Quantification of Ecosystem Carbon Exchange Characteristics in a Dominant Subtropical Evergreen Forest Ecosystem

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Abstract: CO₂ fluxes were measured continuously for three years (2003-2005) using the eddy covariance technique for the canopy layer with a height of 27 m above the ground in a dominant subtropical evergreen forest in Dinghushan, South China. By applying gapfilling methods, we quantified the different components of the carbon fluxes (net ecosystem exchange (NEE)), gross primary production (GPP) and ecosystem respiration (R_{eco}) in order to assess the effects of meteorological variables on these fluxes and the atmospherecanopy interactions on the forest carbon cycle. Our results showed that monthly average daily maximum net CO₂ exchange of the whole ecosystem varied from -3.79 to $-14.24 \mu mol m^{-2} s^{-1}$ and was linearly related to photosynthetic active radiation. The Dinghushan forest acted as a net carbon sink of -488 g C m⁻² y⁻¹, with a GPP of 1448 g C m⁻² y⁻¹, and a R_{eco} of 961 g C m⁻² y⁻¹. Using a carboxylase-based model, we compared the predicted fluxes of CO_2 with measurements. GPP was modelled as 1443 g C $m^{-2} y^{-1}$, and the model inversion results helped to explain ca. 90% of temporal variability of the measured ecosystem fluxes. Contribution of CO₂ fluxes in the subtropical forest in the dry season (October-March) was 62.2% of the annual total from the whole forest ecosystem. On average, 43.3% of the net annual carbon sink occurred between October and December, indicating that this time period is an important stage for uptake of CO_2 by the forest ecosystem from the atmosphere. Carbon uptake in the evergreen forest ecosystem is an indicator of the interaction of between the atmosphere and the canopy, especially in terms of driving climate factors such as temperature and rainfall events. We found that the Dinghushan evergreen forest is acting as a carbon sink almost year-round. The study can improve the evaluation of the net carbon uptake of tropical monsoon evergreen forest ecosystem in south China region under climate change conditions.

Key words: Dinghushan, eddy covariance, gap filling, CO_2 fluxes, net ecosystem exchange

1. Introduction

A recent study using biomass inventory data from China suggests that all forests in China are weak carbon (C) sources, with an emission rate of $0.022 \text{ Pg C y}^{-1}$ (Fang *et al.*, 2001; Piao

et al., 2009). The natural forests in China serve as weak carbon sinks, with an estimated 0.1 Pg C during the past decade (Fang *et al.*, 2001; Fang and Chen, 2001). Research conducted during the last few years; however, indicate that subtropical monsoon evergreen forests, which are representative of the forests in southern China at the regional scale, play a major role in CO_2 uptake due to their mature vegetation layers and also because of their evergreen nature (Yan *et al.*, 2006; Zhou *et al.*, 2006).

CO₂ is a major constituent of the greenhouse gases and its concentration in the atmosphere is directly influenced by human activities (Schimel, 1995; Houghton et al., 2001; Rannik et al., 2002), with significant impacts on global climate. Recent studies have confirmed the important role played by terrestrial vegetation in the current global climate change, particularly, the role of forests in the global carbon cycle (Global Change Newsletter, 1995). Thus, ecologists have an important role in evaluating CO₂ fluxes from terrestrial ecosystems. Previous studies have relied on chamber techniques or cuvettes to evaluate leaf-level or ecosystem level CO2 exchange processes of vegetation communities (Edwards and Sollins, 1973; Keller et al., 1986). However, such techniques are inherently limited, because they alter the local environment (Baldocchi et al., 1988). Chambers may also not apply when observing net CO_2 fluxes from the forest canopy or long-term, continuous measurements. Under such circumstances, the eddy covariance technique is more appropriate, and provides an alternative means for measuring CO₂ fluxes between the biosphere and the atmosphere. It is a non-invasive and non-destructive micrometeorological method which reveals continuous integrated signals with low spatial (typically 0.05 to 1 km²) but high time resolution (usually 30 minutes). It is a sound way to evaluate CO₂ uptake by the forest. Most of the flux towers in the existing world-wide network with long-term data are in North America and Europe. In the past decade, the flux tower network in Asia has been rapidly growing (Lee et al., 2004; Yu et al., 2006; Saigusa et al., 2008; Mizoguchi et al., 2009). Tower measurements of CO₂ fluxes over the dominant subtropical forest have been made since 2002 in South China by direct eddy covariance method within the Chinaflux network. The establishment of the Chinaflux network was based on the

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recognition that understanding of the gas-exchange processes between vegetation and the atmosphere is extremely important in global biogeochemical cycles and also in predicting future climate.

China's subtropical zone has unique features, which include the following: (1) A humid and warm climate, contrary to other regions at the same latitude around the globe that are extremely arid. (2) A long disturbance history, with intensive human activity in large areas that have left almost no mature oldgrowth forest. (3) The rapid industrialization in China during the past 20 years, especially in the southern part of the country, but was accompanied by the creation of large areas of young forest or rapid conversion of bare land in mountainous areas into forest. (4) Presence of evergreen forest, which differs significantly from other forests in terms of the carbon cycle, because it is stimulated by abundant precipitation and warm temperatures. Previous studies on the country's forest carbon budgets using forest inventory data (Fang and Chen, 2001; Wang et al., 2001) and process -based models (Cao et al., 2003) have been conducted. However, uncertainties still exist regarding the contributions of subtropical evergreen forests to the overall carbon budget.

Dinghushan Ecological Station, now known as Dinghushan Biosphere Reserve was established as a part of the Network of Biosphere Reserves organized by UNESCO in 1979. Since then measurements of microclimate, biomass, water balance, nutrient cycle, etc, have been carried out continuously. The Dingshuan Ecological Station forest is composed of dominant monsoon subtropical evergreen forest. The forest has been preserved very similar to its original form according to the Buddhist and local geomantic tradition, which regard the forest as a holy site. This subtropical monsoon forest has become an ideal research hot spot. Such regions of environmental/industrial transition are more sensitive to global climate change and the use of the eddy covariance technique could provide valuable net CO_2 flux data for assessing the role of these forests in the global C budget, i.e. whether they are a sink or source of carbon.

Various strategies have been applied to the eddy covariance method to describe spatial and temporal variation of ecosystems or at large scales (Potter et al., 1993; Running and Hunt, 1993; Bonan, 1995; Sellers et al., 1996; Chen et al., 1999; Liu et al., 1999), including numerous models used to study biophysical transport of trace gases, water and energy between land surface and the atmosphere. A standardized data processing is needed for an effective comparison across biomes and for underpinning inter-annual variability. However, consistent or standardized methodologies based on flux network observations have not yet been demonstrated. On the other hand, especially for this study site, the modeling analysis is a very important tool for measuring carbon exchange at a high temporal resolution for the unique climate features listed as above. Additionally, our flux tower in southern China, as a new member of Chinaflux network, is very important to the complete integration of flux research across all of China. A complete range of modeling work has yet to be completed at the Dinghushan site. We hypothesize that the Dinghushan forest plays a role as a carbon sink in the global C budget. We hypothesize that the seasonal variations in NEE in Dinghushan forests are largely driven by meteorological factors such as temperature, precipitation, and solar energy, and by vegetation characteristics. We also hypothesized that carbon is accumulated during the hot-humid season and the forest acts as a very weak carbon sink in dry season, but the carbon exchange rate is not greatly reduced in dry season with the less water, e.g. less soil moisture because of the lag effects of droughts.

The objectives of the study were: (1) to combine the EUROFLUX NEE calculation methodology with the Reichstein *et al.* (2005)-and Owen *et al.* (2007)-developed models to quantify a long-term measurement of forest CO_2 fluxes in a dominant subtropical evergreen forest ecosystem in southern China, (2) to compare measured net CO_2 fluxes using the eddy covariance technique with model predictions, and (3) identify the role of evergreen forests in the regional CO_2 budget.

2. Materials and methods

a. Site descriptions

The study site was located in the Dinghushan Biosphere Reserve, Guangdong Province, South China. The reserve is located between $23^{\circ}09'21''$ and $23^{\circ}11'30''N$ and $112^{\circ}30'39''$ and $112^{\circ}33'41''E$, with a total area of 1156 ha. The Reserve experiences a typical subtropical monsoon humid climate, with an average annual temperature of $20.9^{\circ}C$. The highest and lowest extreme temperatures recorded are $38.0^{\circ}C$ and $-0.2^{\circ}C$, respectively. The average annual rainfall is 1927 mm, of which more than 80% falls during the wet season (April-September) and the remaining during the dry season (October-March). Annual mean relative humidity is 82% (Tang *et al.*, 2006).

The rock formations are composed of sandstone and shale belonging to the Devonian Period. The predominant soil type is lateritic red earth, soil pH ranges between 4.5- 6.0 and a rich humus layer is common. The Biosphere Reserve contains a more than 400-year-old mature forest, which is subtropical monsoon evergreen broad-leaved forest dominated by Castanopsis chinensis, Schima superba, Cryptocarya chinensis, Cryptocarya concinna and Machilus chinensis, and its prophase succession communities, such as coniferous Masson pine forest and coniferous and broad-leaved mixed forest, which exist together. The flora of the Biosphere Reserve includes 260 families, 864 genera, and 1740 species of wild plants. The coniferous and broad-leaved mixed forest that was examined in the present study is about 100 years old, with dominant canopy species including Schima superba, Castanopsis chinensis, Pinus massoniana, a mean canopy height of 17 m above the ground, and a maximum of leaf area index of approximately 6.5.

b. CO₂ flux measurements via eddy covariance methodology

An open-path eddy covariance system was used from 2003

to 2005 at the study site to measure energy, latent heat and carbon dioxide exchange; the methods are described by Li et al. (2008a). The observation mast (cross-section $80 \text{ cm} \times 80 \text{ cm}$) was 38 m tall, the eddy covariance measurement height was 27 m, and sensors used for the measurements were the LI-7500 (LI-COR Inc., USA) open path CO₂ analyzer and CSAT3 sonic anemometer (Campbell Scientific, Inc., USA). Air temperature, CO₂ and water vapour concentrations as well as the wind velocity were sampled at a 10 Hz frequency. Covariance of the vertical velocity component and of the CO₂ concentration was computed every half hour. Planar fit rotation (Wilczak et al., 2001) and quality tests (Foken and Wichura, 1996) in the updated flux methodology (Foken et al., 2004) were applied. Based on the methods, a data-screening procedure was used to remove periods with weak turbulence when u* was less than 0.2 m s^{-1} .

We calculated the net ecosystem exchange rate (NEE) directly from flux data following the EUROFLUX methodology (Aubinet et al., 2000; including also updates by Lee et al., 2004; Mauder and Foken, 2006). A negative value of NEE means a net flux of CO₂ from the atmosphere to the ecosystem in the tower footprint, i.e., a gain in carbon by the ecosystem indicating that the ecosystem is a sink for carbon. The procedure of gap filling, using the marginal distribution sampling method, as well as the method for partitioning ecosystem respiration (Reco) and gross photosynthesis (GPP) from net CO₂ fluxes (NEE), using a short-term temperature dependent method, was carried out as described by Reichstein et al. (2005) and Owen et al. (2007). A negative value of NEE also indicates that the fluxes of gross phorosynthesis are greater than ecosystem respiration fluxes. All flux rates are reported either as μ mol CO₂ m⁻² s⁻¹ or as g C m⁻² per time unit

c. Meteorological data collecting

Meteorological data were also collected at seven levels in the canopy at 4, 9, 15, 21, 27, 31 and 36 m above the ground, in addition to three or five layers underneath the ground surface. 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 Company, Michigan, USA). PAR (Photosynthetic photon flux density) was measured with sensors Li190SB (LI-COR Inc., USA) and LQS70-10 (Apogee, Logan, UT, USA). Temperature, humidity (HMP45C, Campbell Inc., USA and IRTS-P, Apogee, Logan, UT, USA), wind velocity (A100R, Vector, UK) and wind direction (W200P, Vector, UK) were measured at every level. Soil temperature was measured at five depths of 5, 10, 15, 20 and 40 cm or 20, 40, 60, 80 and 100 cm with two types of probes (105-T and 107-L, Campbell Inc., USA) and soil moisture (CS616, Campbell Inc., USA) was measured at three depths of 5, 20 and 40 cm. All these routine meteorological signals were directly recorded with the data loggers (3 CR10X and 1 CR23X, Campbell Inc., USA). All recorded data were averaged into 30 minute mean values.

d. Physiologically-based process model

In order to simplify the characteristics of ecosystem fluxes, a physiologically-based process model was utilized. The model applied to describe light interception and leaf gas exchange is single-layered and defines sun and shade light classes for canopy foliage. We used the measured $\mathbf{R}_{\mathrm{eco}}$ from the night measurements to estimate the $R_{\rm eco}$ during the light measurements; and then obtained $GPP = NEE + R_{eco}$. Based on the assumptions, LAI had little influence with respect to evergreen forests (cf. Owen et al., 2007). We relaxed the data requirements for model inversions, obtaining parameter estimates for Vcuptake, the leaf carboxylation capacity (μ mol m⁻² leaf area s^{-1}), using the Dinghushan site seasonal maximum LAI value. The model inversion method does not require separation of parameterization and validation processes. Radiation distribution in the model onto sun and shaded leaves is described according to Chen et al. (1999) with (an effect of foliage clumping index) assumed at 0.7 for evergreen forest. The light interception of the sunlit and shaded leaves is used along with absorption and emission of long-wave radiation, convective heat loss and latent heat loss through transpiration to calculate the energy balance of leaves in two classes (sunlit and shaded). The simulation of gross photosynthesis follows Farquhar and von Caemmerer (1982) as modified for field applications by Harley and Tenhunen (1991). Model inversions for parameter estimation are based on Ribulose-1,5-bisphosphate-carboxylaseoxygenase (Rubisco) enzyme reactions where the rate of CO_2 fixation is limited by either the regeneration of Ribulose-1,5biphosphate (RuBP) at low light intensity and/or high internal CO₂ concentration; or by Rubisco activity and CO₂/O₂-concentration at saturated light and low internal CO₂ concentration (cf., Reichstein 2001). Further details about the physiological model are described in Owen et al. (2007) and Li et al. (2008a). Differing from Owen et al. (2007) in which the parameters were estimated on a ten day basis, parameter determination in this study was carried out for each day. The parameter Vcuptake1*, the average leaf carboxylation capacity at 25°C, (single parameter model inversion, notation consistent with Owen et al. (2007)) was estimated for daily flux measurements at the Dinghushan site. The daily basis estimation was expected to reveal a distinct pattern that may have been hidden in a 7 or 10 day estimation.

e. Statistical analysis

Nonlinear and linear regressions for the GPP and NEE model fitting were performed with the SigmaPlot 2002 version 8.0 statistical package. In order to smooth daily CO_2 flux values to visualize the pattern of annual daily GPP, NEE and R_{eco} using SigmaPlot, we chose the negative exponential smoother with a sampling proportion of 0.1 and a polynomial degree of 1.

2005. Daily mean soil moisture, soil temperature at 5 cm depth and daily precipitation are shown in Fig. 2. The patterns of

monthly daytime mean solar radiation, mean vapor pressure

3. Results

a. Climate

Figures 1 and 2 show the prevailing climatic conditions in Dinghushan during the three year period between 2003 and



Fig. 1. Variations of monthly daytime mean values in (a) PPFD (photosynthetic photon flux density) measured from 1100 to 1300 LST, (b) air temperature, (c) VPD (water vapor pressure deficit) and (d) wind speed at the Dinghushan site at 38 m height aboveground during 2003 to 2005.



Fig. 2. Temporal course of daily mean soil moisture and soil temperature at 5 cm depth, and daily precipitation at the Dinghushan site from 2003 to 2005.

soil temperature. In terms of temperature and precipitation, the general annual climate pattern includes a hot-humid season (April-September) and a cool-dry season (October-March) (Figs. 1 and 2). Monthly mean air temperature varied between 20.3 and 27.8°C in the hot-humid season with frequent typhoon, storm or extreme rainy events and 11.0 and 23.4°C in the cooldry season with relatively few occurrences of freezing or extremely high temperatures. The mean annual total precipitation for this study period is 1876 mm. During the observation period, the mean maximum monthly daytime value of solar radiation was 420.3 W m⁻²; the mean maximum monthly daytime value of VPD was 1.4 kPa and yearly variations in the range of 0.2 to 1.4 kPa. Wind speed was generally no more than 4 m s^{-1} and the average annual wind speed during the daytime was 2.3 m s^{-1} .

b. Ecosystem fluxes

Results of the flux separation in the period of 2003-2005 are illustrated in Fig. 3. It shows the daily course of GPP, Reco and NEE. Monthly average NEE, R_{eco} and GPP values are presented in Table 1. Based on the daily course, one finds a clear picture of the seasonal change of ecosystem fluxes. The ecosystem acted as a daily carbon sink except for a short period in 2005 (DOY 77-DOY117) when it acted as a weak carbon source. The winter time also performed a strong role in carbon uptake. NEE exhibited a clear pattern with little interannual variation (Table 1, Fig. 4). Monthly means of NEE pooled over the three years characterize the NEE pattern of an average year (Fig. 4a). The ecosystem acted as a CO₂ sink year-round with an average of $-40.7 \text{ g C m}^{-2} \text{ month}^{-1}$ and a total carbon sequestration of 488 g C m⁻²y⁻¹ (Fig. 4). The net CO₂ exchange budget in the cool-dry season, e.g. October and December were much more negative indicating a strong carbon sink activity, while



Fig. 3. Pattern of daily ecosystem CO₂ fluxes. Gross primary production (GPP; bold solid line), ecosystem respiration (R_{eco}; grey solid line) and net ecosystem exchange (NEE; grey dashed line). For ease of visualization of the seasonal changes, fluxes were smoothed as described in section 2.

the hot-humid season, e.g. April was less negative indicating a weak carbon sink activity. Generally, 38% ($-184.4 \text{ g C m}^{-2} \text{ v}^{-1}$) of the annual carbon sink occurred during the hot-humid season, while contribution of CO₂ fluxes in the cool-dry season was 62% ($-304 \text{ g C m}^{-2} \text{ y}^{-1}$) of the annual total. The daily net CO2 exchange was very large in October, November and December (Figs. 4a and 4b), indicating that this time period is an important stage for uptake of CO₂ by the forest ecosystem

Table 1. Monthly average CO₂ fluxes. Units for NEE, R_{eco} and GPP are μ mol m⁻² s⁻¹, standard error is provided in parentheses, negative NEE values indicate that the Dinghushan forest is a carbon sink.

Month of year	2003						2004					2005						
	NEE		R _{eco}		GPP		NEE		R _{eco}		GPP		NEE		R _{eco}		GPP	
1	-2.01	(1.54)	1.41	(0.53)	3.42	(1.23)	-1.56	(1.35)	1.23	(0.46)	2.79	(1.62)	-1.14	(1.20)	1.65	(0.45)	2.79	(1.19)
2	-0.39	(1.17)	2.60	(1.40)	2.99	(1.28)	-0.92	(1.26)	1.72	(0.51)	2.64	(1.20)	-0.37	(1.81)	2.51	(1.28)	2.88	(1.45)
3	-2.19	(2.57)	2.39	(0.57)	4.58	(2.73)	-0.33	(1.15)	2.10	(0.32)	2.43	(1.06)	-0.15	(1.46)	2.33	(1.09)	2.48	(1.04)
4	-1.01	(1.96)	2.89	(0.49)	3.89	(2.03)	-0.45	(1.53)	3.76	(0.63)	4.22	(1.68)	0.19	(1.69)	3.06	(0.33)	2.87	(1.84)
5	-1.59	(1.54)	3.02	(0.33)	4.61	(1.38)	-0.73	(1.48)	4.50	(0.52)	5.23	(1.46)	-0.95	(1.07)	2.83	(0.69)	3.78	(1.36)
6	-0.80	(1.50)	2.65	(0.24)	3.45	(1.65)	-1.74	(1.09)	3.24	(0.52)	4.98	(1.01)	0.09	(1.14)	3.58	(0.66)	3.50	(1.41)
7	-0.90	(0.81)	3.70	(0.50)	4.60	(0.89)	-1.14	(0.49)	3.60	(0.14)	4.74	(0.50)	-1.06	(1.13)	3.44	(0.52)	4.50	(1.25)
8	-0.46	(1.01)	4.10	(0.58)	4.56	(1.20)	-0.97	(1.47)	2.88	(0.47)	3.84	(1.57)	-1.15	(1.25)	4.02	(0.78)	5.17	(1.55)
9	-1.22	(1.73)	2.70	(0.25)	3.92	(1.74)	-2.78	(1.65)	2.41	(1.03)	5.19	(1.29)	-1.48	(1.48)	3.34	(0.35)	4.82	(1.63)
10	-2.43	(1.67)	2.32	(1.11)	4.75	(1.30)	-2.97	(0.61)	1.64	(0.56)	4.61	(0.65)	-2.85	(0.78)	2.80	(0.50)	5.65	(0.96)
11	-2.00	(1.24)	1.98	(0.49)	3.99	(1.11)	-2.29	(0.90)	1.53	(0.46)	3.82	(0.77)	-1.99	(1.02)	2.43	(0.48)	4.42	(0.86)
12	-2.59	(0.69)	1.26	(0.23)	3.85	(0.71)	-1.74	(1.20)	1.37	(0.39)	3.11	(1.17)	-1.80	(0.99)	1.64	(0.46)	3.44	(1.20)



Fig. 4. (a) Monthly average net ecosystem exchange of CO_2 (NEE) from 2003 to 2005 and accumulated NEE. Vertical bar shows the standard errors. (b) Portion of the total NEE variance attributed to each month.

from the atmosphere. In all, these results indicate that the Dinghushan evergreen forest is acting as a carbon sink in the global C budget.

Interannual variation of the annual budget of NEE, GPP, and R_{eco} and their modelled values is presented in Table 2. The measured NEE varied from -373 to -516 g C m⁻² y⁻¹, respectively (Table 2), measured GPP varied from 1411 to 1483 g C m⁻² y⁻¹, and measured R_{eco} ranged from 915 to 1023 g C m⁻² y⁻¹ over the three years.

Figure 5a shows the relationship between monthly averaged daily NEE and incident photosynthetic active radiation (PAR), both using averages for the time period of 1100 to 1300 LST, typically when the potential maximum photosynthetic capacity occurs. The NEE ranged from -3.79 to -14.24 µmol m⁻² s⁻¹

and was linearly related to PAR (NEE = $-0.0081 \times PAR$, R² = 0.60, P < 0.001). The pattern of total monthly precipitation shows there was a gap that separated the precipitation distribution into two sets. Linear regression shows that precipitation affected NEE at the significant level of P = 0.01 (Fig. 5b). Ecosystem respiration (R_{eco}) exhibited an exponential relation with soil temperature at the 5 cm depth (Fig. 6a). Nonlinear regression was applied to test the relationship between R_{eco} and its interaction with soil temperature (T_{soil}) and soil moisture (θ), which can be described as R_{eco} = 0.0872 × T_{soil} + 7.44 × θ – 0.68 (R² = 0.63, P < 0.001) (Fig. 6b). Again, a linear regression was applied to test the relationship between GPP and air temperature, it shows an exponential relation with air temperature (Fig. 7). This supports that the seasonal variations

Table 2. Annual budgets of measured and modelled NEE, R_{eco} , and GPP. Integrated CO₂ flux values shown are in g C m⁻².

Year	Measaured NEE	Modelled NEE	NEE R ²	Measured GPP	Modelled GPP	GPP R ²	Measured R_{eco}	Modelled R _{eco}	$R_{eco} R^2$
2003	-539	-514	0.90	1483	1479	0.92	944	965	0.90
2004	-537	-516	0.89	1452	1448	0.89	915	932	0.88
2005	-388	-373	0.91	1411	1402	0.93	1023	1029	0.92
Average	-488	-467	-	1448	1443	-	961	975	-



Fig. 5. Correlations between measured monthly daytime net CO_2 fluxes (NEE) and (a) monthly average midday PAR and (b) total monthly precipitation. PAR and NEE measurements were averaged during the midday (e.g., 1100 - 1300 LST, when the photosynthetic signal is the strongest).



Fig. 6. Correlations between monthly ecosystem respiration (R_{eco}) , mean soil temperature and mean soil moisture.



Fig. 7. Correlation between monthly mean GPP and monthly daytime mean air temperature.

in NEE in Dinghushan forest are largely driven by temperature.

c. Process-based model parameter and modelled GPP

The influences on carbon exchange of forest ecosystems are complicated due to ecological processes with high spatial and



Fig. 8. Comparison of modeled GPP and measured GPP for the physiologically-based process model applied over the three years (2003-2005).

temporal variability. In order to simplify those multiple variables to describe the characteristics of this evergreen forest, we introduced the process-based physiological model to quantify the capacity of carbon uptake. As a test, the parameters of Vcuptake1* were estimated in 2004 and are shown in Fig. 8. Figure 8 shows that the parameter Vcuptake1*, which is the maximum uptake capacity, followed the daily GPP (Fig. 8). The other two years (2003 and 2005) follow a similar pattern for the relationship between Vcuptake1* and GPP (data not shown). Along with the parameter estimation, the daily GPP was also modelled (Fig. 9). Yearly budgets of modelled NEE, R_{eco} , and GPP for the three consecutive years are listed in Table 2. One finds the modelled daily GPP can explain more than 90% of the variation of measured eddy GPP.

4. Discussion and conclusion

Environmental conditions influence the carbon exchange processes between forest ecosystems and the atmosphere. Gap filling methods and model inversion helped us to recognize the CO₂ exchange characteristics of the evergreen forest in Dinghushan in lower subtropical China, which can be partly explained by meteorological factors. CO₂ fluxes were dependent mainly on the variation in PAR, which is similar to findings in a previous study (Rannik et al., 2002). Figure 1a showed the pattern of PPFD which partly explains the pattern of carbon uptake in Fig. 3. The PPFD values in the hot-humid season were lower than in winter time due to foggy or cloudy days that frequently occurred in the spring or summer (Yu et al., 2008), which resulted in a strong carbon sink in winter time. The daily maximum average CO_2 uptake capacity by the forest occurring between 11:00 am and 1:00 pm is -14 μ mol m⁻² s⁻¹ (Fig. 5), and the incident potential maximum is -20 umol m⁻² s⁻¹, which was similar to previous studies in temperate deciduous broad-leaved forest and black spruce forest (Baldocchi and Vogel, 1996; Michael et al., 1997) and lower than the range of 18-27 μ mol m⁻² s⁻¹ found in boreal aspen forest (Black, 1996). Responses to amounts of precipitation by



Fig. 9. Estimated daily GPP during 2004 from eddy covariance measurements (open circles) and annual course for estimated daily Vcuptake1* (solid line) obtained from inversion of the physiology-based model.

assimilation of atmospheric CO₂ showed the NEE has a strong relationship with precipitation during drought conditions (Reichstein *et al.*, 2002). In the Dinghushan site, the relationship between monthly NEE and precipitation was not so strong (P = 0.01, significant, Fig. 5b), suggesting that precipitation was not the dominated factor to control CO₂ uptake. On the other hand, rainfall events have significant effects on CO₂ uptake by stimulating soil respiration and reducing plant photosynthesis (Davidson *et al.*, 1998; Michael *et al.*, 2002; Wright *et al.*, 2006). Many rainfall events during the wet season could explain why this forest ecosystem acted as a relative weak carbon sinks. Finally, these climate factors can influence carbon exchange processes between the forest ecosystem and the atmosphere.

Understanding the ecosystem respiration is very important to quantify the ecosystem fluxes, and environmental variables

such as soil temperature, soil water content, air temperature, PAR and air humidity significantly affect ecosystem CO₂ exchange (Lloyd and Taylor, 1994; Davidson et al., 1998; Li et al., 2008b). Correlations of R_{eco} and soil temperature and soil moisture are presented in Figs. 6a and 6b. It suggests that 55% of the variation in ecosystem respiration can be explained by soil temperature. Considering soil temperature and soil moisture, 63% of the variation can be explained, and therefore we can infer that ecosystem respiration was controlled by abiotic and biotic factors due to its high heterogeneity. Zhou et al. (2006b) reported that the dynamic underground biomass was also affected by the change from carbon sink to source along with the seasonal change. From March to May, CO₂ exchange capacity was weak and the ecosystem was found to be a weak carbon sink, whereas during September to November, it proved to be a strong carbon sink. Alternatively, it proved that carbon accumulates during the hot-humid season, whereas the forest acts as a very weak carbon sink in the dry season. In summary, the Dinghushan forest plays a role as a carbon sink in the global C budget.

For the consecutive years of 2003 to 2005, the annual NEE was -539, -539 and -388 g m⁻² y⁻¹, respectively. Our observations showed the carbon gain pattern in Dinghushan in the winter/dry season was quite different from summer/humid season for this subtropical region in China. Inter-annual differences in net ecosystem exchange (NEE) in the Dinghushan forest ecosystem studied here-as reflected in the processes of photosynthesis (GPP) and ecosystem respiration (Reco)-depended more on seasonal climate factors, like air temperature, rather than precipitation. Extreme weather events and vegetation characteristics, such as biomass and LAI conditions, also contribute to inter-annual variability in NEE. Particularly, we noticed a large interannual variation of NEE during our three years of study (i.e., 30% reduction in 2005, despite no major changes in environmental conditions during the three years) that can be explained by the physical damage from two landslides and more frequent typhoons in 2005, which reduced LAI and green biomass. Generally, the net carbon sink at Dinghushan was larger than a Mediterranean evergreen forest at the Puéchabon in the south of France (ca. $-250 \text{ g C m}^{-2} \text{ y}^{-1}$) (Allard et al., 2008). These findings suggest that the dominant monsoon subtropical evergreen forest in Dinghushan could be a good model forest for the net carbon uptake under the Kyoto protocol for southern China.

Model inversion results showed that the modelled GPP agrees well with the estimated GPP by eddy covariance measurement, and hence we concluded that the model inversion is also a good tool for estimating GPP.

In summary, the eddy covariance measurement technique was a good instrument to provide an overall picture of the carbon dynamics in the evergreen forest in south China. The quantification of CO_2 exchange proved the evergreen forest played a role as a carbon sink year-round, indicating that the evergreen forest ecosystem is very important in China and should be investigated further in the sphere of climate change.

The old-growth forest soil accumulates carbon in Dinghushan (Zhou et al., 2006a); and it can be inferred that the behavior of the canopy of the old-growth forest is consistent with the soil carbon change during the process of forest succession. Atmosphere-canopy interactions in Dinghushan forests enhanced carbon uptake via the interconnections of meteorology, atmospheric chemistry and forest carbon cycle. In the face of global warming, the carbon gain function of the evergreen forest ecosystem in lower subtropical China is often thought to be a very important ecosystem service. Therefore the evergreen forest ecosystem in Dinghushan is a good reference for reforestation plans in response to the Kyoto Protocol and greenhouse gas emissions, especially in harmonizing the demand of economical development and environmental protection in south China. Studies on the interactions between the canopy and atmosphere and their regulation of carbon dioxide emissions can improve both our understanding of terrestrial ecosystems and our ability to predict regional-and global-scale ranges in atmospheric chemistry.

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