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SPECIAL FEATURE: ORIGINAL ARTICLE

Lessons learned from CarboEastAsia: Carbon and water cycles in East Asian terrestrial ecosystems

Substantial amounts of carbon are sequestered during dry periods in an old-growth subtropical forest in South China

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Abstract A number of continuous eddy covariance measurements and long-term biomass inventories had proved that old-growth forests are carbon sinks worldwide. The present study estimated the net ecosystem productivity (NEP) for an old-growth subtropical forest at the Dinghushan Biosphere Reserve in South China to investigate the temporal pattern of carbon sequestration, both seasonally and annually. The measured NEP over 7 years (from 2003 to 2009) showed that this forest was a net carbon sink, ranging from 230 (in 2008) to 489 g C m^{-2} $year^{-1}$ (in 2004). The greatest value of NEP was found in the driest year and the lowest value in the wettest year during the study period. Within a year, NEP during the dry season was about 81.4 % higher than for the wet season. Accordingly, the dry season at seasonal scale and dry years at interannual scale are key periods for carbon sequestration in this forest. The strong seasonality of ecosystem or soil respiration (ER or SR) compared with gross primary productivity (GPP) resulted in substantial amounts of carbon being sequestered during dry seasons. A decrease of GPP and an increase of ER or SR demonstrated the lower carbon uptake in rainy years. From this study, we conclude that GPP and living biomass carbon increment are not overriding parameters controlling NEP. The variations in ER or SR driven by the rainfall scheme were the dominant factor determining the magnitude of NEP in this forest in South China.

Keywords Gross primary productivity · Net ecosystem productivity · Old-growth forest · Respiration · Temporal pattern

Introduction

Carbon uptake in old-growth forests had traditionally been considered to be balanced by respiration, therefore resulting in negligible carbon sink (Odum 1969; Jarvis et al. 1989; Melillo et al. 1996). However, continuous eddy covariance measurements and long-term biomass inventories since the late 1990s have proved that old-growth forests are significant carbon sinks worldwide (Phillips et al. 1998; Knohl et al. 2003; Zhou et al. 2006; Luyssaert et al. 2008; Lewis et al. 2009; Tan et al. 2011).

Old-growth forests are assumed to be insignificant carbon sinks based on two primary theories: (1) tree growth function, and (2) balance between assimilation and respiration. Applying these two theories to estimate carbon uptake is in conflict with the results by continuous eddy covariance measurements. Little evidence holds that the net ecosystem productivity (NEP) tends to zero when forests develop to an advanced stage. On the contrary, large atmospheric carbon uptake above the forest canopy was found in old-growth forests. In many old-growth forests, larger than expected NEP was found by long-term biomass inventories (Phillips et al. 1998; Knohl et al. 2003) and increasing amounts of accumulated soil organic carbon

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(SOC) were found by long-term SOC measurements (Zhou et al. 2006). Recently, old-growth forests were reported to be global carbon sinks by Luyssaert et al. (2008), Lewis et al. (2009), and Tan et al. (2011). Although many studies had proved that old-growth forests were carbon sinks, the temporal pattern of net carbon uptake (NEP) by old-growth forests remains uncertain from previous studies (Tian et al. 1998; Botta et al. 2002; Saleska et al. 2003; Zhang et al. 2010).

The magnitude of NEP is the balance between gross primary production (GPP) and ecosystem respiration (ER). Both GPP and ER are affected by climatic and biological factors (Stoy et al. 2009), and these factors vary on different time scales from diurnal to century (Richardson et al. 2007). On the short time scale, variations in NEP are predominantly influenced by incoming photosynthetically active radiation (PAR) and temperature (Stoy et al. 2005). A long-term record of carbon exchange in a boreal black spruce forest has shown that the interactions between soil thaw and water table depth provide critical control of carbon exchange on the seasonal to decadal time scales (Dunn et al. 2007). Welp et al. (2007) reported that interannual variations in NEP of deciduous broadleaved forests are more sensitive to temperature variation than for evergreen needle-leaved forests. Yuan et al. (2009) found that interannual variations in NEP are closely related to ER for deciduous broadleaved forests, and to GPP for evergreen needle-leaved forests globally. In subtropical and tropical regions, forests had often been considered to show little seasonal and interannual variations in NEP because of abundant rainfall and consistently warm temperature (Holdridge 1947; Richard 1996). To date, seasonal and interannual variations in NEP have not been well studied in subtropical and tropical forests.

Tower measurements of carbon dioxide (CO_2) flux (denoted as carbon flux in the present study) have been carried out in an old-growth subtropical forest in South China since 2002 by the direct eddy covariance method within the Chinaflux network. Eddy covariance provides an alternative means for carbon uptake estimation by measuring carbon fluxes between the biosphere and the atmosphere. This study uses measurements of carbon fluxes and soil respiration for this forest to investigate the temporal pattern of NEP, considering both seasonal and interannual variations in carbon fluxes.

Materials and methods

Study site description

The study was carried out in the Dinghushan Biosphere Reserve located in central Guangdong Province, South China, between 23°09′21″ and 23°11′30″N and 112°30′39″ and 112°33′41″E. The total area of the reserve is 11.56 km^2. Most of the Dinghushan area is covered with rolling hills and low mountains, with altitude ranging from 100 to 700 m. The region is characterized by typical subtropical monsoon humid climate, with average 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 1,700 mm, of which more than 80 % falls during the wet season (April–September) and less than 20 % during the dry season (October–March). The mean annual relative humidity is 82 %, and the mean annual wind speed is 1.4 m s^{-1}.

The predominant soil type is lateritic red earth. Soil pH ranges from 4.5 to 6.0, and a rich humus layer is common. Favored by the subtropical monsoon climate and long history of protection, the Dinghushan Biosphere Reserve has well-protected old-growth forest (monsoon evergreen broadleaved forest) and its prophase successional forests. The forest stand age of the monsoon evergreen broadleaved forest as examined in previous study is more than 400 years (Zhou et al. 2006), being dominated by *Castanopsis chinensis*, *Schima superba*, *Cryptocarya chinensis*, *Cryptocarya concinna*, and *Machilus chinensis*. The canopy height is about 22 m, and the mean leaf area index (LAI) is 4.9 in the dry season and 5.6 in the wet season. The flora includes 260 families, 864 genera, and 1740 species of wild plants (Yan et al. 2006).

Flux instrumentation and measurements

A 38-m-tall tower (DHFTL01) was established in the subtropical evergreen broadleaved forest. The forest stand is large enough with more than 5 km fetch available in every direction. Carbon fluxes were measured by eddy covariance systems at height of 27 m on the tower, using a 3D sonic anemometer (CSAT3; Campbell Scientific Inc., Logan, UT) and open-path CO_2/H_2O analyzer (Li7500; Li-cor Inc., Lincoln, NE). The signals from the sensors were sampled at 10 Hz, and directly recorded using the synchronous device for measurement (SDM) technique by a data logger (CR5000; Campbell).

Solar radiation was measured at the top of the tower (CM11, CNR1; Kipp&Zonen). Rainfall was measured at the top of the tower (52203; R.M. Young). PAR (the photosynthetic photon flux density) was measured with Li190SB (Li-cor) and LQS70-10 (Apogee) sensors. Temperature, humidity (HMP45C; Campbell and IRTS-P: Apogee), wind velocity (A100R; Vector), and wind direction (W200P; Vector) were measured at seven layers at 4, 9, 15, 21, 27, 31, and 36 m above the ground. Soil temperature (105-T and 107-L; Campbell) and soil moisture (CS616; Campbell) were measured at 5 layers at 5, 10, 20, 40, and 60 cm depth under the ground. All these routine meteorological signals were directly recorded with the data loggers (3 CR10X and 1 CR23X; Campbell). All recorded data were 30-min mean values. More extensive description of the instrumentation and measurements can also be found in Yu et al. (2006).

Flux calculations and corrections

Carbon fluxes were calculated using the covariance of vertical wind velocity and the density of CO_2 for every 30 min; further details of this method were reported in the previous study (Zhang et al. 2006). We used a program to process raw 30-min flux data as follows: (1) the three-dimensional coordinate rotation of the wind velocity component was applied to set the mean vertical to zero ($w = 0$) (Baldocchi et al. 2000; Wilczak et al. 2001); (2) the Webb-Pearman-Leuning correction was used to eliminate the influence of air density fluctuations resulting from heat and water vapor transfer (Webb et al. 1980); (3) the storage below eddy covariance height was calculated by using the temporal change in CO_2 concentration above the canopy measured with LI-7500 (Hollinger et al. 1994; Carrara et al. 2003); (4) abnormal data were filtered from the dataset, including rainfall days, periods of system failure, negative CO_2 fluxes at nighttime, and low-turbulence fluxes ($u^* < 0.2$ m s^{-1}) at nighttime; (5) data gaps were filled by means of the nonlinear regression method (Falge et al. 2001; Zhang et al. 2006). For small gaps (<2 h), the missing data were linearly interpolated. Larger gaps, such as daytime and nighttime gaps, were treated separately when filling the gaps in the carbon fluxes datasets. Satisfactory measurements in the present study were obtained for carbon fluxes after quality assessment and quality control, with bad records in daytime and nighttime <8 and <23 %, respectively. The net ecosystem exchange (NEE, g C m^{-2} timescale^{-1}) was converted into NEP (=−NEE).

Parts of the data NEE and the partitioned components of GPP and ER have been used in previous study (Yu et al. 2008). ER was calculated as the sum of daytime ecosystem respiration (ER_{day}) and nighttime ecosystem respiration (ER_{night}), estimated using empirical equations derived from the variables of soil temperature at 5 cm depth and water content in the top 10 cm of soil. GPP was estimated as the sum of NEP and ER; see Yu et al. (2008) for further details.

Soil respiration measurements and calculations

Soil respiration (SR, most of ER) was measured by a static chamber system consisting of a base with an annular collar on which is placed a chamber with volume of length × width × height = 0.5 m × 0.5 m × 0.5 m. The chamber is made from stainless steel with the top being covered by a cotton pad to reduce heat exchange. Six bases were permanently pushed 3 cm into the soil at least 4 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 gastight syringe through a septum-covered access port immediately and every 10 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). For details of the SR (g C m^{-2} timescale^{-1}) calculation, see Yan et al. (2006). SR was measured hourly for each plot between 0900 and 1200 hours once per week from 2003 to 2009 and continuously for 24 h once a month from 2003 to 2005. Analysis of the diurnal SR data collected on one day each month revealed that the average value from 0900 to 1200 hours was very similar to the whole day mean (Yan et al. 2009). At the beginning of 2006, 24-hourly measurements were suspended. We calculated the monthly values of SR rates as the mean SR on the 5 observation days each month before 2006 and the 4 observation days each month after 2006, and applied them to further investigate the seasonal variation in SR.

Tree growth measurements

The dendrometer band data-logger system (RS317-780 5K; BMC Messysteme GmbH, Germany) automatically records tree growth using electrical signals caused by changes in the resistance of a thin metal strip used as a flexure device. The "tape" is a stainless-steel cable with extremely low temperature dependence. The tape glides on a Teflon net around the bark of the tree stem to reduce friction and to protect against icing, resin, and callousing. The dendrometer band is placed at breast height (1.3 m). The beginning of the band is fixed at the tree stem with a stainless-steel screw, whereas the end is fixed where the band overlaps with a stainless-steel spring that is approximately 5 cm long. As the tree stem fluctuates, the spring stretches or shrinks and the measuring sensor point is pulled. This is compatible with a data logger. The accuracy of measurements of changes in diameter at breast height using this system is 0.1 mm. In the present study, one tree from each of the dominant species (three dominated species: *Ca. chinensis*, *S. superba*, and *Cr. Chinensis*) was selected and data were recorded every 6 h from April 2003 to March 2004.

Results

Changes in climatic factors during 2003–2009

As shown in Table 1, the mean annual air temperature was 20.3 °C, ranging from 19.9 °C (in 2008) to 20.6 °C (in 2007) in the period 2003–2009. Little changes in the mean air temperature during whole year, wet season (April–September), or dry season (October–March) were detected, with coefficient of variation (CV) less than 1.5 % (Table 1). On average, the air temperature during wet seasons and dry seasons was 24.7 and 16.0 °C, respectively (Table 1). The mean annual vapor pressure deficit (VPD) was 0.65 kPa, with 0.61 kPa in dry seasons and 0.69 kPa in wet seasons.

A previous study on rainfall time series had showed that the main cycle regularity of rainfall was 7 years at the same study site (Zhou and Yan 2001). The measured rainfall over this period of 7 years (from 2003 to 2009) basically covered the extreme hydrological events, with mean annual rainfall of 1,640 mm (Table 1). Although little changes in the mean annual temperature occurred during this period, annual rainfall showed large variations, with CV of 24.6 % (Table 1). The driest and wettest years were observed to range from precipitation of 1,299.9 mm (in 2004) to 2,361.1 mm (in 2008) (Table 1), consistent with the periodical rainfall behavior at the study site. In the period 2003–2009, about 82 % of rainfall occurred in wet seasons and 18 % in dry seasons, which created a clear difference between wet and dry seasons.

The study site is strongly influenced by the Asian monsoon. Temperature and rainfall showed a positive relationship across seasons, being warmer in wet seasons and cooler in dry seasons (Table 1).

Seasonal and interannual variations of carbon sequestration

Measurements from the Dinghushan flux tower showed that NEP is quite different between wet and dry seasons (Fig. 1). In the period 2003–2009, the mean NEP during dry seasons was 252 ± 38 g C m^{-2}, being about 81.4 % higher than that in wet seasons (139 ± 58 g C m^{-2}). However, the CV values in Table 2 demonstrate that the NEP presented much larger variations in wet seasons (41.6 %) than for dry seasons (15.2 %), indicating that carbon sequestration during dry seasons was quite steady compared with during wet seasons. Within a year, the dry season is an important period for carbon sequestration in this forest (Fig. 1).

As shown in Table 2, although large interannual variations (CV = 22.4 %) in NEP were found, the measured NEP over 7 years showed that it was always a net carbon sink. The annual NEP ranged from 230 (in 2008) to 489 g C m^{-2} $year^{-1}$ (in 2004) with an average of 390 g C m^{-2} $year^{-1}$. Interestingly, the greatest and least NEP occurred in the driest and wettest year, respectively. We found that annual rainfall could explain about 95 % of total variance in the measured NEP over the period of 7 years (Fig. 2). At the interannual scale, a larger carbon uptake was presented in dry years, which therefore was an important period for carbon sequestration in this forest.

Carbon balance at seasonal and interannual scales

The calculated ER averaged over 7 years was 652 ± 32 g C m^{-2} during wet seasons, being more than 2 times than that in dry seasons (323 ± 28 g C m^{-2}). The measured SR at this study site is presented in Table 2,

Table 1 Mean air temperature (°C), amount of annual precipitation (mm), and mean vapor pressure deficit (kPa) in dry season (October–March), wet season (April–September), and whole year

Year	Temperature (°C) (one standard deviation)			Precipitation (mm)			Vapor pressure deficit (kPa) (one standard deviation)		
	Dry season (Oct–Mar)	Wet season (Apr–Sep)	Annual	Dry season (Oct–Mar)	Wet season (Apr–Sep)	Annual	Dry season (Oct–Mar)	Wet season (Apr–Sep)	Annual
2003	15.2 (2.0)	25.1 (2.1)	20.1 (5.5)	190.4	1,148.7	1,339.1	0.61 (0.32)	0.74 (0.20)	0.68 (0.25)
2004	16.2 (3.8)	24.8 (2.2)	20.5 (5.4)	286.9	1,013.0	1,299.9	0.66 (0.38)	0.75 (0.19)	0.71 (0.28)
2005	15.3 (4.9)	24.8 (2.4)	20.1 (6.2)	184.6	1,721.6	1,906.2	0.56 (0.31)	0.65 (0.21)	0.61 (0.26)
2006	16.7 (4.1)	24.4 (2.3)	20.5 (5.1)	365.2	1,464.8	1,830.0	0.61 (0.21)	0.67 (0.20)	0.64 (0.20)
2007	16.7 (3.7)	24.6 (3.1)	20.6 (5.2)	221.4	1,151.8	1,373.2	0.63 (0.35)	0.71 (0.18)	0.67 (0.26)
2008	15.4 (5.4)	24.4 (2.4)	19.9 (6.1)	486.7	1,874.4	2,361.1	0.61 (0.24)	0.61 (0.19)	0.61 (0.20)
2009	16.2 (4.6)	24.7 (3.1)	20.5 (5.8)	317.9	1,056.0	1,373.9	0.57 (0.30)	0.70 (0.21)	0.64 (0.25)
Ave.	16.0	24.7	20.3	293.3	1,347.2	1,640.5	0.61	0.69	0.65
CV (%)	0.7	1	1.4	37.0	25.5	24.6	3.4	5.0	3.7

The climate data were measured on the Dinghushan flux tower during the period from 2003 to 2009

Ave. average, *CV* coefficient of variation

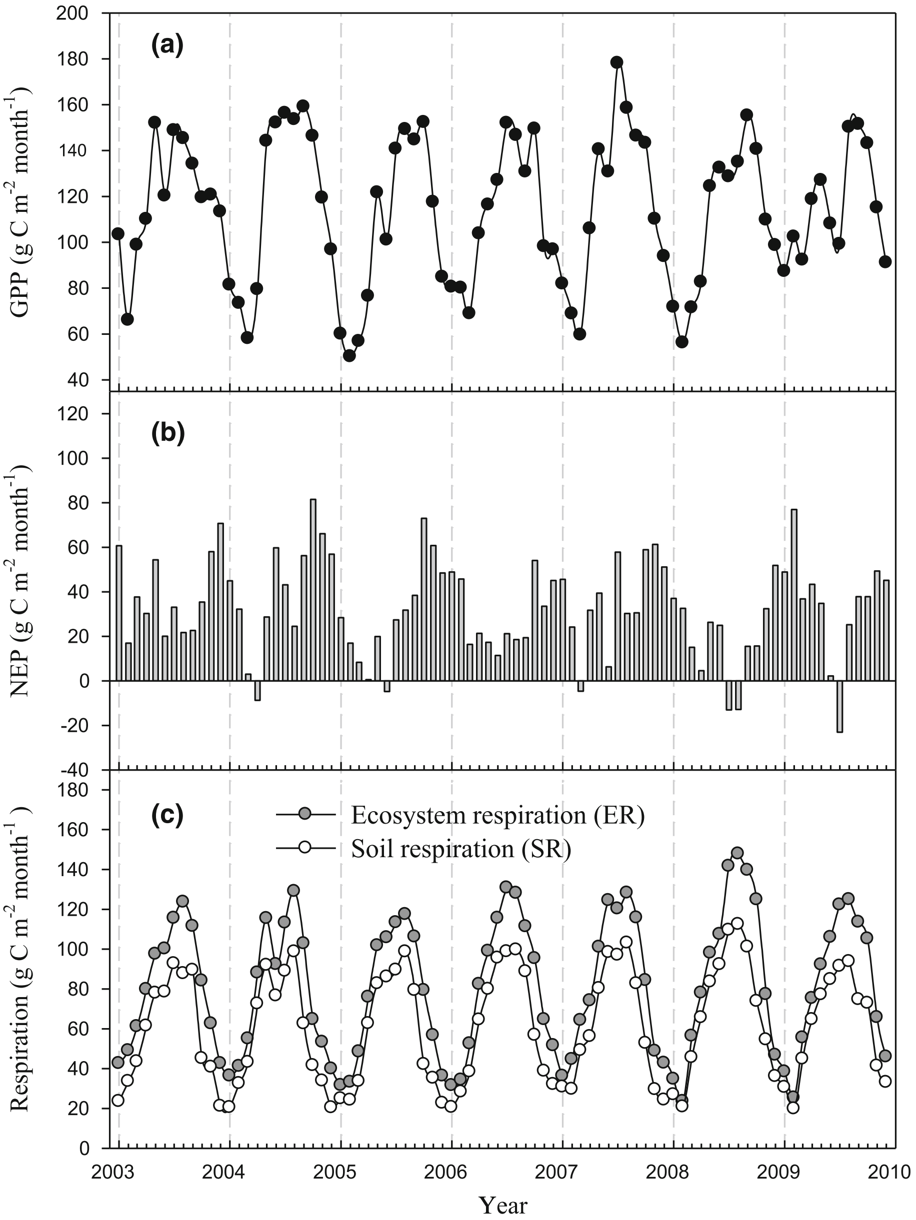

Fig. 1 Seasonal variations of carbon fluxes (g C m^{-2} $month^{-1}$) during the period 2003–2009. Soil respiration (SR) measured by chamber and ecosystem respiration (ER) estimated from flux partitioning are shown in **c**. Seasonal variations of gross primary productivity (GPP) and net ecosystem productivity (NEP) are shown in **a** and **b**, respectively

demonstrating that SR during wet seasons was also 136.4 % higher than for dry seasons. Table 2 also shows that the mean GPP was 790 ± 48 and 575 ± 39 g C m^{-2} for wet seasons and dry seasons, respectively. On average, the GPP during wet seasons was about 37.5 % higher than for dry seasons, being a small difference between wet and dry seasons compared with ER or SR.

At the interannual scale, annual ER varied from 905 (in 2003) to 1,075 g C m^{-2} $year^{-1}$ (in 2008) and annual GPP varied from 1,254 (in 2005) to 1,431 g C m^{-2} $year^{-1}$ (in 2003). Annual ER and GPP changes are plotted against annual rainfall in Fig. 2. It is shown that stronger ER and weaker GPP occurred in wetter years, while stronger GPP and weaker ER occurred in drier years. Therefore, more atmospheric carbon was sequestered in dry years. As a result of the above, large interannual variations in NEP were detected, although small variations in ER and GPP were observed (Table 2).

During the study period, about 17.5 and 43.7 % of GPP was fixed as carbon sink during wet seasons and dry seasons, respectively. At the annual scale, about 28.4 % of GPP was fixed as net carbon sink, whereas the lowest ratio was observed in the year with the highest rainfall (2008, 17.6 %). In contrast, the highest ratio was found in the year with the lowest rainfall (2004, 34.4 %). Carbon sequestration in this forest exhibited strong temporal patterns on seasonal and interannual scales. Substantial amounts of atmospheric carbon were sequestered during the dry periods.

Table 2 Net ecosystem productivity (NEP, g C m^{-2} timescale^{-1}), gross primary productivity (GPP, g C m^{-2} timescale^{-1}), ecosystem respiration (ER, g C m^{-2} timescale^{-1}), and soil respiration (SR, g C m^{-2} timescale^{-1}) in dry seasons (October–March), wet seasons (April–September), and annual period

Year	NEP (g C m^{-2} timescale^{-1})			GPP (g C m^{-2} timescale^{-1})			ER (g C m^{-2} timescale^{-1})			SR (g C m^{-2} timescale^{-1})		
	Dry season (Oct–Mar)	Wet season (Apr–Sep)	Annual	Dry season (Oct–Mar)	Wet season (Apr–Sep)	Annual	Dry season (Oct–Mar)	Wet season (Apr–Sep)	Annual	Dry season (Oct–Mar)	Wet season (Apr–Sep)	Annual
2003	279	182	461	621	810	1,431	341	627	968	207	487	694
2004	285	204	489	575	844	1,419	290	640	930	191	491	682
2005	236	113	349	521	733	1,254	285	620	905	182	498	680
2006	244	109	353	573	776	1,349	329	666	995	214	526	740
2007	236	196	432	557	859	1,416	320	663	983	215	517	732
2008	185	46	231	548	758	1,306	363	712	1,075	257	564	821
2009	295	120	415	631	754	1,385	335	633	968	242	486	728
Ave.	251	139	390	575	791	1,366	323	652	975	215	510	725
CV (%)	15.2	41.6	22.3	6.8	6.1	4.9	8.6	4.9	5.5	12.3	5.6	6.7

The data of NEP, GPP, and ER were estimated from the Dinghushan flux tower, and SR in the old-growth subtropical forest was measured by chamber during the period 2003–2009

Ave average, *CV* coefficient of variation

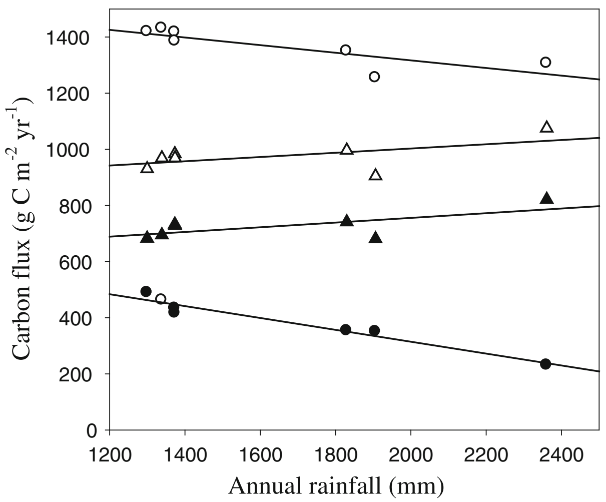

Fig. 2 Linear relationships between carbon fluxes (g C m^{-2} year^{-1}) [net ecosystem productivity (NEP, *filled circles*), gross primary productivity (GPP, *open circles*), ecosystem respiration (ER, *open triangles*), and soil respiration (SR, *filled triangles*)] and rainfall (mm) at the annual scale during the period 2003–2009

Carbon sequestration versus tree growth at seasonal scale

As shown in Fig. 3, tree growth observations at the same study site showed that the three dominant tree species could grow throughout the year. The difference of wood increment between the wet and dry seasons depended on the tree species. Trees of both *Ca. chinensis* and *S. superba* grew fast in the wet season, while no significant difference in *Cr. Chinensis* growth was found between the wet and dry seasons. The mean rate of wood increment of the three tree species in the wet season was 43.8 % higher than in the dry season (Fig. 3), in good general agreement with the variations in GPP within a year. In the period 2003–2009, the GPP during wet seasons was about 37.5 % higher than for dry seasons (Table 2). Although both the measured tree growth and estimated GPP declined in dry seasons, greater carbon sequestration was still found during this period. The seasonal variations in carbon sequestration were opposite to the seasonal dynamics in tree growth.

Discussion

Carbon sequestration in old-growth forests

Most results have shown that old-growth forests in tropical and subtropical regions are carbon sinks, ranging from 100 to 700 g C m^{-2} year^{-1} (Loescher et al. 2003; Vourlitis et al. 2004; Yamamoto et al. 2005; Hutyra et al. 2007; Kosugi et al. 2008). The 6-year average carbon sequestration in an old-growth Asian tropical rainforest was 168 g C m^{-2} year^{-1}, varying from 98 to 235 g C m^{-2} year^{-1} (Zhang et al. 2010). This forest (age >400 years) has been perfectly preserved in the Dinghushan Biosphere Reserve. Continuous carbon sequestration in this forest had also been found in previous studies using different approaches. For comparison, the results from three repeated biomass inventories in 1999, 2004, and 2008 (Zhang et al. 2003; Liu et al. 2007; Wang and Yang 2009) showed that plant biomass carbon was accumulated at a rate of

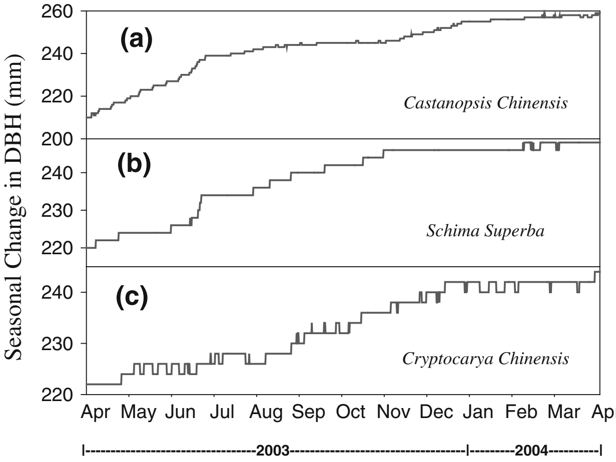

Fig. 3 Measured data by dendrometer band for the three tree species in the old-growth subtropical forest, showing the seasonal patterns of diameter at breast height (DBH, mm) increment from April 2003 to March 2004

360 g C m^2 $year^{-1}$ in the period 1999–2004 and 305 g C m^{-2} $year^{-1}$ during 2004–2008 [0.43 is the convention coefficient of carbon for this forest, as reported by Fang et al. (2003)]. A recent study using a biometric method estimated mean NEP of 115 ± 89 g C m^{-2} $year^{-1}$ during the long period 1982–2004 (Tang et al. 2011). In addition, the measured SOC stock in the top 20-cm soil layer presented a significant increase, with an average rate of 61 g C m^{-2} $year^{-1}$ during the period 1979–2003 (Zhou et al. 2006). Obviously, these studies embodied temporal trends of carbon dynamics and were unable to capture seasonal or interannual variations.

The classical view considers that tropical and subtropical forests have no seasonality of carbon exchange because of abundant rainfall and consistently warm temperature (Holdridge 1947; Richard 1996). However, a terrestrial ecosystem model (TEM) and integrated biosphere simulator (IBIS) predicted that carbon was gained in wet seasons and lost in dry seasons due to soil water limitations on tree growth (Tian et al. 1998; Botta et al. 2002). Observational evidence, however, shows that the actual carbon dynamics are more heterogeneous, with different sites behaving as sources and sinks at different times according to the seasonality of rainfall. Continuous eddy covariance measurements have proved that old-growth tropical forests are carbon sinks in dry seasons and carbon sources in wet seasons (Saleska et al. 2003; Zhang et al. 2010). Our measurements in this forest showed that tree growth and GPP declined in dry seasons, but net carbon was gained in both the wet and dry seasons. Moreover, substantial amounts of atmospheric carbon are sequestered during dry seasons. This variability in behavior suggests a level of complexity in the effects of soil water content on carbon fluxes that is not captured by TEM and IBIS models. At our study site, soil water content at 5 cm depth was 0.17 ± 0.02 and 0.24 ± 0.01 m^3 m^{-3} in dry and wet seasons, respectively. For details of the seasonal variations in soil water content at 5 cm depth, see Li et al. (2012). During dry seasons, many tree species do not suffer from the lower soil water content because they possess several attributes, including dry season deciduous habit, deep roots, and/or large capacity for osmoregulation (Eamus and Prior 2001). Under a given climate condition, whether plants will suffer from the lower soil water content during dry seasons critically depends on the ability to redistribute water from wet to dry parts of the profile (Jackson et al. 2000). Hydraulic redistribution has been demonstrated for many plant species, including tropical and subtropical tree species (Oliveira et al. 2005; Bleby et al. 2010).

At the interannual scale, large variations in annual NEP have been found in forests worldwide. In this forest, the annual NEP was about 390 g C m^{-2} $year^{-1}$ with standard deviation (SD) of 87 g C m^{-2} $year^{-1}$ during the period 2003–2009. The SD value for this forest is lower than the estimate of 105 g C m^{-2} $year^{-1}$ in an old-growth Douglas fir–western hemlock forest (Falk et al. 2008) and higher than the estimate of 56 g C m^{-2} $year^{-1}$ in temperate deciduous forests (Goulden et al. 1996). In boreal aspen forest and spruce forest, the SD of NEP was 99 and 21 g C m^{-2} $year^{-1}$, respectively (Krishnan et al. 2006, 2008). These results suggest that forest type is one of causes for the large variations in annual NEP.

Variables controlling carbon sequestration at seasonal and interannual scales

During the observation period, the average ER during wet seasons was about 101.5 % higher than for dry seasons (Table 2), but the average GPP during wet seasons was only about 37.5 % higher than for dry seasons (Table 2). This forest therefore presented greater NEP during the dry season, although the wet season is a growing season at this study site. High moisture and temperature in wet seasons favor tree growth and also improve biological activity and in turn SR (Yan et al. 2009). A previous study showed that a decrease in light-use efficiency and maximum photosynthesis rate in wet seasons would weaken the differences of GPP between dry and wet seasons (Zhang et al. 2006). It was concluded that carbon uptake by photosynthesis responded more weakly to changes in meteorological factors than did carbon release by respiration at the seasonal scale. Respiration therefore controlled the seasonal pattern of carbon sequestration in this forest. The same results were also found in Amazonia tropical forest and Asian tropical rainforest (Saleska et al. 2003; Zhang et al. 2010).

At the interannual scale, both GPP and ER showed small variations (Table 2), but a large variation in NEP was still found in this forest, with the greatest NEP in the driest year and the lowest NEP in the wettest year (Table 1). A previous study showed that the variations in NEP cannot be fully explained by the prompt responses of plant and ecosystem physiology to weather conditions (PAR, VPD, and temperature) on a long time scale (Ciais et al. 2005). Dunn et al. (2007) demonstrated that hydrological components of the forest ecosystem, particularly the depth of the water table, are the major drivers of interannual variations in NEP in a 160-year-old black spruce forest. In our study, annual rainfall may explain much of the observed interannual variability and trend of NEP in this forest (Fig. 2). During dry periods, hydraulic redistribution allows water to move from deep moist soil to the dry surface soil layer, where plant roots are more abundant. During wet periods, water can also move down from the surface layer to deep layer via roots to minimize loss through surface runoff. The response of NEP in forests to water status has a long time lag and cannot be detected on a short time scale. Consequently, the variations in NEP at interannual scale might be strongly influenced by hydrological components including the water table depth and rainfall pattern.

Conclusions

Based on measurements of eddy covariance, a static chamber system, and a dendrometer band data-logger system (tree growth), the seasonal and interannual variations in NEP in an old-growth forest in South China were investigated. We found the following:

1. NEP over 7 years (from 2003 to 2009) showed that this forest was a net carbon sink with average of 390 g C m^{-2} $year^{-1}$, ranging from 230 (in 2008) to 489 g C m^{-2} $year^{-1}$ (in 2004). The driest year had the greatest NEP, and the wettest year had the lowest NEP. Within a year, NEP during the dry season was about 81.4 % higher than for the wet season.
2. The strong seasonal variations in ER or SR compared with GPP in this forest resulted in substantial amounts of atmospheric carbon being sequestered during dry seasons. A decrease of GPP as well as an increase of ER or SR was driven by superfluous rain, which resulted in less NEP in rainy years.
3. Comparing carbon release by respiration with carbon gain by tree growth, we could conclude that GPP or living biomass carbon increment is not an overriding parameter controlling NEP, while the variations in ER or SR driven by the rainfall scheme were the dominant factor determining NEP in this forest.

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