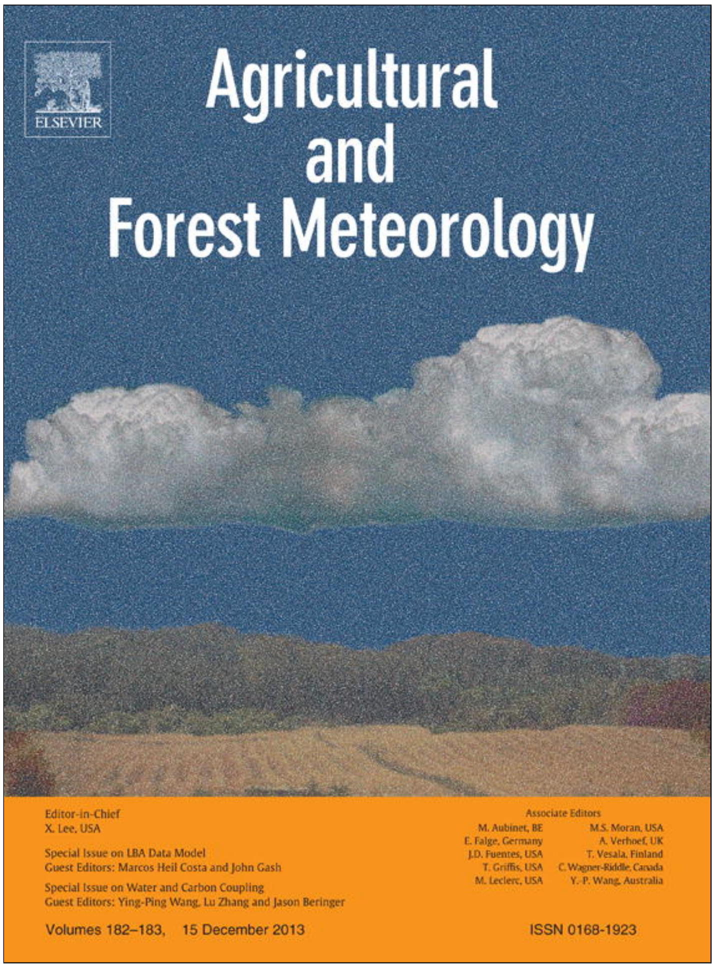
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Seasonal and inter-annual variations in net ecosystem exchange of two old-growth forests in southern China

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ABSTRACT

Old-growth forests can accumulate carbon. However, what controls the rate of net carbon accumulation in those old-growth forests is still poorly understood. Using eddy flux measurements from two old-growth evergreen broadleaf forests (subtropical forest and tropical forest) in southern China, we compared the seasonal and inter-annual variations in the carbon fluxes of those two forests and quantified the major drivers for these temporal variations. The measured flux data showed that the annual net carbon uptake of the subtropical forest was generally much larger than that for the tropical forest. The mean net ecosystem exchange (NEE) over 6 years was $-397 \pm 94\,g\,C\,m^{-2}\,yr^{-1}$ for the subtropical forest and $-166 \pm 49\,g\,C\,m^{-2}\,yr^{-1}$ for the tropical forest with different seasonal variations. The subtropical forest was a carbon sink for most months in a year, while the tropical forest was a carbon source in wet seasons (positive NEE) and a carbon sink in dry seasons (negative NEE). Both forests were stronger carbon sink in dry years, because of much larger reduction in ER than in wet years. At the seasonal scale, GPP in wet seasons was 37.1% higher than that for dry seasons in the subtropical forest, and was only 12.4% higher in the tropical forest. The amplitude of seasonal GPP variation in the tropical forest was much weaker than in the subtropical forest, but the amplitude of the seasonal variation in ER was much larger than in the subtropical forest. The seasonal variation in NEE was largely driven by the variation in monthly ER of the tropical forest, and by both seasonal variations in monthly GPP and ER of the subtropical forest. At inter-annual scale, annual NEE varied tightly with annual rainfall from year to year. Therefore annual rainfall was suggested a fundamental driver of annual carbon sequestration in the subtropical and tropical forests in southern China.

1. Introduction

Net ecosystem exchange (NEE) is a small difference between two large fluxes, gross primary production (GPP) and ecosystem respiration (ER), and the magnitude of net carbon uptake (= –NEE) is usually less than 20% of GPP or ER (Law et al., 2002). Therefore a small variation in GPP or ER can switch an ecosystem between being a source and being a sink. Both GPP and ER are affected by many abiotic and biotic factors, which can vary differently at different time scales (Richardson et al., 2007). At diurnal time scale, variations in GPP and ER are predominantly influenced by incoming photosynthetically active radiation (PAR), vapour pressure deficit (VPD) and air temperature. At seasonal time scale, GPP and ER can also be affected by soil water and temperature, canopy leaf area index (LAI) and litterfall (Stoy et al., 2005; Zhang et al., 2010). At inter-annual time scale, land use history and disturbance, and climate variation can significantly affect GPP and ER, thereby the carbon balance of an ecosystem (Albani et al., 2006). Spectral analysis shows that variations of GPP and NEE are quite similar at weekly and shorter time scales, and becomes quite different at the biweekly and longer time scales across different plant functional types (Stoy et al., 2009; Wang et al., 2011). As a result, variation in NEE is strongly influenced by both GPP and ER due to their direct responses of ecosystems to environmental variables at short-time scale (<weekly). At inter-annual time scale, the dynamics of ecosystems (i.e., phenology, growth pattern or recruitment) and their responses to environmental variables with a frequency longer than one year, such as seasonal rainfall anomaly, extreme summer heat

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and variation of the depth of groundwater table can all significantly affect NEE (Ciais et al., 2005; Dunn et al., 2007). Because our understanding of these dynamics within the ecosystem is much poorer than the direct responses of GPP and ER to environmental drivers at diurnal or seasonal time scales, and the inter-annual variation of NEE often is much more difficult to be accurately simulated than its diurnal or seasonal variations (Siqueira et al., 2006; Wang et al., 2011).

Previous study of two forest types in interior Alaska showed that the inter-annual variation in NEE of deciduous broadleaf forest was more sensitive to temperature variation than evergreen conifer forest (Welp et al., 2007). Yuan et al. (2009) found that the inter-annual variation in NEE is closely related to ER for deciduous broadleaf forests and to GPP for evergreen needleleaf forests globally. However, most previous studies on the seasonal and inter-annual variations in GPP, RE and NEE were on boreal and temperate forests (Barr et al., 2007; Krishnan et al., 2008; Stoy et al., 2009). In the subtropical and tropical regions, the forests had often been considered to have little seasonality in NEE because of abundant rainfall and consistently warm temperature (Holdridge, 1947; Richard, 1996). However eddy covariance measurements have showed that the seasonal variation in NEE was largely driven by ER in an Amazonian tropical forest (Saleska et al., 2003) and an Asia tropical rain forest (Zhang et al., 2010). These two studies revealed that the dry season is an important period for carbon sequestration in tropical forest ecosystems, while a north Australian tropical savanna showed an essential carbon 'neutral' in the dry season being resulted from lower GPP due to water limitation (Eamus et al., 2001; Hutley et al., 2005). To date, no studies have been made on the inter-annual variation of NEE in subtropical or tropical forests that accounts for more than 40% of the global GPP (Beer et al., 2010) and always net carbon uptake over the last two decades (Zhou et al., 2006; Pan et al., 2011; Tan et al., 2011).

Two old-growth forests, the subtropical evergreen broadleaf forest (age >400 years) and tropical seasonal rain forest (age >180 years), have been perfectly preserved in the Dinghushan Biosphere Reserve and Menglun Nature Reserve, respectively. Previous studies showed that these two old-growth forests are significant carbon sinks (Zhou et al., 2006; Tan et al., 2011). However, the major drivers of seasonal and inter-annual variations of these carbon sinks have yet to be quantified. The objectives of this study therefore are to (1) compare the seasonal and inter-annual variations of GPP, RE and NEE at two old-growth evergreen broadleaf forests in southern China; (2) identify the major biotic and abiotic drivers of the seasonal and inter-annual variations of GPP, RE and NEE of these two forests. We hypothesized that there were no pronounced differences of temporal variations in net carbon uptake between the tropical and subtropical forests because of the similar climate condition and no significant water stress in most years experienced by both forests in southern China. We also tested the hypothesis that GPP do not vary markedly neither between wet season and dry season, nor from year to year in old-growth forests based on previous studies in tropical forests (Saleska et al., 2003; Hutyra et al., 2007; Kosugi et al., 2008). This may be possible because of the full canopy cover throughout the year in tropical and subtropical forests.

2. Materials and methods

2.1. Site descriptions

The subtropical forest site (23°10′16″ N, 112°31′48″ E) is located in the Dinghushan Biosphere Reserve in central Guangdong Province, southern China. The total area of the reserve is 11.56 km^2, and most area is coved with rolling hills and low mountains, with an altitude above the sea level ranging from 100 to 700 m. The region is characterized by a typical subtropical monsoon humid climate, with a mean annual temperature of 20.5 °C. The highest and lowest monthly mean temperatures are 28.0 °C in July and 12.0 °C in January, respectively. The average annual rainfall is 1700 mm, of which more than 80% falls during wet seasons (April–September). The predominant soil type is lateritic red earth. Soil pH ranges from 4.5 to 6.0 with a rich humus layer at ground. The forest is more than 400 years old (Zhou et al., 2006), and is dominated by *Castanopsis chinensis*, *Schima superba*, *Cryptocarya chinensis*, *Cryptocarya concinna*, and *Machilus chinensis*. The canopy height is about 22 m and the mean LAI is about 4.9 in dry seasons and 5.6 in wet seasons. The flora includes 260 families, 864 genera, and 1740 species of wild plants (Yan et al., 2006).

The tropical forest site (21°55′39″ N, 101°15′55″ E) is located in the Menglun Nature Reserve in Xishuangbanna, Southern China. The climate is strongly seasonal with two air masses alternating between wet and dry seasons within a year (Zhang, 1966). During wet seasons (April–September), 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 during dry seasons (October–March). 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, about 87% of which falls during wet seasons. The soil is lateritic derived from siliceous rocks, such as granite and gneiss, with a pH from 4.5 to 5.5. 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 have the canopy with 40 m in height on average. 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) include *Garcinia cowa*, *Knema erratica*, *Ardisia sinoaustralis* (Cao et al., 1996). LAI varies from 4.0 to 6.0 within a year (Zhang et al., 2010).

2.2. Measurements

As part of the ChinaFLUX network, a 38 m-tall flux tower (DHS tower) and a 70 m-tall flux tower (XSBN tower) were established in the subtropical forest site and the tropical forest site, respectively. An eddy covariance system (EC) with 3D sonic anemometer (CSAT3; Campbell Scientific Inc., Lincoln, NE, USA) and an infrared open-path gas analyzer (Li-7500; Li-Cor Inc.), were mounted at 27.0 m on the DHS tower and 48.8 m on the XSBN tower, respectively. Seven levels of air temperature, relative humidity (HMP45C; Campbell Scientific Inc., Lincoln, NE, USA), photosynthetically active radiation (LQS70-10; Apogee) and wind speed (A100R; Vector) sensors were mounted along each tower to obtain canopy profiles. Solar radiation and net radiation was measured with radiometers (CM11, CNR1; Kipp & Zonnen). Precipitation was recorded by a rain gauge (52,203; R.M. Young) at the top of both the DHS tower and XSBN tower. In each forest stand, soil temperature and moisture were measured with thermocouple (105T; Campbell Scientific Inc., Lincoln, NE, USA) and time-delay reflectometer (CS616; Campbell Scientific Inc., Lincoln, NE, USA), respectively. Routine meteorological data were recorded at 30 min intervals by data loggers (CR10X & CR23X; Campbell Scientific Inc., Lincoln, NE, USA), and the measured windspeed in each of three directions, concentrations of CO_2 and water vapour were recorded at a frequency of 10 Hz using a data logger (CR5000; Campbell Scientific Inc., Lincoln, NE, USA).

The forests are quite uniform within 5 km surrounding the flux towers at both sites, and footprints as estimated by Mi et al. (2006) varies from 130 m to 3 km, depending on the atmospheric stability. Therefore the fetch meets the requirement for eddy flux measurements at both sites. Spectral analysis showed that the contribution to total flux was negligible from high frequency (>1 Hz), and the measured fluxes are reliable and representative of the forest within a few km^2 around the tower, as demonstrated by Mi et al. (2006).

2.3. Flux data corrections and calculations

To ensure the reliable processing of flux data, ChinaFLUX has developed a series of proven methodologies for carbon fluxes data quality assessment and quality control (QA/QC) including coordinate rotation, WPL correction, canopy storage calculation, nighttime flux correction, and gap-filling and flux participation (Yu et al., 2006). Prior to obtaining the seasonal and annual fluxes, the energy closure ratio at the two sites was examined and all exceeded 0.7 (Li et al., 2005; Zhang et al., 2010). The three-dimensional coordinate rotation of wind velocity component was applied to set mean vertical on zero (Wilczak et al., 2001; Finnigan et al., 2003; Zhu et al., 2005). The WPL correction was used to eliminate the influence of air density fluctuations resulting from heat and water vapor transfer (Webb et al., 1980). The storage below EC height was calculated by using the temporal change in CO_2 concentration above the canopy measured with Li-7500 (Carrara et al., 2003). The abnormal data points were excluded from flux calculations, including periods of system failure, the negative CO_2 fluxes at nighttime and very stable night condition ($u^* < 0.2\ m\ s^{-1}$). The data gaps were filled by means of the nonlinear regression method (Falge et al., 2001). NEE was partitioned into GPP and RE using the method as described by Reichstein et al. (2005). Further details of QA/QC and flux partitioning can be found in Yu et al. (2006). Fluxes of NEE and the partitioned components of GPP and RE have been used in previous studies (Tan et al., 2011; Yan et al., 2012). However, analyses of seasonal or inter-annual variations in these three fluxes have not been studied before. Because of a large gap caused by 3D sonic anemometer failure, flux data in 2005 for DHS and in 2009 for XSBN were not included in the present study. Gaps in the other years as used in this study are less than 13% for both sites.

Estimates of NEE based on eddy covariance are affected by various sources of systematic bias and random uncertainty. Dragoni et al. (2007) indicated that the overall uncertainty of annual NEE was dominated by the data processing procedures, especially the gap-filling. For the continuous fluxes measurements of ChinaFLUX, Liu et al. (2012) estimated the uncertainty of annual NEE of 5.3–23.6 $g\ C\ m^{-2}\ yr^{-1}$ due to the selection of respiration and light-response models for Chinese forest ecosystems, and found that the estimates of the estimated seasonal and annual NEE were quite similar using different gap-filling methods. They also evaluated the uncertainty in nighttime CO_2 flux using different u^* thresholds and the effect on the estimates of annual NEE using a bootstrapping approach. Their results suggested that uncertainty of annual NEE was about 14.8 (5.8–22.4) $g\ C\ m^{-2}\ yr^{-1}$ from nighttime data correction with different u^* threshold values for the different forest ecosystems in ChinaFLUX.

2.4. Soil respiration and litterfall measurements

Soil respiration (SR) was measured using a static chamber system, which consists of a base with an annular collar on which is placed the chamber with a volume of length × width × height of 0.5 m × 0.5 m × 0.5 m. The six bases were permanently pushed 3 cm into the soil at least four weeks before the first sampling. The sample tube was connected to the upper part of the chamber. Two small electric fans were installed for air mixing inside the chamber. During measurements, the chamber was water sealed by filling water into the pedestal's trough where the chamber sits. Gas sample was taken using a gas-tight syringe (100 mL) at 0, 10, 20, 30, and 40 min after chamber closure. Five gas samples were collected for laboratory analysis during each measurement. Samples were analyzed for CO_2 concentration using an HP4890D gas chromatograph (Agilent, Wilmington, DE, USA) equipped with flame ionization detectors (Wang and Wang, 2003). The details of SR calculation see Yan et al. (2006). Hourly SR was measured for each plot between 9:00 and 12:00 h once per week from 2003 to 2009. Our previous study has demonstrated that SR measured from 09:00 to 11:00 is representative of the daily mean SR (Yan et al., 2009). The monthly values of SR were calculated from the four observation days each month.

Ten 1 m^2 square litter traps were placed in each forest stand randomly. The trap was made of a plastic net that allows water to percolate easily but retain litter. The trap was installed at 50 cm above the ground. The litter material in the trap was collected monthly, and was air dried, then separated into leaves, branches, barks and flower and fruit. The unidentified fine litter material was combined with flower and fruit litter. All litter material was dried in an oven at 65 °C until constant weight was obtained. The final dry weight of each component in all samples was converted into the litter carbon input (LCI, $g\ C\ m^{-2}$). The convention coefficient of carbon for each litter component at the subtropical forest and tropical forest was reported by Fang et al. (2003) and Lü et al. (2006). The mean proportion of carbon content in all litter components was 47.5% for the subtropical forest and 46.6% for the tropical forest.

3. Results

3.1. Changes of rainfall and temperature at the seasonal or inter-annual scale

The measured rainfall over the 7-year study period includes the extreme hydrological events (2003 is the driest year and 2008 is the wettest year) with a mean annual rainfall of 1640.5 mm for the subtropical forest site and 1394.3 mm for the tropical forest site (Fig. 1). Both sites showed the different inter-annual variations in rainfall with a coefficient of variation of 24.6% for the subtropical site and 14.2% for the tropical site. The mean annual air temperature was 20.3 °C at the subtropical site and 20.2 °C at the tropical site with small inter-annual variation (coefficient of variation <2%) at both sites.

Both sites are strongly influenced by the Asian monsoon and experience similar seasonal variations of rainfall with distinctive wet and dry seasons within a year (Fig. 1). Total rainfall during wet seasons (April to September) accounts for 82% of the annual rainfall in the subtropical site and 86% in the tropical site from 2003 to 2009 on average. The mean air temperature was 16.0 °C during dry seasons and 24.7 °C during wet seasons at the subtropical site, and was 17.6 °C during dry seasons and 22.9 °C during wet seasons at the tropical site. As a result, the climate at the subtropical site is warmer and wetter during wet seasons but cooler during dry seasons than the tropical site.

3.2. Seasonal and inter-annual variations in carbon fluxes of the two forests

The measured NEE from flux towers showed that both the old-growth forests were the net carbon sinks (negative values) annually over the study periods. The annual net carbon uptake (= –NEE) of the subtropical forest was more than twice as much as that of the tropical forest (Table 1). The annual net carbon uptake of the subtropical forest varied from 230 to 489 $g\ C\ m^{-2}\ yr^{-1}$ with a mean rate of 397 $g\ C\ m^{-2}\ yr^{-1}$ from 2003 to 2009. For the tropical forest, the annual net carbon uptake varied from 199 to 232 $g\ C\ m^{-2}\ yr^{-1}$ with a mean rate of 166 $g\ C\ m^{-2}\ yr^{-1}$ from 2003 to 2008. Compared with the net carbon uptake, the annual GPP and ER were very different in magnitude and seasonal variation at the two forests (Table 1). Both annual GPP and ER were much larger in the tropical forest

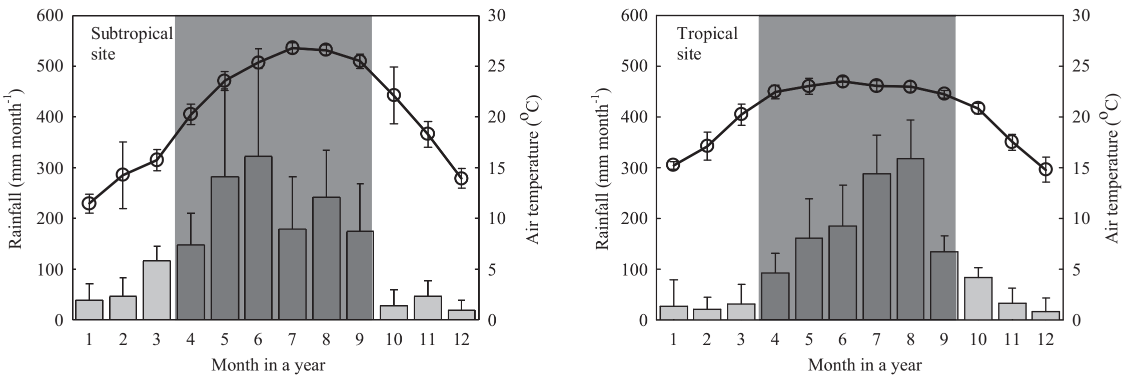

Fig. 1. The mean monthly rainfall (mm) represented by bars and air temperature (°C) represented by solid line with dots during 2003–2009 at the subtropical and tropical sites. Both sites had a distinctive wet season and dry season within a year. The wet season (April–September) was marked by the shade area in each of the graphs.

than those for the subtropical forest. The mean annual GPP was 2331 g C m^{-2} yr^{-1} in the tropical forest from 2003 to 2008, or about 68% higher than that in the subtropical forest. The annual ER in the tropical forest ranged from 1909 to 2447 g C m^{-2} yr^{-1}, or more than twice as much as that in the subtropical forest from 2003 to 2008. As a result, the annual NEE/GPP ratio is 7.1% and 28.7% for the tropical and subtropical forests, respectively. The difference in NEE/GPP ratios between the two forests largely resulted from their difference in ER and its responses to biotic and abiotic factors at annual time scale.

Measurements also showed that the seasonal variation in monthly NEE was quite different at the two forests (Fig. 2). Monthly NEE varied much more strongly in the tropical forest than in the subtropical forest. The small seasonal variation in NEE resulted from similar variations in the monthly GPP and ER at the subtropical forest, whereas the strong seasonal variation in NEE was largely driven by the variation in the monthly ER in the tropical forest, as the seasonal variation in the monthly GPP was quite small at the tropical forest. In the subtropical forest, NEE was negative for most months during the study period, and the mean net carbon uptake in dry seasons was about 81.4% higher than that in wet seasons. The tropical forest was a carbon source in wet seasons (positive NEE) and a carbon sink in dry seasons (negative NEE) (Fig. 2). Because the magnitude of carbon uptake in dry seasons was always larger than carbon release in wet seasons, the old-growth tropical forest was still a net carbon sink annually over the study period. The monthly GPP in wet seasons is 37.1% higher than that for dry seasons in the subtropical forest, but only 12.4% higher in the tropical forest. Therefore the monthly GPP of the subtropical forest was more variable within a year than in the tropical forest. On the other hand, the monthly ER was found to be more variable in the tropical forest than in the subtropical forest. As a result, the seasonal variation of NEE was driven by the variation of ER in the tropical forest, and by both seasonal variations of GPP and ER in the subtropical forest.

3.3. Responses of NEE to aboveground litterfall and soil respiration

NEE is a balance between GPP and ER. Generally, it varies with GPP or ER or both. Meanwhile, aboveground litterfall representing about 60–80% of aboveground net primary production (NPP) and the substrate for soil carbon decomposition; and SR accounts for more than 80% of ER in the subtropical forest (Yan et al., 2006; Tang et al., 2011) or the tropical forest (Sha et al., 2005; Tang et al., 2010). Both variables were measured independently of eddy covariance, and can be used as an independent evidence of the responses of NEE to the derived GPP or ER from eddy covariance measurements.

To evaluate the responses of NEE to aboveground litterfall and SR at the seasonal scale, a linear regression of the monthly deviation in NEE (ΔNEE, defined as a difference between monthly NEE and mean monthly NEE during the study period) was used against the monthly deviation in LCI (ΔLCI) or SR (ΔSR) in both forests (Fig. 3). As shown in Fig. 3, ΔNEE was positively correlated with either ΔLCI or ΔSR, which suggested that the net carbon uptake by each of both forests decreased with an increase of LCI or SR. In the tropical forest, ΔLCI could explain about 52% ($R^2 = 0.52$, $n = 72$, $P < 0.001$) of total variance in ΔNEE, being greater than that in the subtropical forest ($R^2 = 0.41$, $n = 70$, $P < 0.001$, aboveground litterfall data for two months with strong influences of typhoon were excluded). ΔSR could also explain total variance in ΔNEE of the tropical forest ($R^2 = 0.55$, $n = 72$, $P < 0.001$) more than subtropical forest ($R^2 = 0.37$, $n = 72$, $P < 0.001$). By comparing the magnitude of linear regression slope, we conclude that the response of NEE to

Table 1
Annual rainfall (mm), net ecosystem exchange (NEE, g C m^{-2} yr^{-1}), ecosystem respiration (ER, g C m^{-2} yr^{-1}), and gross primary productivity (GPP, g C m^{-2} yr^{-1}) of the subtropical and tropical forests during the study period. Negative flux represents a net carbon uptake by the ecosystem. Ave. for mean annual flux and cv for coefficient of variation in %. One standard error of the flux is also shown after "avg." with ±.

Year	Rainfall (mm)		NEE (g C m^{-2} yr^{-1})		ER (g C m^{-2} yr^{-1})		GPP (g C m^{-2} yr^{-1})	
	Subtropical	Tropical	Subtropical	Tropical	Subtropical	Tropical	Subtropical	Tropical
2003	1339	1244	−461.7	−143.9	968.9	2294.2	1430.6	2438.1
2004	1300	1308	−488.6	−181.7	930.0	2190.9	1418.5	2342.6
2005	–	1369	–	−133.7	–	2238.5	–	2372.2
2006	1830	1392	−353.1	−206.0	995.8	1940.2	1348.9	2146.3
2007	1373	1266	−432.6	−231.7	983.6	1909.0	1416.2	2140.8
2008	2361	1679	−230.3	−99.3	1075.0	2446.5	1305.3	2545.7
2009	1375	–	−415.7	–	968.8	–	1384.5	–
Ave.	1596 ± 422	1376 ± 159	−397.0 ± 93.7	−166.1 ± 49.3	978.0 ± 48.5	2169.9 ± 208.8	1384.0 ± 48.6	2330.9 ± 161.1
c.v.	26.5%	11.5%	23.6%	29.7%	4.9%	9.6%	3.5%	6.9%

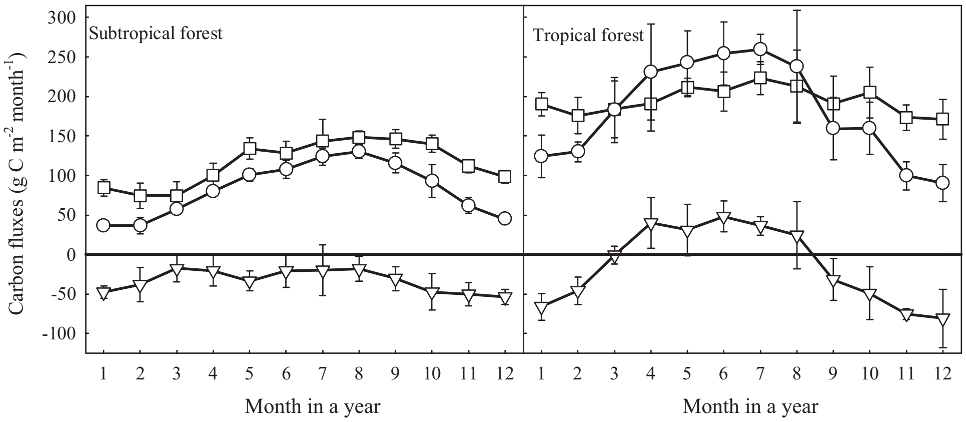

Fig. 2. The mean monthly carbon fluxes of the subtropical and tropical forests during 2003–2009. Solid lines with triangles are net ecosystem exchange (NEE, g C m^{-2} $month^{-1}$). Solid lines with circles and squares represent for ecosystem respiration (ER, g C m^{-2} $month^{-1}$) and gross primary production (GPP, g C m^{-2} $month^{-1}$), respectively.

LCI or SR in the tropical forest was much stronger than that in the subtropical forest. If SR (the largest component of ER) was considered as an alternative variable of ER, this result supports our above findings that the seasonal variation of NEE was largely driven by the variation of ER in the tropical forest, and by both seasonal variations of GPP and ER in the subtropical forest.

At the annual scale, annual NEE was positive to annual LCI or annual SR in both forests (Table 2), which meant more annual aboveground litter input or annual SR would lead to a decrease of annual net carbon uptake by each of both forests. However this decrease was significant ($P < 0.001$) for the subtropical forest only, not for the tropical forest (Table 2). Therefore at the inter-annual scale, LCI and SR were two major drivers of NEE in the subtropical forest.

3.4. Response of NEE to climatic variables

NEE of a forest can also be affected by climatic variables, such as energy and water relations and so on through their influences on GPP and ER. At the seasonal scale, monsoon climate condition in the two study sites resulted in much rainfall and high temperature in the wet season (Fig. 1). However NEE in the wet season was much greater than that in the dry season for both forests (Fig. 2). Therefore, all selected energy or water related factors were positively correlated with NEE at the seasonal scale except for VPD (Table 3). VPD was negative to NEE in the subtropical forest, but positive in the tropical forest. The water relations (rainfall or soil moisture) explained more seasonal variations in NEE than energy factors (air temperature and incoming PAR) at the subtropical forest, while air and soil temperature explained more seasonal variations in NEE than other selected climatic variables in the tropical forest (Table 3). A multiple linear regression was used to investigate the impacts of all selected climatic variables on NEE. All of them together could explain about 69% ($P < 0.001$) and 71%% ($P < 0.001$) of the seasonal variations in NEE of the subtropical and tropical forests, respectively.

The inter-annual variations of incoming energy factors, such as PAR and temperature, were usually quite small at the subtropical and tropical forest sites in southern China, while annual NEE of both forests showed a large variation (Table 1). No significant correlation between annual NEE and any of energy factors was found (Figure not shown). However the greater annual NEE usually occurred in the rainy years and smaller annual NEE in the dry years for the both forests (Fig. 4). Annual rainfall or annual mean soil moisture could explain about 95% ($P = 0.001$) and 67% ($P = 0.048$) of the inter-annual variations in NEE of the subtropical and tropical forests, respectively. However statistic analysis showed that there was no significant correlation between annual NEE and annual rainfall or annual mean soil moisture for the tropical forests.

3.5. Responses of GPP and ER to soil temperature or moisture

To understand why the measured NEE of both forests was varied in such a way at the seasonal or inter-annual scales, we analyzed

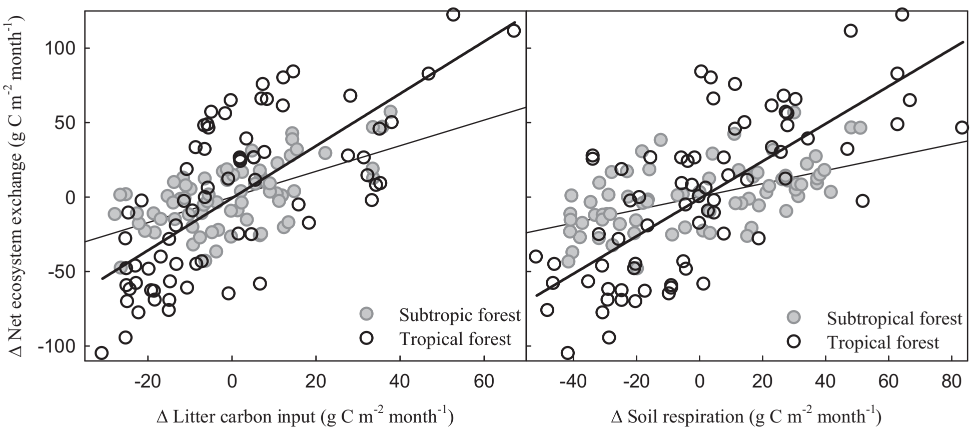

Fig. 3. Relationship between monthly deviation (defined as a difference between monthly value and mean monthly value during the study period) in net ecosystem exchange (ΔNEE, g C m^{-2} month $^{-1}$) and monthly deviation in soil respiration (ΔSR, g C m^{-2} $month^{-1}$) or litter carbon input (ΔLCI, g C m^{-2} $month^{-1}$) during the study period in the subtropical or tropical forest. Linear regression was shown as a solid line.

Table 2
Linear regressions between annual net ecosystem exchange (NEE(y), g C m^{-2} yr^{-1}) and annual litter carbon input (LCI(x_1), g C m^{-2} yr^{-1}) or soil respiration (SR(x_2), g C m^{-2} yr^{-1}) of the subtropical and tropical forests during the study period. r^2 is correlation squared and p is the significance level.

Factor	Subtropical forest	r^2	p	Tropical forest	r^2	p
LCI (x_1)	$y = 0.883x_1 - 804.1$	0.97	<0.001	$y = 0.037x_1 - 181.5$	0	0.967
SR (x_2)	$y = 1.826x_2 - 1726.1$	0.98	<0.001	$y = 0.409x_2 - 673.4$	0.74	0.028

Table 3
Linear regressions between the monthly net ecosystem exchange (NEE(y), g C m^{-2} month^{-1}) and climatic variables, including the monthly mean vapour pressure deficit (VPD, kPa), photosynthetically active radiation (PAR, mol m^{-2} month^{-1}), monthly mean air temperature (T_a, °C) and soil surface temperature (T_s, °C), monthly rainfall (R, mm month^{-1}) and monthly mean soil moisture (SM, %) at the subtropical and tropical forests during the study period. R^* represents the monthly rainfall date excluding the points of monthly rainfall over 300 mm (which represented the data points observed during typhoon period with very high rainfall).

Abiotic factor	Subtropical forest	r^2	p	Tropical forest	r^2	p
VPD(x_3)	$y = -25.44x_3 - 16.57$	0.08	0.015	$y = 92.85x_3 - 52.53$	0.16	0.001
PAR (x_4)	$y = 0.01x_4 - 33.65$	0.01	0.947	$y = 0.193x_4 - 160.74$	0.31	<0.001
T_a (x_5)	$y = 1.28x_5 - 59.17$	0.10	0.007	$y = 12.83x_5 - 273.87$	0.60	<0.001
T_s (x_6)	$y = 1.35x_6 - 60.47$	0.07	0.022	$y = 11.92x_6 - 248.96$	0.45	<0.001
R (x_7)	$y = 0.08x_7 - 43.04$	0.29	<0.001	$y = 0.28x_7 - 46.25$	0.34	<0.001
R^* (x_8)	$y = 0.18x_8 - 52.30$	0.44	<0.001	$y = 0.37x_8 - 52.85$	0.42	<0.001
SM (x_9)	$y = 2.97x_9 - 95.23$	0.58	<0.001	$y = 4.74x_9 - 119.67$	0.21	<0.001

the responses of two substantial biological processes (GPP and ER) of NEE to soil temperature and soil moisture, which are very two important parameters to determine the variations in ecosystem GPP and ER. To compare the response sensitivity of GPP or ER of the two forests, the monthly deviations (defined as a difference between monthly value and mean monthly value during the study period) was used in Fig. 5.

At the seasonal scale, Fig. 5 showed that the monthly deviation in GPP (ΔGPP) or ER (ΔER) of the two forests showed a significant positive linear correlation with the monthly deviation ($P < 0.001$) with the monthly deviation in soil temperature (ΔST) or moisture (ΔSM). In the subtropical forest, about 37–87% of variations in monthly ΔGPP or ΔER were explained by monthly ΔST or ΔSM, which was greater than that in the tropical forest (about 27–53%). Comparing linear regression slopes, we found that the response of monthly ΔGPP to monthly ΔST or ΔSM was weaker than that of monthly ΔER for both forests. ER therefore was the major driver of NEE in both forests at the season scale. The linear regression slope of monthly ΔER to monthly ΔST was about 24% higher than that of monthly ΔGPP In the subtropical forest, or about four times greater than that in the tropical forest. Therefore NEE in the subtropical forest was also driven by GPP. As a result, the seasonal variation in NEE was driven by the variation in ER of the tropical forest, and by both seasonal variations in GPP and ER of the subtropical forest, which was consistent with the result as presented earlier.

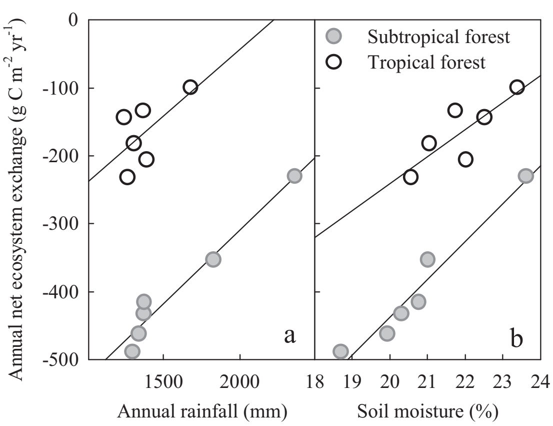

Fig. 4. Linear regression between annual net ecosystem exchange (g C m^{-2} yr^{-1}) and annual rainfall (mm, a) or annual mean soil moisture (%, b) of the subtropical or tropical forest during the study period. Linear regression was shown as a solid line.

At inter-annual scale, annual mean soil temperature had no significant effects on GPP or ER of both forests because of its small inter-annual variation. Fig. 6 showed the responses of annual ΔGPP or ΔER to annual ΔSM. In the subtropical forest, annual ΔGPP was negatively correlated with annual ΔSM, while annual ΔER was positively correlated with ΔSM. Therefore GPP decreased and ER increased with increasing annual soil moisture in rainy year, annual net carbon uptake therefore decreased because of greater sensitivity of ΔER than ΔGPP to ΔSM in the subtropical forest. In the tropical forest, both annual ΔGPP and ΔER were positive to annual ΔSM, but the sensitivity or the slope of the linear regression of annual ΔER to annual ΔSM was greater than annual ΔGPP (Fig. 6). As a result, annual net carbon uptake also decreased with high annual soil moisture in rainy year in the tropical forest.

4. Discussion

4.1. Seasonal carbon fluxes in subtropical and tropical forest

Seasonal variation in NEE was traditionally considered to be weak in subtropical and tropical forests because of warm and moist climate throughout a year (Holdridge, 1947; Richard, 1996). However the recent two studies (Zhang et al., 2010; Yan et al., 2012) have shown that the dry season was an important period for net carbon uptake by the subtropical and tropical forests within a year. In this study, both forests were carbon sinks in the dry season. In the wet season, the subtropical forest was a weak carbon sink, whereas the tropical forest was a carbon source. Our result in tropical forest was consistent with a previous study carried out in an Amazonian tropical forest (Saleska et al., 2003), but contrary to the result observed in a north Australian tropical savanna (Eamus et al., 2001; Hutley et al., 2005). Results in this study suggested that NEE of the tropical forest varied more seasonally than that in the subtropical forest, even though both forests experienced similar climate condition strongly influenced by seasonal monsoon (Yan et al., 2011). Therefore the hypothesis that no pronounced differences of temporal variations in net carbon uptake between the two forests at the seasonal scale was found to be false.

Many previous studies have shown that the seasonal variation in NEE of tropical forests (Saleska et al., 2003; Zhang et al., 2010) and deciduous broadleaf forest (Stoy et al., 2008) was mainly driven by ER. In the tropical forest we studied here, the greater seasonality of NEE was also mainly driven by ER, because of smaller seasonal variation in GPP. In the subtropical forest, the smaller seasonal variation in NEE resulted from the very similar seasonal variations in GPP and

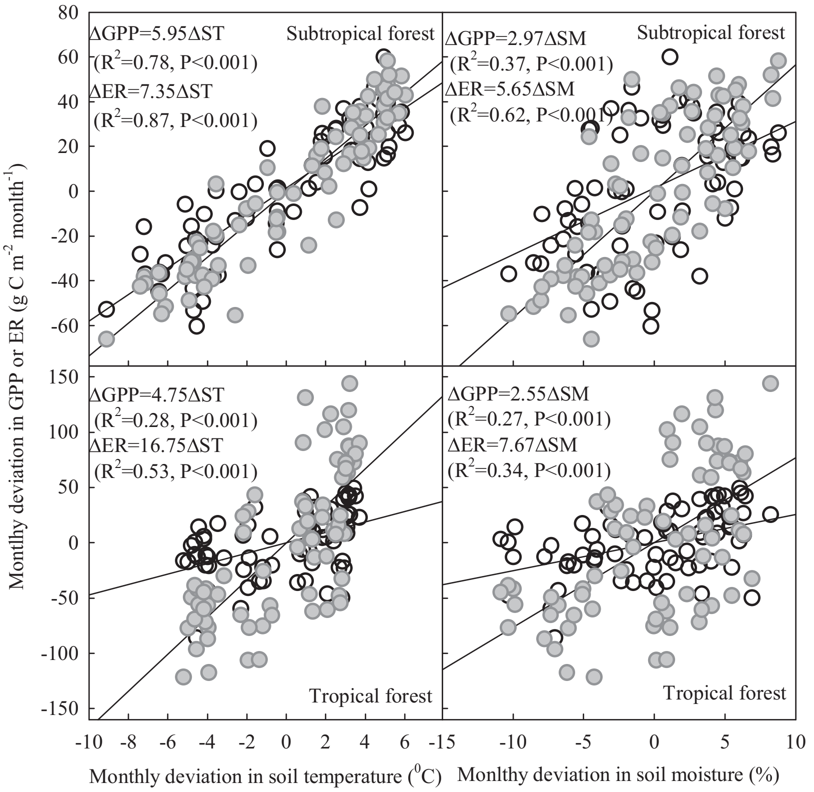

Fig. 5. Linear regression between monthly deviation (defined as a difference between monthly value and mean monthly value during the study period) in gross primary productivity (ΔGPP, g C m^{-2} $month^{-1}$) or ecosystem respiration (ΔER, g C m^{-2} $month^{-1}$) and monthly deviation in soil temperature (ΔST, °C) or moisture (ΔSM, %) at the subtropical or tropical forest site. The filled and open circles represent ΔGPP and ΔER, respectively. Least-square linear regression is shown as a solid line.

ER (Fig. 2). The different seasonal variations in NEE between the subtropical and tropical forests were determined by the different responses of GPP and ER of both forests to climatic variables. Previous studies showed that soil temperature and moisture are the two major climatic factors affecting the seasonal patterns of GPP and ER (Falk et al., 2008), but this effect varied across different forest ecosystems (Jarvis et al., 2001; Van Dijk and Dolman, 2004; Yuan et al., 2009). However the variation in soil temperature and moisture drivers becomes progressively less important at longer time scales (Richardson et al., 2007). Generally, the response of GPP and ER to soil temperature and moisture in tropical forest was weaker than the temperate forest or boreal forest (Yuan et al., 2009). In this study, the response of GPP in the subtropical forest soil temperature or moisture was stronger than that in the tropical forest, which agreed well with the general results. However the response of ER to soil temperature and moisture in the subtropical forest was much weaker than that in the tropical forest, which was contrary to the general results.

The sensitivity of ER was about 24–80% higher than that of GPP to soil temperature and moisture in the subtropical forest, and about three to four fold higher in the tropical forest. As a result, the subtropical forest became a small carbon sink and the tropical forest became a carbon source in wet seasons when both soil temperature and moisture were much higher than in dry seasons. Because of the quite small responses of GPP to soil temperature and moisture in the tropical forest, the seasonal variation in GPP of the subtropical forest was much stronger than the tropical forest. Therefore the hypothesis that GPP do not vary markedly between wet season and dry season was found to be correct in the tropical forest, but false in the subtropical forest.

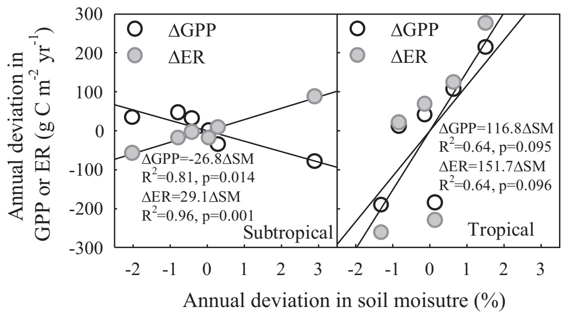

Fig. 6. Linear regression between annual deviation (defined as a difference of annual value and mean annual value during the study period) in soil moisture (%) and annual deviation in gross primary productivity (g C m^{-2} yr^{-1}) or ecosystem respiration (g C m^{-2} yr^{-1}) of the subtropical or tropical forest during 2003–2009. Linear regression was shown as a solid line.

4.2. Inter-annual carbon fluxes in subtropical and tropical forest

At inter-annual scale, the fractions of GPP fixed as net carbon uptake annually in both forests were higher in the dryer years and lower in the wetter year than the mean annual fraction over the study period. On average, this fraction is about 28.7% in the subtropical forest and 7.1% of GPP in the tropical forest. This very low fraction found in the tropical forest was out of the range of 23–83%, which was summarized from 60 data points across the different forest types (DeLucia et al., 2007). Amount of annual net carbon uptake by both forests was highest in the driest year during the study period (Table 1). The result was consistent with finding that the net carbon uptake by a Hainich deciduous old-growth forest was still large during the extremely dry year of 2003 (Granier et al., 2007).

As compared with annual NEE (Table 1), annual GPP in subtropical or tropical forests was quite steady with relatively small inter-annual variations, which agreed with the hypothesis that GPP do not vary markedly from year to year in the old-growth forests. However annual ER varied strongly with annual rainfall or soil moisture from year to year. Both forests showed a positive correlation between annual ER and annual rainfall during the study period, while the responses of annual GPP to annual rainfall were quite different between the two forests. In the subtropical forest, more annual rainfall reduced annual GPP due to a higher fraction of cloudy days. Less annul GPP but greater annual ER therefore contributed to a weak carbon sink in rainy years. In the tropical forest, more annual rainfall increased annual GPP due to alleviating water limitation, because this increasing carbon fixed by GPP was smaller than increasing carbon release by ER with warm and moist conditions, a weak carbon sink was still found in rainy years (Fig. 6). This different response of GPP to annual rainfall may result from the difference in tree height between the two forests. The canopy height is about 22 m in the subtropical forest (Yan et al., 2012) and more than 40 m in the tropical forest (Cao et al., 1996). In dry years, cavitation during water transport from root to leaf can occur, and result in a reduction in leaf photosynthesis (Koch et al., 2004). Therefore taller trees in the tropical forests were more sensitive to change in annual rainfall than shorter trees in the subtropical forest. The previous studies (Li et al., 2012; Liu et al., 2012; Yan et al., 2012) have also reported that the seasonal drought has no significant effects on the subtropical trees growth.

Annual NEE exhibited the strong inter-annual variations in both forests due to the different variations in annual GPP and ER. As a result of the quite different responses of annual GPP and the very similar responses of annual ER to annual rainfall, the correlations between annual GPP and ER were very different in both forests at the inter-annual scale. Annual GPP and ER is negatively correlated in the subtropical forest, but positively correlated in the tropical forest. That positive correlation between GPP and ER was also found in an old-growth forest (the Gifford Pinchot National Forest) in southern Washington State (Falk et al., 2008). The negative correlation between GPP and ER has not been found previously. Inter-annual variations in carbon fluxes of different biomes resulted from the different responses of carbon fluxes to climate factors. For example, in the boreal forests, variation of NEE was related to inter-annual variation in spring temperature and leaf emergence, summer drought and soil water supply in late growing season (Barr et al., 2007; Krishnan et al., 2008). In the temperate deciduous forests, variation of NEE was attributed to a combination of factors including occurrence of summer drought, soil temperature and winter snow (Goulden et al., 1996). Inter-annual variations in winter temperature and snow water were found to explain significantly inter-annual variations of growing season length and NEE at a subalpine forest (Hu et al., 2009). Inter-annual variations of NEE was found to be related to spring precipitation and soil moisture in a savanna and grassland (Lawrence et al., 2002; Ma et al., 2007). In the peatland, soil temperature and water table variations in growing season were found to be major contributor to the inter-annual variation of NEE (Teklemariam et al., 2010). Our results in this study suggested that annual rainfall was a major driver for the inter-annual variations of NEE of the subtropical and tropical forests.

5. Conclusions

Here we presented the seasonal and inter-annual variations in GPP, ER and their difference at a subtropical or tropical forest in southern China. Their responses to biotic and abiotic factors were also evaluated in this study. The following two conclusions can be drawn: (1) at the seasonal scale, the subtropical forest was a carbon sink for most months, while the tropical forest was a carbon source in wet seasons and a carbon sink in dry seasons. The seasonal variation in NEE was largely driven by the variation in monthly ER of the tropical forest, and by both seasonal variations in monthly GPP and ER of the subtropical forest. These different contributions of GPP and ER to the seasonal variations in NEE of the two forests resulted from their different responses to soil temperature and moisture; (2) measurements of eddy covariance during the period of 6 years showed that the two old-growth forests located in seasonal climates were always a net sink annually, with a mean NEE of $-397 \pm 94\,g\,C\,m^{-2}\,yr^{-1}$ for the subtropical forest and $-166 \pm 49\,g\,C\,m^{-2}\,yr^{-1}$ for the tropical forest. At inter-annual scale, annual NEE varied tightly with annual rainfall or soil moisture from year to year. This resulted from the different responses of annual GPP and ER to annual rainfall. Therefore annual rainfall was a major driver of annual carbon sequestration in the subtropical or tropical forests in southern China.

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