest

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ABSTRACT

Tropical rain forests play important roles in the global carbon cycle. We report a six-year eddy covariance carbon flux campaign in a primary tropical seasonal rain forest in southwest China. An unexpected seasonal pattern of net ecosystem carbon exchange was detected, with carbon lost during the rainy season and stored in the dry season. Strong seasonality of ecosystem respiration was suggested to primarily account for this seasonal pattern. The annual net uptake of CO_2 by the forest varied from 0.98 to 2.35 metric tons of carbon per hectare between 2003 and 2008. 6-year averaged sink strength was 1.68 metric tons of carbon per hectare.

1. Introduction

A “missing sink” in global carbon cycling, first raised by Reiners (1973) and then advanced by Bolin (1977), Wong (1978), Woodwell et al. (1978) and Woodwell (1983), is uncertain, although enormous efforts have been devoted to this field in recent years. Mid- and high- latitudes of the northern terrestrial hemisphere was suggested be the main contributor to the “missing sink” by numerous reports (Tans et al., 1990; Kauppi et al., 1992; Wofsy et al., 1993; Dixon et al., 1994; Ciais et al., 1995; Goulden et al., 1996a; Keeling et al., 1996; Fan et al., 1998; Valentini et al., 2000; Fang et al., 2001). However, this perspective was recently disputed by both terrestrial and ocean observations which suggested the “missing sink” was in low-latitude land (Stephens et al., 2007).

Tropical land has most often been treated as a carbon source in the global cycle (Woodwell et al., 1978). Large land-use change induced carbon losses, combined with the nearly balance state of primary tropical rain forests suggested that tropical land was overall a carbon source. But, well protection of tropical rain forest and “sink state” of old-growth forests suggest further inquiries into roles of old-growth tropical rain forests in global carbon balance (Zhou et al., 2006; Luyssaert et al., 2008).

There are three tropical rain forest zones around the world, African, Amazonian, and Asia (Whitmore, 1975). Tropical Amazonia is the largest and best-studied rain forest. Most results from this area show old-growth tropical rain forests are carbon sinks, ranging 1–5 tC ha^{-1} yr^{-1} (Fan et al., 1990; Grace et al., 1995; Malhi et al., 1998; Loescher et al., 2003; Vourlitis et al., 2004; Hutyra et al., 2007). In tropical Africa, carbon storage of intact tropical forest has increased over the past 40 years (Lewis et al., 2009). For tropical Asia, an even larger carbon sink of 5–7 tC ha^{-1} yr^{-1} has been suggested (Kosugi et al., 2008; Yamamoto et al., 2005a; Yamamoto et al., 2005b).

Seasonal rain forest is one type of tropical rain forest found at upper limits of latitude and altitude in the Asian tropics (Zhu, 2004, 2006). This area includes northern Thailand, Laos, Vietnam, Cambodia, and Xishuangbanna (in southern Yunnan Province of China). We chose to investigate the net carbon balance of forest in this area.

In this study, we report six years (2003–2008) of eddy covariance carbon flux measurements in a tropical seasonal rain forest in Xishuangbanna, southwest China. Our primary objective was to investigate: (1) if the forest was a carbon sink or source, (2) the seasonal and inter-annual variation of the ecosystem carbon fluxes.

2. Methods

2.1. Site description

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 mass

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movements alternating during the year (Zhang, 1966). Between May and October, the tropical southern monsoon from the Indian Ocean delivers some 80% of the annual rainfall, while the dry and cold air of the southern edges of the subtropical jet streams dominates the climate from November and April (Cao et al., 1996). In this monsoonal climate, there are three distinct seasons: humid hot rainy season (May–October), foggy cool dry season (November–February), and hot dry season (March–April).

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 (Fig. 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). A permanent ecological research plot was established in the Reserve in 1994 by the Xishuangbanna Forest Ecological Research Station, and is also part of the Chinese Ecosystem Research Network. The plot is located on a flat area approximately 40 m wide between two hills extending from east to west. The slopes to the south and north of the site are about 20°. The lateritic soil is derived from siliceous rocks, such as granite and gneiss, with a pH value from 4.5 to 5.5. A stream (about 1 m wide) dissects the site and the length of the valley is about 2 km. This valley is a typical site for tropical seasonal rain forest (Cao et al., 2006). This tropical rain forest differs from tropical Asian lowland rain forest because some tree species are deciduous. The richness of species is lower than that of Malaysian rain forests, higher than Australian and African rain forests, and similar to tropical forests on Barro Colorado Island, Panama (Cao et al., 2006; Zhu, 2006).

Climate records collected over 40 years at a weather station (560 m above sea level), 5 km southeast of the study site, show a mean annual air temperature of 21.7 °C, with maximum monthly temperature of 25.7 °C in June and minimum of 15.9 °C in January. The mean annual rainfall is 1487 mm, of which 1294 mm (87%) occurs in the rainy season, with 193 mm (13%) in the dry season. Class A pan evaporation varies between 1000 and 1200 mm y^{-1}. The mean annual wind speed is 0.5 m s^{-1} (Liu et al., 2005).

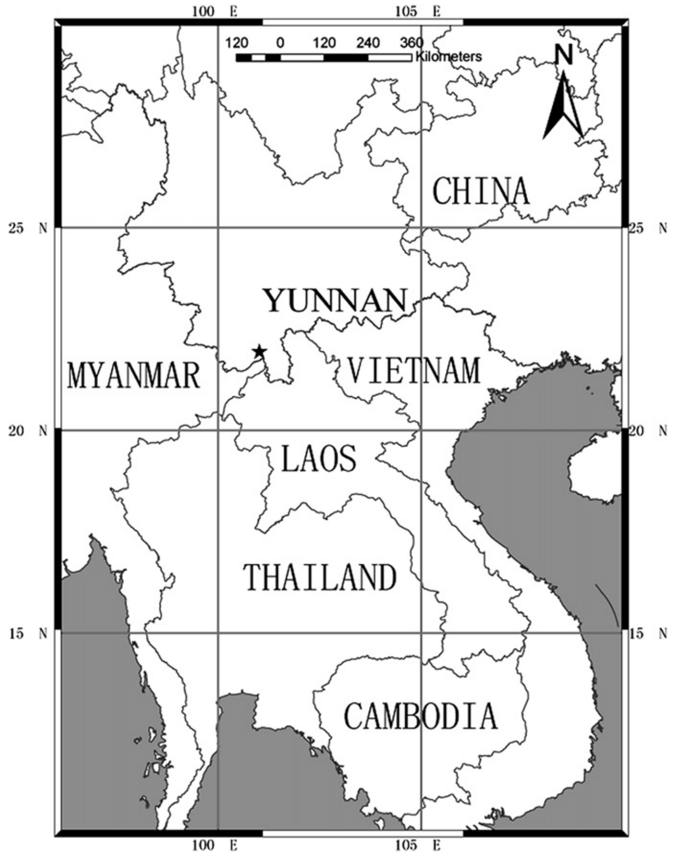

Fig. 1. Geographic location of our study site (indicated by a star).

This permanent ecological research plot is in the center of the nature reserve; it shows no signs of recent anthropogenic disturbance other than hunting trails. With large logs, many epiphytes, uneven size distribution of plants, and emergent trees, this tropical seasonal rain forest can be considered primary, or “old-growth” (Tan et al., 2010).

2.2. Instrumentation and measurements

A 70-m tower was established at the center of the 1 ha permanent plot. An eddy covariance system with 3-D sonic anemometer (Model CSAT-S, Campbell Scientific Inc., Logan, UT, USA) and an infrared open-path gas analyzer (Model LI-7500, Li-Cor Inc., Lincoln, NE, USA), was mounted at 48.8 m on the tower. Seven levels of air temperature, relative humidity (Model HMP45C, Campbell Scientific Inc.), photosynthetically active radiation (Model LQS7010-SUN, APOGEE, Logan, UT, USA) and wind speed (Model A100R, Vector Instrument, RHYL, U.K.) sensors were mounted lower on the tower to obtain canopy profiles. Solar radiation and net radiation was measured with radiometers (Model CM11 and Model CNR-1, Kipp & Zonnen, Delft, Netherlands). Precipitation was recorded by a rain gauge (Model 52203, RM Young, Traverse City, MI, USA) at the top of the tower. Soil temperature and moisture were measured with thermocouples (Model 105T, Campbell Scientific Inc.) and time-delay reflectometers (Model CS616, Campbell Scientific Inc.). Routine meteorological data were recorded (Model CR10X & CR23X dataloggers, Campbell Scienctific Inc.) at 30-min intervals. The eddy flux data were recorded at frequency of 10 Hz (Model CR5000 datalogger, Campbell Scientific Inc.). The leaf area index was measured by a canopy analyzer (Model Li-2000, Li-Cor Inc.).

2.3. Calculations

Vapor pressure deficit was calculated from relative humidity and air temperature. The empirical equation used to obtain saturated vapor pressure was from Jones (1992),

$$e_s = 0.61078\exp\left(\frac{17.269T}{T+237.30}\right) \tag{1}$$

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). F_c was calculated as the mean covariance between fluctuations in vertical wind velocity (ω) and the density of CO_2 (c) (Baldocchi et al., 1988),

$$F = \rho\overline{\omega'c'} \tag{2}$$

where ρ is air density, primes denote deviations from the mean, and the over-bar signifies a time average (30-min averaging period). F_s is calculated as (Hollinger et al., 1994),

$$\delta Fs = \frac{\delta c}{\delta t}\cdot z_r \tag{3}$$

where δc is variation in 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,

$$\mathrm{NEE} = F_c + F_s \tag{4}$$

Negative values of NEE indicate CO_2 flux from air into the forest, and *vice versa*.

2.4. Flux data quality assessment and quality control (QA/QC)

There are several difficulties related eddy covariance based carbon flux measurements. Eddy covariance systems attenuate the true turbulent signals at sufficiently high and low frequencies (Moore, 1986). Physical size of instruments, instrument separation distances, and the inherent time response of instruments can lead to information loss (Goulden et al., 1997; Massman and Lee, 2002). Terrain irregularity can induce drainage flow events under stable condition (Tóta et al., 2008; Campos et al., 2009). Shear-generated gravity waves are a common motion type in the canopy at nighttime (Mahrt, 1982; Fitzjarrald and Moore, 1990; Massman and Lee, 2002). Large vertical gradients in CO_2 concentration exist near the ground due to the lack of vigorous turbulent mixing during nighttime can lead to significant advection term (Sun et al., 1998; Mahrt et al., 2001). Canopy heterogeneity may cause local thermal circulations driven by different surface radiative cooling (Lee, 1998; Campos et al., 2009). Perturbations in net radiation induced by cloud cover variations can alter the canonical form of turbulence, inducing nonstationarity (Cava et al., 2004; Campos et al., 2009). Moreover, there are uncertainties regarding the turbulent field and how to rotate coordinate system (Massman and Lee, 2002; Sun et al., 2007). Though continuous data collection was carried out, the average data coverage during a year is only 65% due to system failure or data rejection (Falge et al., 2001). A standard gap-filling procedure was necessary for inter-site and inter-annual carbon flux comparison, but it is still not available. The eddy covariance footprint expands rapidly as air becomes increasingly stratified (Schimid, 1994) and can extend beyond the vegetation type under investigation. The air stability over a forest often exceeds the range over which the Monin–Obukhov similarity are valid (Massman and Lee, 2002). Thus, quality assessment and quality control of eddy flux data are necessary for sites with complex canopy structure and terrain (Foken, 2008). Ten steps of QA/AC were carried out to obtain annual and seasonally summed ecosystem carbon fluxes:

01) Ecosystem energy closure test. The first law of thermodynamics stipulates that energy can only be transferred from one form to another. The energy balance closure for an ecosystem can be written as:

$$\mathrm{LE} + H = R_n - G - S - Q \tag{5}$$

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, all expressed in energy units. As S and Q were always treated as invariant, so in plotting LE + H against R_n–G, we expected the slope of the regression to be near one and the line to intercept the origin. R_n and G were measured directly by net radiometer and duplicate soil heat flux plates, respectively; LE and H were measured by eddy covariance system (CSAT-3, and Li-7500). The result in our site shows that LE + H represent near 70% of the R_n–G in the forest.

02) Turbulent spectra and cospectra testing. According to Kolmogorov's law, the spectral density can be plotted as a function of frequency:

$$nS(n) = \alpha\varepsilon^{2/3}n^{-2/3} \tag{6}$$

where α is the Kolmogorov constant and ε is the dissipation rate. Before spectra analysis, time series were linearly detrended and means removed. Power spectra and cospectra were calculated with Matlab software using the FFT method (Math Works Inc., Natick, MA, USA). Time series were divided into 12 equal segments. The spectra were multiplied by frequency and normalized by the variance (or covariance) of the entity. Power spectra and cospectra obeyed the −2/3 and −4/3 power law in our site.

03) Turbulence integrity test. Monin–Obukhov similarity theory suggests that the dimensionless variance can be explained as a function of stability index $(-(z-d)/L)$ with an exponent of 1/3, also called flux-variance similarity (Foken and Wichura, 1996). This flux-variance similarity is characteristic of atmospheric turbulence (Stull, 1988; Kaimal and Finnigan, 1994). In our site, flux-covariance similarity obeys the 1/3 rule with relatively high correlation coefficients.

04) Footprint assessment. We estimated the flux source area or "footprint" with the statistical source area model of Schimid (1994). Three required input variables were z_m/z_0, z_m/L, and S_v/u^*. z_m was calculated from roughness length (z_o) and zero-plane displacement (d), L was Monin–Obukhov length, S_v is variance of horizontal wind direction. We point out that the footprint analysis shows that in our site the eddy flux footprint included not only tropical seasonal rain forest, but also part of the nearby evergreen broadleaf forest, which occurred at higher elevations.

05) Exclusion of spikes. Physically impossible values were excluded before calculating averages, variances, and covariances. The limits for physical exclusion were established with TK2 software (Department of Micrometeorology, University of Bayreuth, Germany). A spike detection algorithm was applied here (Vickers and Mahrt, 1997). Any values exceeding 5.5 times standard deviation within a moving window of 10 values were excluded. In addition, turbulent fluxes outside the range [−3,3] ($\mathrm{mg\,CO_2\,m^{-2}\,s^{-1}}$) during rainfall were also excluded.

06) Averaging and detrending. It is necessary for us to choose an effective averaging time period (T) in order to obtain the turbulent fluctuation:

$$w'(t) = w(t) - \overline{w} \tag{7}$$

$$\overline{w(t)} = \overline{w} = \frac{1}{T}\int_0^T w(t)\mathrm{d}t \tag{8}$$

where $w(t)$ is a time series, over-bar means averaging, and primes indicate fluctuations. In our study, a 30 min interval was initially chosen and the effectiveness of this interval was tested (Sun et al., 2006). We used a linear detrending method, which instead of subtracting the mean from the signal in a period of 30 min we determine the line of best fit over the period and subtract that.

07) Density correction and axis rotation. In this study, three-dimensional coordinate rotation was applied to the wind vector to remove the effect of instrument tilt and irregularity of the airflow (Tanner and Thurtell, 1969). Flux data were corrected for variations in air density caused by heat and water vapor fluxes (Webb et al., 1980).

08) Nighttime flux underestimation correction. The moving point test method (MPT) was used to objectively determine the

friction velocity (u^*) threshold (Gu et al., 2005). The average u^* for the entire dataset was 0.13 m s^{-1} (Table 1).

09) Data availability. The percentage of daytime (daytime was defined with photosynthetically active radiation at least 10 μmol m^{-2} s^{-1} following Goulden et al., 1996b) data remaining spike and rainfall data exclusion was about 75% (Table 1). For nighttime, however, only about 25% of data remained after u^* threshold filtering.

10) Gap-filling. Gap-filling was necessary to obtain annual sums of carbon exchange. The most widely used methods for gap-filling are mean diurnal variation (MDV), and nonlinear regression (NLR) (Falge et al., 2001). In daytime, data was binned with windows of 10 days and the Michaelis–Menten equation was used for gap-filling. In nighttime, the regression between soil temperature and ecosystem respiration using a Lloyd–Taylor equation was very poor for a windows of 10 days. As the MDV method will introduce a considerable error in estimating annual fluxes of ecosystem respiration and NEE when data are limiting, e.g. only 25% in our site. Therefore, we accomplished nighttime data gap-filling with the NLR method and an enlarged window of one month.

More recently, several studies suggested that most appropriate average time to compute carbon flux during nighttime is less than the widely suggested 30 min (Campos et al., 2009). The nighttime carbon flux can switch sign when using too long averaging time scales in tropical rain forest (Culf, 2000). Under stable night, ecosystem carbon flux may affect by wave-like motion (Cava et al., 2004). Because friction velocity (u^*) itself is highly dependent on temporal scales, the use of u^* as the scale for correcting nocturnal carbon dioxide fluxes is not appropriate (Acevedo et al., 2009). In this study, we still use the traditional 30 min averaging time and u^* correction for convenient in inter-annul and inter-site comparison.

2.5. *Flux partitioning*

The flux term NEE was partitioned into two important components of ecosystem carbon exchange, photosynthetic carbon uptake (termed in gross ecosystem exchange, GEE) and respiratory carbon release (termed in total ecosystem respiration, RE). Day-time RE was estimated using an empirical equation including nighttime soil temperature, nighttime RE, and daytime soil temperature. Total ecosystem respiration was defined as follows:

$$RE = RE_{night} + RE_{day} \tag{9}$$

where RE_{night} and RE_{day} were night-time and day-time ecosystem respiration, respectively.

GEE were calculated according to the equation:

$$GEE = NEE - RE \tag{10}$$

Table 1
Threshold friction velocity (m s^{-1}) for low turbulence determined by the moving point test method (u^*_L), percentage of daytime data remaining after spike and rainfall data exclusion (%Day), and percentage of data remaining after nighttime u^*-threshold filtering (%Night).

Year	2003	2004	2005	2006	2007	2008
u^*_L	0.13	0.13	0.14	0.13	0.13	0.13
%Day	79%	74%	68%	73%	78%	77%
%Night	27%	25%	20%	25%	27%	26%

3. Results

Our site was dominated by the Indian summer monsoon. Although it is a tropical area, the seasonality of climate was significant (Fig. 2). Solar radiation was highest in the dry-hot sub-season (March and April). In the rainy season (May to October), solar radiation was reduced during frequent rainfall events, and, in the fog-cool sub-season (November to following February), by dense fog (Tan et al., 2010; Zhang, 1966). Net radiation varied little throughout the year. In contrast to solar radiation, reduced net radiation was observed at dry-hot sub-season. This pattern was probably caused by enhanced reflectivity due to a local phonological pattern termed “intensive leaf change” (Fig. 2d). Mean soil and canopy temperatures had significant annual variations, being higher in the rainy season than in the dry season. The annual soil and canopy temperature ranges were nearly 10 °C. Most temperatures during the fog-cool sub-season were below 18 °C. Therefore, this area was suggested be too cool to support a typical tropical rain forest (Zhu, 2006). Annual rainfall in our site is about 1490 mm. More than 86% of annual rainfall was occurred in the rainy half year (May to October), based on 40 years monitoring at a meteorological station 5 km from our site (Tan et al., 2010). So, an obvious dry season was observed. In the dry season, soil volumetric water content was usually lower than 0.2 m^3 m^{-3}. The lowest observed soil moisture; less than 0.1 m^3 m^{-3} and persisting for 8 days, was during the dry-hot sub-season of 2004. However, the soil moisture

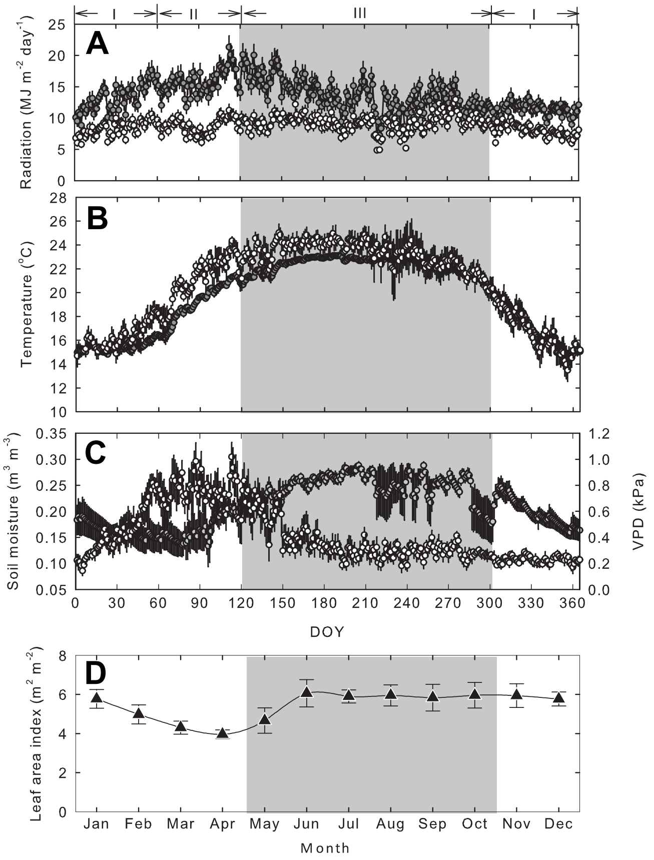

Fig. 2. Six-year mean seasonal variations of environmental factors in our study site. I, II, and III represents fog-cool sub-season, dry-hot sub-season and rainy season, respectively. Shaded area indicates the rainy season. (A) Daily summed solar radiation (dark grey circles) and net radiation (white circles); (B) Daily averaged canopy temperature (white circles) and air temperature at height of 26 m (dark grey circles); (C) Daily averaged soil water content (dark grey circles) and air vapor pressure deficit (white circles). (D) Leaf area index. The error bar represents six-year standard error.

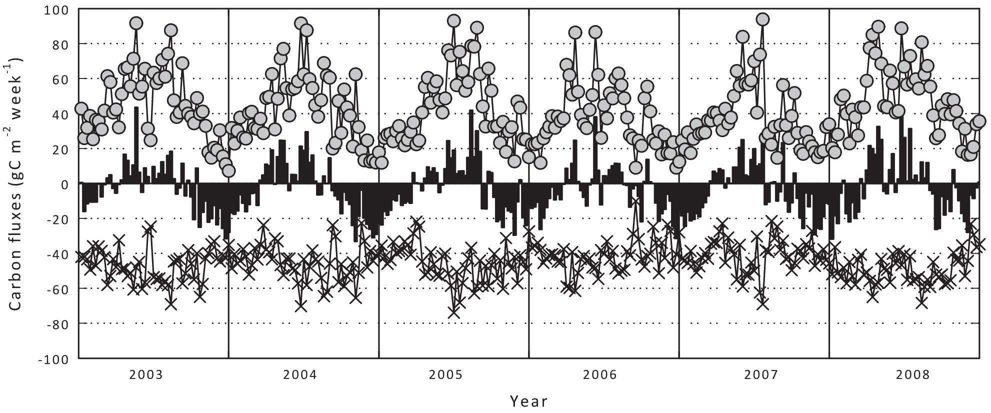

Fig. 3. Weekly binned net ecosystem CO_2 exchange (NEE) (vertical bar), ecosystem respiration (RE) (filled symbols connected by lines), and gross ecosystem CO_2 exchange (GEE) (solid line) during six years (2003–2008) at Xishuangbanna tropical seasonal rain forest.

reported by da Rocha et al. (2004) in Amazonia was never less than 0.3 m^3 m^{-3}. And hence, the tropical rain forest was once oppugned to be existed in this area with extremely low annual rainfall and strong seasonality (Zhu, 2006). High temperature and low humidity lead to high vapor pressure deficit during the dry-hot sub-season. Moisture stress (high VPD and low soil moisture) in dry-hot sub-season is a strong selective pressure on this forest ecosystem, and in dry years, we expect it to experience moderate to severe drought.

The ecosystem carbon exchange was expected to show significant seasonality, as does the climate. Weekly binned carbon balance, including gross ecosystem exchange, total ecosystem respiration and net ecosystem carbon exchanges, are shown in Fig. 3. The warm and wet rainy season provides an optimal environment for ecosystem carbon metabolism (photosynthesis and respiration). During the dry season, in contrast, these processes proceed at slower rates. The detailed description of monthly variation of net ecosystem carbon exchange is shown in Fig. 4. Distinctive carbon net sink periods (January to March, and September to December) and source periods (April to August) can be seen in the figure. Though the sink/source pattern was slightly different from the seasonal pattern (shaded areas), the rainy season was mostly a carbon source and the dry season a carbon sink. Woody increment data from tropical rain forests suggest that carbon accumulation (sink effect) will be reduced during dry seasons (Goulden et al., 2004; Miller et al., 2004). Ecosystem models (such as TEM and IBIS) indicate that ecosystem carbon sink strength will increase during rain seasons (Saleska et al., 2003). Together, these suggest that an unexpected seasonal pattern of NEE occurs at our site.

The inter-annual variation of carbon exchange in tall forests has been a challenging and little-investigated issue in ecosystem ecology (Barford et al., 2001). Table 2 shows the year-to-year variation of NEE, GEE, and RE. Our studied ecosystem was carbon sink in each year. The average carbon sink strength during 2003–2008 was −1.68 tC ha^{-1} yr^{-1}. The inter-annual variation of carbon exchange (including NEE, GEE and RE) was substantial. The largest carbon sink strength was observed in 2007, while GEE and RE in that year were moderate. The smallest carbon sink strength was observed in 2008, with the largest GEE and RE observed in that year.

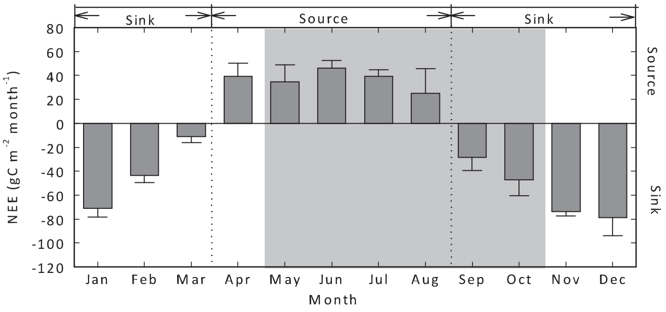

Fig. 4. Six-year averaged seasonal variation of net ecosystem CO_2 exchange (NEE). Shaded area represents the rainy season. The error bar was standard error of six years.

4. Discussion

The classical view of tropical rain forests includes little or no seasonality in phenology or production, as they primarily occur in areas with abundant rainfall and consistently warm temperature (Holdridge, 1947; Richard, 1996). In Caxiuana, an eastern Amazonian tropical rain forest, no seasonality of carbon exchange was observed (Carswell et al., 2002), but terrestrial Ecosystem Model (TEM) and Integrated Biosphere Simulator (IBIS) suggest that carbon was released in the dry season due to water limitations on photosynthetic carbon uptake (Tian et al., 1998; Botta et al., 2002). Moreover, an unexpected seasonal pattern of carbon flux, which ecosystem was a carbon sink in the dry season and a carbon source in the rainy season, was reported by several studies (Goulden et al., 2004; Hutyra et al., 2007; Saleska et al., 2003). The unexpected seasonal carbon exchange pattern was supported by remotely sensed data, indicating that the Amazonian rain forest was "green-up" in dry season (Huete et al., 2006) and in a dry year (Saleska et al., 2007). This unexpected seasonal pattern was attributed to enhanced photosynthesis in the dry season with increased insolation (less cloud cover), but not constrained by water stress. The possibility of water stress was excluded there because extensive tree roots allow continuous access to deep soil water (da Rocha et al., 2004; Nepstad et al., 1994; Oliveira et al., 2005). Deep-soil water resources can allow plants to avoid water stress in dry seasons, and even in dry years. In the Amazonian dry season, leaf

Table 2
The annual carbon flux of Xishuangbanna tropical seasonal rain forest. NEE was net ecosystem carbon exchange. *RE* is total ecosystem respiration which summed from nighttime data after *u**-friction threshold filtering. *GEE* is gross ecosystem carbon exchange. NEE, RE, and GEE units are tC ha^{-1} yr^{-1}.

Year	2003	2004	2005	2006	2007	2008
NEE	−1.47	−1.87	−1.36	−2.10	−2.35	−0.98
RE	22.95	21.95	22.39	19.41	18.92	24.81
GEE	−24.42	−23.82	−23.75	−21.51	−21.27	−25.79

flush coincides with maximum insolation, and enhanced photosynthesis was subsequently expected in this ecosystem generally free from water stress (Asner et al., 2004; Carswell et al., 2002; Keller et al., 2004; Rice et al., 2004; Saleska et al., 2003).

An unexpected seasonal pattern of carbon exchange was also observed at our site (Fig. 4). Carbon was uptake mainly in the dry season with release during the rainy season. Our site was located on the northern edge of Far East tropical rain forest region near Tropic of Cancer, with a strongly seasonal climate (Fig. 2). Here, strong seasonality of carbon exchange would be expected. However, ecosystem release of carbon during the rainy season, with abundant rainfall (more than 80%), was unexpected. So, the first question we pose is if water stress was absent from our site. Actually, ecosystem water stress was just sounding when during dry season. In Southeast Asia, affected by the monsoon background climate, a distinctive near two month long dry-hot sub-season with high temperature, high water vapor deficit, and low soil moisture occurs (Fig. 2). The local ecosystem phenology termed “intensive leaf change” suggests that water limitation can stress this ecosystem. In our site, upper-layer canopy trees shed their leaves intensively (less than 10% of leaves remain in mid-April) around the dry season (Fig. 2). This phenology was only observed in trees of tall stature. This is consistent with the hydraulic limitation hypothesis (Ryan et al., 2006). The climatic data also suggest that water stress in the dry season is unavoidable here. Annual rainfall in our site was only about 1500 mm, far less than in Amazonian rain forests. It is perhaps surprising that a relatively low rainfall can support an ecosystem with biomass and diversity similar to Amazonian forests (Cao et al., 1996; Tan et al., 2010). In addition, 86% of the annual rainfall occurs in wet season. Only about 220 mm rain falls during the dry half year. To survive in such an environment, an ecosystem adaptation of “intensive leaf change” has evolved. The second question we pose is whether leaf flushing coincides with maximum insolation during the dry season. Photosynthetically active radiation was highest in the dry-hot sub-season and early rain season (Fig. 2). Lower insolation in mid- and latter-rainy season was attributed to rain- and cloud-induced short sunshine hours. In fog-cool sub-season, a sub-season in dry season, dense and persistent fog was suggested to reduce sunshine hours (Liu et al., 2005). During the period of peak irradiance, the “intensive leaf change” occurred (Fig. 2d). Forest was not “greening-up” but “yellowing-down” in the peak irradiance stage.

As mentioned and discussed above, the mechanism, which fully explained unexpected seasonal pattern of carbon flux in Amazonian, was not available in our site. To address the cause of the unexpected seasonal pattern of carbon exchange in our forest, net ecosystem carbon exchange was partitioning into two parts, gross photosynthetic carbon uptake and total ecosystem respiratory carbon release (Fig. 3). Ecosystem photosynthesis was enhanced, not weakened in the rainy season due to adequate moisture, high leaf-area index and leaf photosynthetic capacity (Song et al., 2006). Lower photosynthesis observed in the fog-cool sub-season was attributed to lower temperature then. The annual temperature range in our site was around 10 °C. The coldest month temperature was about 13 °C. Lower temperature will suppress photosynthesis-related enzymes (Schulze et al., 2005) and reduce the ecosystem photosynthesis. In dry-hot sub-season, ecosystem was warmer but there is less leaf area, limiting photosynthesis then. Ecosystem respiration, which strongly correlated with temperature at seasonal scale, also peaked in the rainy season. Ecosystem respiration is dominated by soil efflux (Reichstein et al., 2005). Previous data from our site shows that soil respiration is primarily controlled by litterfall decomposition and fine root turnover in (Sha et al., 2005). The soil organic matter carbon pool was near equilibrium, with carbon input (predominantly from litterfall) equaling output. So, ecosystem litterfall input and decomposition dominate ecosystem respiration at seasonal and annual scales. Litterfall input peaks in the dry-hot sub-season when “intensive leaf change” takes place. The shed leaves were not immediately decomposed at a high rate as moisture is low, detritus material was desiccated and decomposition was reduced (Saleska et al., 2003). The decomposition process was accelerated by subsequent rainfall. Temperature, moisture, litterfall quality, litterfall quantity, and time were dominant ecological factors affecting litterfall decomposition (Chapin et al., 2002). The peak litterfall in the dry-hot sub-season does not persist for long, because most of the litterfall is leaf material and the turnover time for leaves in our site is only 3–4 months (Zheng et al., 2006). The litter is mostly decomposed by the later rainy season. Reduced litterfall substrate coincides with lower temperature, so a reduction of ecosystem respiration was both expected and observed in the following fog-cool sub-season (Fig. 3). This is also why high respiration temperature sensitivity (Q_{10}; the rate change under a 10 °C temperature change) of 3.72 was observed in our site. The Q_{10} contains information from litterfall accumulation from the previous sub-season.

Net ecosystem carbon exchange is the balance between gross photosynthetic carbon uptake (GEE) and total respiratory carbon release (RE). Though GEE and RE were both increasing in the rainy season, the change of RE was larger than GEE and a net carbon source was observed. In dry season, the change of RE was smaller than GEE and a net carbon sink was observed. In summary, the stronger seasonality of RE compared to GEE leads the unexpected seasonal pattern of NEE at our site.

5. Conclusions

We conducted eddy covariance flux measurement over six years (2003–2008) in a tropical seasonal rain forest in southwestern China. To obtain defensible annual carbon fluxes at our site, 10 steps of QA/QC were carried out. The 6-year average carbon sink strength of this tropical seasonal rain forest was 1.68 tC ha^{-1} yr^{-1}, varied from 0.98 to 2.35 tC ha^{-1} yr^{-1}. An unexpected seasonal pattern of net ecosystem carbon exchange was observed during these years. Carbon was lost in the rain season and gained in the dry season. Though GEE and RE have similar seasonal patterns, higher in the wet season and lower in the dry season, the seasonality of RE was stronger than that of GEE. The increased RE in the rain season exceeded that of GEE, a net carbon source was detected then, and *vice versa*. The strong seasonality of RE appears to be connected with the local phenology of “intensive leaf change”. Our study can also inform the debate over drought sensitivity of tropical forests.

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