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Environmental controls over carbon exchange of three forest ecosystems in eastern China

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Abstract

Net ecosystem productivity (NEP) was continuously measured using the eddy covariance (EC) technique from 2003 to 2005 at three forest sites of ChinaFLUX. The forests include Changbaishan temperate mixed forest (CBS), Qianyanzhou subtropical coniferous plantation (QYZ), and Dinghushan subtropical evergreen broad-leaved forest (DHS). They span wide ranges of temperature and precipitation and are influenced by the eastern Asian monsoon climate to varying extent. In this study, we estimated ecosystem respiration (RE) and gross ecosystem productivity (GEP). Comparison of ecosystem carbon exchange among the three forests shows that RE was mainly determined by temperature, with the forest at CBS exhibiting the highest temperature sensitivity among the three ecosystems. The RE was highly dependent on GEP across the three forests, and the ratio of RE to GEP decreased along the North–South Transect of Eastern China (NSTEC) (i.e. from the CBS to the DHS), with an average of 0.77 ± 0.06. Daily GEP was mainly influenced by temperature at CBS, whereas photosynthetic photon flux density was the dominant factor affecting the daily GEP at both QYZ and DHS. Temperature mainly determined the pattern of the interannual variations of ecosystem carbon exchange at CBS. However, water availability primarily controlled the interannual variations of ecosystem carbon exchange at QYZ. At DHS, NEP attained the highest values at the beginning of the dry seasons (autumn) rather than the rainy seasons (summer), probably because insufficient radiation and frequent fog during the rainy seasons hindered canopy photosynthesis. All the three forest ecosystems acted as a carbon sink from 2003 to 2005. The annual average values of NEP at CBS, QYZ, and DHS were 259 ± 19, 354 ± 34, and 434 ± 66 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, respectively. The slope of NEP that decreased with increasing latitude along the NSTEC was markedly different from that observed on the forest transect in the European continent. Long-term flux measurements over more forest ecosystems along the NSTEC will further help verify such a difference between the European forest transect and the NSTEC and provide insights into the responses of ecosystem carbon exchange to climate change in China.

Keywords: ChinaFLUX, eastern Asian monsoon, ecosystem respiration (RE), eddy covariance, gross ecosystem productivity (GEP), net ecosystem productivity (NEP), North–South Transect of Eastern China (NSTEC)

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Introduction

Forests play an important role in global carbon cycle (Tans *et al*., 1990; Malhi *et al*., 1999; Valentini *et al*., 2000; Barford *et al*., 2001; Fang *et al*., 2001). Carbon exchange between the forest ecosystem and the atmosphere is one of the key processes that need to be assessed in the context of the Kyoto Protocol (IPCC, 2001). Net ecosystem productivity (NEP) between the biosphere and the atmosphere results from the balance between the assimilatory influxes due to foliage photosynthesis (gross

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ecosystem productivity, GEP) and the respiratory effluxes from autotrophs and heterotrophs (ecosystem respiration, RE). These flux processes are substantially subject to the environmental conditions and climate change (Malhi *et al.*, 1999; Law *et al.*, 2002).

The potential of natural and planted forests in China for carbon sequestration has been addressed recently in the literature (e.g. Fang *et al.*, 2001; Guan *et al.*, 2006; Wen *et al.*, 2006; Zhang *et al.*, 2006a, b). There is, however, much uncertainty in the quantitative estimation of such potential. Fang *et al.* (2001) pointed out that the planted forest (afforestation and reforestation), which absorbed 0.45 $\mathrm{Pg\,C\,yr^{-1}}$, was the primary reason for the increase in carbon absorption by the terrestrial ecosystems in China. For years, the old-growth forest was traditionally treated as negligible carbon sink in the classic ecological theory, because its NEP was considered to be in equilibrium and at the maximum of carbon sequestration capacity under certain environmental and climatic conditions (Odum, 1969). However, some recent studies suggested that the carbon uptake of old forests was underestimated in the global carbon cycle (Zhou *et al.*, 2006). Currently, about 18.21% (or 175 million hectares) of the total land area of China is covered by forest, and the planted forest area is 5.52% (or 53 million hectares). The forest carbon storage in China is, therefore, assumed to play an important role in global carbon cycle (Fang *et al.*, 2001). However, so far very few studies have addressed the role of CO_2 sequestration by different natural and planted forests in China based on eddy covariance (EC) measurements (Yu *et al.*, 2006).

Because of the influence of the eastern Asian monsoon, the climate in Asia differs from that in Europe and in North America, with apparent latitudinal gradients of temperature and precipitation along the North–South Transect of Eastern China (NSTEC) (Yu *et al.*, 2006). A vegetation sequence is distributed along the NSTEC, including the cold temperate coniferous forest, temperate mixed forests, warm temperate deciduous broadleaf forest, subtropical evergreen coniferous forest, evergreen broadleaf forest, and tropical rainforest from the north to the south. Comparison of the carbon exchange of different forests can help understand the environmental controls of ecosystem carbon sequestration in eastern China and elucidate the response and adaptation of these forests to climate change.

Estimation of the carbon exchange at the ecosystem level has been approached by means of the EC technique (Baldocchi *et al.*, 2001). The long-term carbon flux observation of ChinaFLUX provides us much information on the responses of ecosystem carbon exchange to climate change in China (Yu *et al.*, 2006, 2008). The main objectives of this study were to quantify the seasonal and interannual patterns of RE, GEP, and NEP at three forest ecosystems in ChinaFLUX selected along the NSTEC, and to explore their responses to climatic variables. We also compared the difference in the latitudinal trend of NEP of eastern China with that of the European continent.

Materials and methods

Site descriptions

As a part of the ChinaFLUX network, the eddy fluxes of carbon dioxide and water vapor were measured at three forests sites in eastern China since late 2002. These forests are Changbaishan temperate mixed forest (CBS), Qianyanzhou subtropical coniferous plantation (QYZ), and Dinghushan subtropical evergreen broadleaved forest (DHS), with a stand age of 200, 23, and 100 years, respectively. The mean annual temperatures from 1985 to 2005 were 3.6, 17.9, and 21.0 °C for CBS, QYZ, and DHS, respectively. The average annual precipitation over these 20 years was 695, 1485, and 1956 mm, respectively. All the three forests have been treated as natural reservation area without human management (fertilization, irrigation, etc.). Table 1 gives site descriptions, and more details of the site information are available in the literature (Wen *et al.*, 2006; Yu *et al.*, 2006, 2008; Zhang *et al.*, 2006a, b).

Measurements and instrumentation

CO_2 fluxes were measured with EC systems from January 1, 2003, to December 31, 2005 (Yu *et al.*, 2006). The EC systems consisted of open-path infrared gas analyzers (Model LI-7500, LICOR Inc., Lincoln, NE, USA) and 3-D sonic anemometers (Model CSAT3, Campbell Scientific Inc., Logan, UT, USA). The signals of the instruments were recorded at 10 Hz by CR5000 datalogger (Model CR5000, Campbell Scientific Inc.) and then block-averaged over 30-min intervals for analyses and archiving.

The meteorological variables were measured simultaneously with the eddy fluxes. Global radiation and net radiation were measured with radiometers (Model CM11 and Model CNR-1, Kipp & Zonnen, Delft, the Netherlands). Photosynthetic photon flux density (Q_P) above and within the canopy was measured with a quantum sensor (Model LI190SB, LICOR Inc.) and five quantum sensors (Model LQS7010-SUN, APOGEE, Logan, UT, USA), respectively. Air temperature and relative humidity profiles were measured with shielded and aspirated probes (Model HMP45C, Campbell Scientific Inc.) at different heights above and within canopy. Vapor pressure deficit (VPD) was calculated as

Table 1 Site descriptions

Sites	CBS	QYZ	DHS
Location	42°24′N, 128°05′E	26°44′N, 115°03′E	23°10′N, 112°34′E
Elevation (m)	738	102	300
Topography	Flat	Hilly	Hilly
Mean annual temperature (°C)*	3.6	17.9	21.0
Annual precipitation (mm)*	695	1485	1956
Predominant species	*Pinus koriaensis*, *Tilia amurensis*, *Acer mono*, *Quercus mongolica*, *Fraxinus mandshurica*	*Pinus massoniana* Lamb, *Pinus elliottii* Engelm, *Cunninghamia lanceolata* Hook	*Schima superba*, *Castanopsis chinensi*, *Pinus massoniana*
Stand age (years)	~200	23	~100
Canopy height (m)	26	12	20
Leaf area index (LAI)	6.1	3.5	4.0
Soil type†	Montane dark brown forest soil	Red soil	Lateritic red soil, yellow soil
Soil texture†	16% (2.0–0.05 mm) 59% (0.05–0.002 mm) 25% (<0.002 mm)	17% (2.0–0.05 mm) 68% (0.05–0.002 mm) 15% (<0.002 mm)	18% (2.0–0.05 mm) 63% (0.05–0.002 mm) 19% (<0.002 mm)
Soil organic matter ($\mathrm{g\,kg^{-1}}$)†	87.5	21.4	37.7
Soil pH†	5.0	4.7	3.8
Height of the eddy covariance system (m)‡	41.5	39.6	27.0
Air temperature and humidity (m)‡	2.5, 8.0, 22.0, 26.0, 32.0, 50.0, 61.8	1.6, 7.6, 11.6, 15.6, 23.6, 31.6, 39.6	4, 9, 15, 21, 27, 31, 36
Soil temperature (cm)‡	0, 5, 10, 20, 50, 100	2, 5, 20, 50, 100	5, 10, 20, 50, 100
Soil moisture (cm)‡	5, 20, 50	5, 20, 50	5, 20, 50

*The values are the averages from 1985 to 2005.

†Data source: database of Chinese Ecosystem Research Network (CERN).

‡The height and depth indicate the location of the sensors mounted.

the difference between the saturation and actual vapor pressures at the given temperature based on the measured relative humidity and air temperature. Precipitation was recorded with a rain gauge (Model 52203, Rm Young, Traverse City, MI, USA) above the canopy. Soil temperature and soil moisture were measured using thermocouple probes (Model 105T, Campbell Scientific Inc.) and water content reflectometers (Model CS616, Campbell Scientific Inc.), respectively. All micrometeorological measurements were recorded at 30-min intervals with dataloggers (Model CR10X & CR23X, Campbell Scientific Inc.). Detailed information on routine meteorological variables is summarized in Table 1.

Flux calculation and correction

The flux of NEP ($\mathrm{mg\,CO_2\,m^{-2}\,s^{-1}}$) between the biosphere and the atmosphere was calculated using Eqn (1), which ignored all advective terms in the mass conservation equation:

$$\mathrm{NEP} = -\left(\overline{w'\rho_c'(z_r)} + \int_0^{z_r} \frac{\partial \bar{\rho}_c}{\partial t}\mathrm{d}z\right), \tag{1}$$

where the first term inside the parentheses on the right-hand side of Eqn (1) is the eddy flux of CO_2, and the second term is the CO_2 storage below the height of EC observation (z_r); w represents the vertical wind velocity ($\mathrm{m\,s^{-1}}$), ρ_c represents the CO_2 concentration (in $\mathrm{mmol\,m^{-3}}$) fluctuations, and primes are the deviations from the time-averaged mean. The overbar indicates a time-averaged mean.

Determination of NEP required accurate rate of change of CO_2 storage calculations (Hollinger *et al.*, 1994; Baldocchi *et al.*, 2000; Finnigan, 2006). Storage below the EC height (S_c) was estimated by the simple method using the temporal change in CO_2 concentration above the canopy measured with LI-7500 (Carrara *et al.*, 2003; Zha *et al.*, 2004).

$$S_c = \frac{\Delta c(z_r)}{\Delta t}\Delta z_r, \quad (2)$$

where S_c is the storage flux, $\Delta c(z)$ the change in CO_2 at height z_r, Δt the time period, and Δz_r the height of the layer. The long-term sum of the storage flux was assumed to be zero (Baldocchi *et al.*, 2000). The monthly sum of storage at our sites was generally less than $\pm 4\,\mathrm{g\,C\,m^{-2}\,month^{-1}}$, and the 3-year integral storage flux was −33, −38, and $-45\,\mathrm{g\,C\,m^{-2}}$ for CBS, QYZ, and DHS, respectively. The storage flux was too low to bias the annual sum of NEP, and the annual sum of the storage approached zero as the data coverage (i.e. the ratio of remaining data after quality control) got better.

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

For QYZ and DHS, the topography is more complex than that at CBS which is flat. The relative altitude is 20–50 m at QYZ, and the terrain of DHS is much complicated than that of the other two sites. With the FSAM (flux source area model), Mi *et al.* (2006) indicated that the footprint was 181, 120, and 129 m for CBS, QYZ, and DHS under unstable conditions, respectively, while 3070, 1655, and 1908 m under stable conditions, respectively. Generally, the fetch of each site could satisfy the requirement of footprint and >70% flux came from the target ecosystems that EC applied (Mi *et al.*, 2006). During the data processing, we excluded the data under stable conditions with a reasonable u_* threshold ($\mathrm{m\,s^{-1}}$) which was helpful to reduce the effect of insufficient fetch and turbulence. The energy balance closure was 83%, 77%, and 82% at CBS, QYZ, and DHS, respectively (Li *et al.*, 2005). The characteristics of the instrument, and the quality and reliability of the flux measurements of ChinaFLUX were reported elsewhere (Wen *et al.*, 2005; Sun *et al.*, 2006b). At QYZ site, Wen *et al.* (2005) indicated that the distributions of both co-spectral and power-spectral followed the theoretic laws, and there was no obvious loss of high-frequency flux.

Because of the difference in experimental setup and methodology used for the spatial integration in advective flux measurement (Feigenwinter *et al.*, 2008), the generally acceptable approach was still not available for advective flux estimation, resulting in difficulty in correcting eddy flux with a single tower. In this study, we still used Eqn (1) to estimate the NEP and neglected all other advective terms.

Under the stable conditions during night-time (global radiation $<1\,\mathrm{W\,m^{-2}}$), the canopy storage and advection were likely to cause underestimation of CO_2 fluxes measured by the EC system. Therefore, we screened the night-time flux data by using site-specific thresholds of friction velocity (u_*) (i.e. 0.15, 0.20, and $0.25\,\mathrm{m\,s^{-1}}$ for CBS, QYZ, and DHS, respectively), above which the parameters of an exponential regression between night-time RE and soil temperature did not change anymore. In this case, the night-time RE values with u_* lower than the thresholds were excluded. We removed negative fluxes at night-time (i.e. apparent 'photosynthesis'), and spurious data caused by rainfall, water condensation or system failure. The average night-time and daytime data coverage was 40% and 78% at CBS, 13% and 82% at QYZ, 24% and 69% at DHS, respectively. The average data coverage during the 3 years (i.e. 2003–2005) was 59%, 47%, and 47% for CBS, QYZ, and DHS, respectively.

Gap filling

The data gaps were filled mainly by means of the nonlinear regression method (Falge *et al.*, 2001). For small gaps (<2 h), the missing data was linearly interpolated. Larger gaps, such as daytime and night-time gaps, were treated separately when filling the gaps in the CO_2 data sets. The missing daytime flux data were estimated as a function of Q_P using the Michaelis–Menten equation with a 10-day moving window:

$$\mathrm{NEP} = \frac{\alpha Q_p \mathrm{GEP_{sat}}}{\alpha Q_p + \mathrm{GEP_{sat}}} - \mathrm{RE_{day}}, \quad (3)$$

where α is the ecosystem apparent quantum yield ($\mathrm{mg\,CO_2\,\mu mol^{-1}}$ quantum), Q_p is the photosynthetic photon flux density ($\mathrm{\mu mol\,quantum\,m^{-2}\,s^{-1}}$), $\mathrm{GEP_{sat}}$ is the asymptotic GEP at saturating light ($\mathrm{mg\,CO_2\,m^{-2}\,s^{-1}}$), and $\mathrm{RE_{day}}$ is the average daytime RE ($\mathrm{mg\,CO_2\,m^{-2}\,s^{-1}}$). Terms α, $\mathrm{GEP_{sat}}$, and $\mathrm{RE_{day}}$ represent the fitted parameters with the observed valid data using the nonlinear regression of MATLAB 7.0.

Because of no photosynthesis during the night-time, the night-time NEP is in effect the night-time ecosystem respiration ($\mathrm{RE_{night}}$, $\mathrm{mg\,CO_2\,m^{-2}\,s^{-1}}$). The missing $\mathrm{RE_{night}}$ was estimated using the Lloyd and Taylor model (Lloyd & Taylor, 1994):

$$\mathrm{RE_{night}} = R_{\mathrm{ref}} e^{E_0\left(\frac{1}{T_{\mathrm{ref}}-T_0} - \frac{1}{T_K - T_0}\right)}, \quad (4)$$

where R_{ref} and E_0 represent the fitted parameters with the observed valid data. R_{ref} stands for the ecosystem respiration rate at the reference temperature (T_{ref}, 10 °C), and E_0 is the parameter that essentially determines the temperature sensitivity of ecosystem respiration. T_K is the air or soil temperature (°C). For CBS, the soil temperature at 5 cm was used, while the air temperature was used for QYZ (Yu *et al*., 2005) and DHS, because it gave better regressions (i.e. higher R^2 values) than soil temperature (Yu *et al*., 2005). The parameter T_0 was set at $-46.02\,^{\circ}\mathrm{C}$ (Reichstein *et al*., 2002).

The Lloyd and Taylor equation is usually adopted to estimate $\mathrm{RE}_{\mathrm{night}}$. However, soil moisture may also affect $\mathrm{RE}_{\mathrm{night}}$, especially for the ecosystems suffered from seasonal droughts (e.g. at QYZ in 2003) (Yu *et al*., 2005; Wen *et al*., 2006). Therefore, temperature and soil water content were also taken into account in the estimation of $\mathrm{RE}_{\mathrm{night}}$:

$$\mathrm{RE}_{\mathrm{night}} = R_{\mathrm{ref}} \mathrm{e}^{\ln(Q_{10})(T_{\mathrm{a}}-T_{\mathrm{ref}})/10}, \tag{5}$$

$$Q_{10} = a + bT_{\mathrm{a}} + cS_{\mathrm{w}} + dS_{\mathrm{w}}^2, \tag{6}$$

where Q_{10} is the temperature sensitivity of respiration, T_{a} is the air temperature, S_{w} is the soil water content ($\mathrm{m^3\,m^{-3}}$), and a, b, c, and d are the site-specific parameters fitted with the valid data of the whole year, in which $b<0$ and $d \leq 0$. There was a significant difference in $\mathrm{RE}_{\mathrm{night}}$ estimated from Eqn (4) and Eqns (5) and (6) in 2003 at QYZ, while the estimates were similar for other two sites and in other years. The parameters were subsequently used to estimate $\mathrm{RE}_{\mathrm{day}}$.

A simple Monte-Carlo simulation was performed to estimate the uncertainty of the annual sums of NEP using the described nonlinear regression method. First, different sets of uniformly distributed pseudorandom numbers were produced with MATLAB 7.0, then 5–60% of the data were removed from the prefilled dataset with an increment of 5% data every time. After this, the described nonlinear regression method was applied to fill the artificial gaps and recalculate the annual sums of NEP. This procedure was repeated 100 times for each gap percentage in every year. The standard deviations for annual NEP were 6.5, 8.2, and $5.8\,\mathrm{g\,C\,m^{-2}}$ at CBS, QYZ, and DHS, respectively.

We also used the mean diurnal variations method (MDV) (Falge *et al*., 2001) and the marginal distribution sampling method (MDS) (Reichstein *et al*., 2005) to fill the gaps and estimate the annual sums of $\mathrm{CO_2}$ fluxes, which might provide another uncertainty estimation of the dependence of the annual sums on gap-filling methods. The estimated annual sums of NEP with the MDV method were always higher than that those estimated with both the nonlinear regression and the MDS method, while the results from the nonlinear regression and the MDS method were comparable. The average difference between the MDV and the nonlinear regression method was 72.5, 23.8, and $69.5\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for CBS, QYZ, and DHS, respectively, while the difference between the MDS and the nonlinear regression method was 6.4, −10.5, and $23.8\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for CBS, QYZ, and DHS, respectively. However, the seasonal variation and magnitude of annual NEP derived from the three gap-filling methods were similar.

Flux partitioning

To estimate the GEP, we estimated the $\mathrm{RE}_{\mathrm{day}}$ with the relationships between the $\mathrm{RE}_{\mathrm{night}}$ vs. soil temperature and water content [Eqns (4)–(6)]. The ecosystem respiration (RE, $\mathrm{mg\,CO_2\,m^{-2}\,s^{-1}}$) was defined as follows:

$$\mathrm{RE} = \mathrm{RE}_{\mathrm{night}} + \mathrm{RE}_{\mathrm{day}}. \tag{7}$$

GEP was estimated according to the equation:

$$\mathrm{GEP} = \mathrm{NEP} + \mathrm{RE}. \tag{8}$$

At the half-hour scale, the units for $\mathrm{CO_2}$ flux were $\mathrm{mg\,CO_2\,m^{-2}\,s^{-1}}$, while at daily, monthly, and annual scales, the units were converted into $\mathrm{g\,C\,day^{-1}}$, $\mathrm{g\,C\,month^{-1}}$, and $\mathrm{g\,C\,yr^{-1}}$, respectively. In this study, the negative sign of flux values represents $\mathrm{CO_2}$ release into the atmosphere, and the positive sign indicates $\mathrm{CO_2}$ entering the biosphere.

Results

Seasonal and interannual variations of environmental variables

Figure 1 demonstrates the seasonal and interannual variations of monthly mean air temperature (T_{a}, at the height of the EC system at each site, see Table 1), monthly mean VPD, monthly cumulative photosynthetic photon flux density (Q_{p}), monthly mean soil water content (S_{w}, 5 cm depth), and monthly cumulative precipitation (P) from 2003 to 2005 at the three observation sites. The seasonal trend of temperature was in good phase with that of precipitation at CBS. The annual mean temperature at CBS in 2005 was lower than that in 2003 and 2004. Likewise, Q_{p} was lower during the summer of 2005 than that during the corresponding period in the previous 2 years. The VPD at CBS showed a bimodal curve with higher VPD in spring and autumn. Soil water content remained at a relatively high level at CBS mostly due to the low evapotranspiration resulted from the low annual temperature and the strong water retention of soils, which had a large fraction of clay particles (Table 1).

In contrast, seasonal distributions of precipitation and temperature were asynchronous at QYZ site.

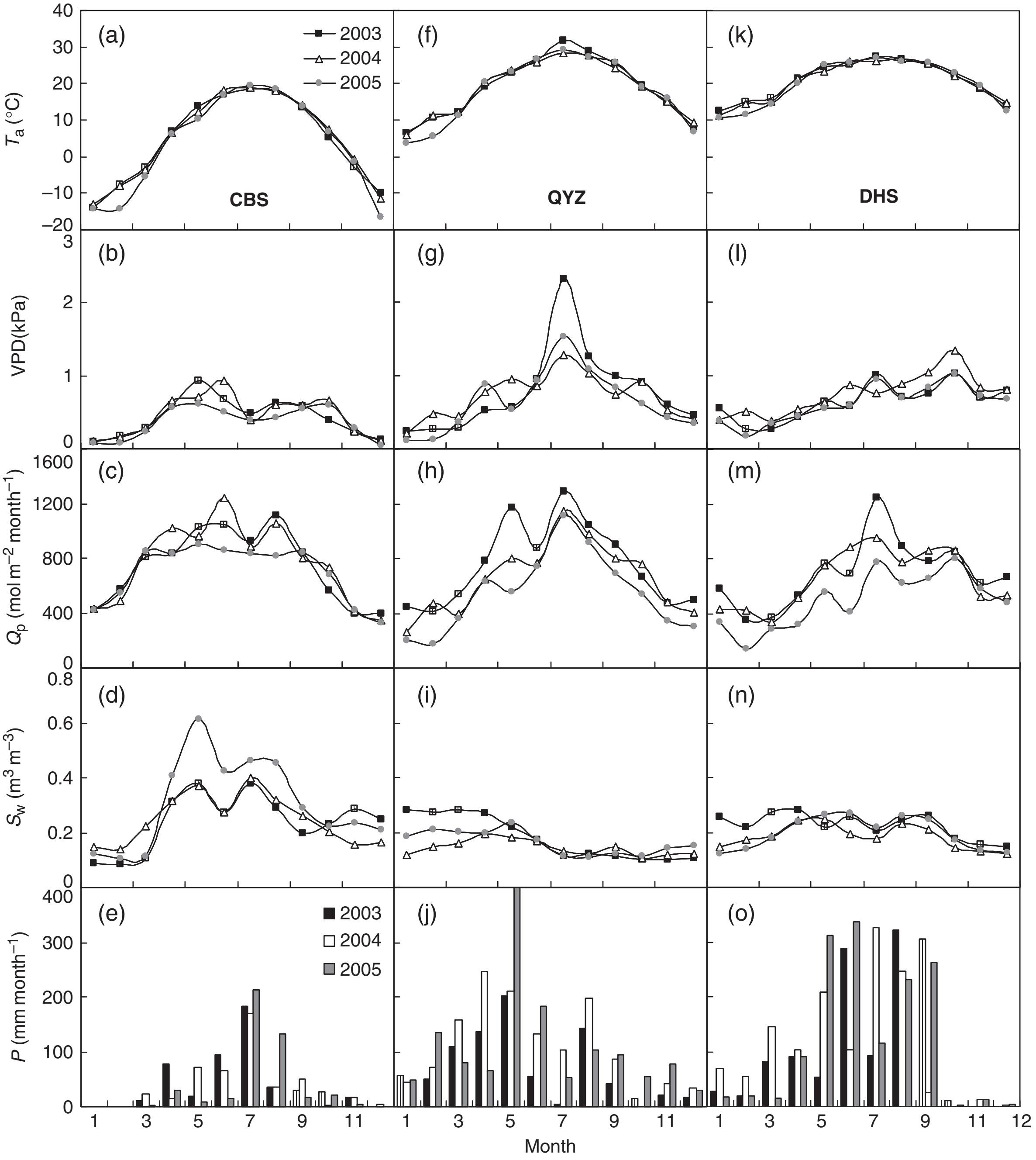

Fig. 1 Seasonal and interannual variations of monthly mean air temperature (T_a), vapor pressure deficit (VPD), monthly cumulative photosynthetic photon flux density (Q_p), monthly mean soil water content (S_w, 5 cm depth), and monthly cumulative precipitation (P) from 2003 to 2005 at CBS (a–e), QYZ (f–j), and DHS (k–o) sites.

Precipitation decreased, to some degree, in July at QYZ, whereas air temperature reached the maximum as VPD increased significantly. The unsynchronized seasonality between temperature and precipitation was marked with high temperatures, less rainfall, and high VPD during the midseason, resulting in a regional drought in summer and the early onset of plant senescence in autumn at QYZ (Wen *et al*., 2006). In 2003, QYZ experienced such an extreme drought stress. On the one hand, both temperature and precipitation exceeded the long-term normal (Sun *et al*., 2006a; Wen *et al*., 2006). On the other hand, VPD was obviously higher than that in 2004 and in 2005. According to the meteorological record, the cumulative precipitation from October to December in

2002 was 406 mm, which was nearly half of the total precipitation in 2003 and resulted in a higher antecedent soil water content before summer in 2003 than in 2004 and in 2005. However, due to the influence of the extreme high temperature and VPD, postsummer soil water content in 2003 was identical to that in the other 2 years. Under such conditions, some plants also senesced. In 2004 and 2005, the annual mean temperature and annual precipitation were close to the long-term averages. The annual precipitation in 2005 was the highest among the 3 years, but Q_P values were the smallest.

According to the long-term statistical data, there exist a distinct rainy season (usually from April to September) and a dry season (usually from October to March) in each year at DHS. Precipitation during the dry season only accounted for 12% of the annual amount across the 3 years. During the rainy season, both temperature and precipitation attained the highest values while the fog also occurred frequently. The highest VPD appeared in October because the temperature was still high, while the precipitation was low. The higher Q_P usually appeared in the late half of the year. Similar to QYZ, Q_P at DHS was lower in 2005 than in 2003 and in 2004. Although the precipitation at QYZ and DHS was higher than that at CBS, the soil water content at QYZ and at DHS was generally lower than that at CBS, which probably resulted from higher evapotranspiration in the subtropical forest than that in the temperate forest, and combined with higher clay and organic matter contents of the soil at CBS than those at QYZ and DHS (Table 1).

Because of the difference in the extent of influence from the eastern Asia monsoon climate, the three forest ecosystems showed distinct variations in seasonal and interannual patterns of meteorological conditions across the 3 years. Meanwhile, there appeared to be a latitudinal trend of the mean annual temperature and annual precipitation at CBS, QYZ, and DHS sites along the NSTEC, which spans about 19° in latitude (Fig. 2).

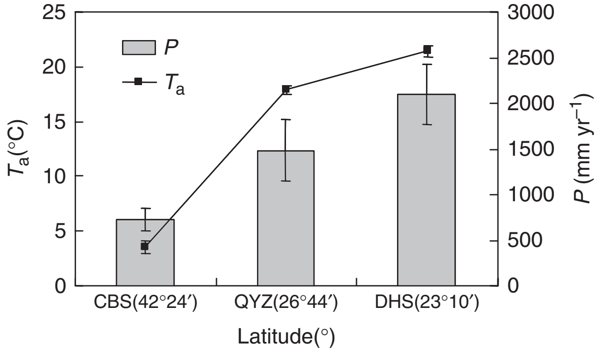

Fig. 2 Latitudinal trends of the mean annual temperatures (T_a) and annual precipitation (P) at CBS, QYZ, and DHS sites along the North–South Transect of Eastern China (NSTEC). Note that the values are the averages from 1985 to 2005. The error bars indicate the standard deviation.

Environmental control over ecosystem respiration and gross ecosystem productivity

Figure 3 shows the relationship between temperature and ecosystem respiration (RE) of the forests at CBS, QYZ, and DHS. EC measurements of the night-time RE were quite scattered. A bin width of 1 day with a minimum bin size of $n = 5$ was used in the fitting procedure to reduce the effect of heteroscedasticity and to provide equal weighting in the parameter estimation (e.g. Griffis *et al.*, 2003). Comparison of the response of RE to temperature among the three forests showed that most variations of RE can be interpreted by the change in temperature, especially in the years without drought stress. Figure 3 also indicates that both the RE at the reference temperature and the temperature sensitivity of RE for the temperate forest (e.g. CBS) were higher than those for the two subtropical ecosystems (e.g. QYZ and DHS). Temperature-driven increase in RE can be dampened by low soil water content (Rustad *et al.*, 2001; Conant *et al.*, 2004). According to the results of Yu *et al.* (2005) and Wen *et al.* (2006), RE would be overestimated only if the effect of temperature were considered during drought stress, especially for the ecosystems that suffered from seasonal drought like QYZ in 2003. Figure 3d also shows that RE is depressed at higher temperature at QYZ in 2003. Therefore, it is necessary to take the soil water effect into account in the estimation of RE during drought stress (Xu & Qi, 2001; Reichstein *et al.*, 2002).

GEP is usually influenced by radiation, temperature, and moisture conditions (Aubinet *et al.*, 2001; Law *et al.*, 2002; Griffis *et al.*, 2003). Partial correlation analysis indicated that temperature dominantly affected the daily GEP of CBS (Fig. 4), whereas Q_P appeared to be the dominant factor at QYZ and DHS (Fig. 5). This was mostly because CBS had larger seasonal variation in temperature from the growing season to the dormancy season, while the temperature was not a constraint for subtropical forest ecosystems at QYZ and DHS.

Figure 4 shows that the daily GEP at CBS increased exponentially with the temperature. The relationship could be described using a modified Van't Hoff model as given below:

$$\mathrm{GEP} = \mathrm{GEP_{ref}} e^{B(T_K - T_{\mathrm{ref}})}, \tag{9}$$

where $\mathrm{GEP_{ref}}$ (g C m^{-2} day^{-1}) is the GEP rate at the reference temperature (T_{ref}, 0 °C), B is a fitted site-specific parameter, and T_K is the air temperature (°C). Both $\mathrm{GEP_{ref}}$ and B were fitted with the data of the whole year.

The parameters of the Van't Hoff model for the CBS forest in each year are summarized in Fig. 4. The GEP

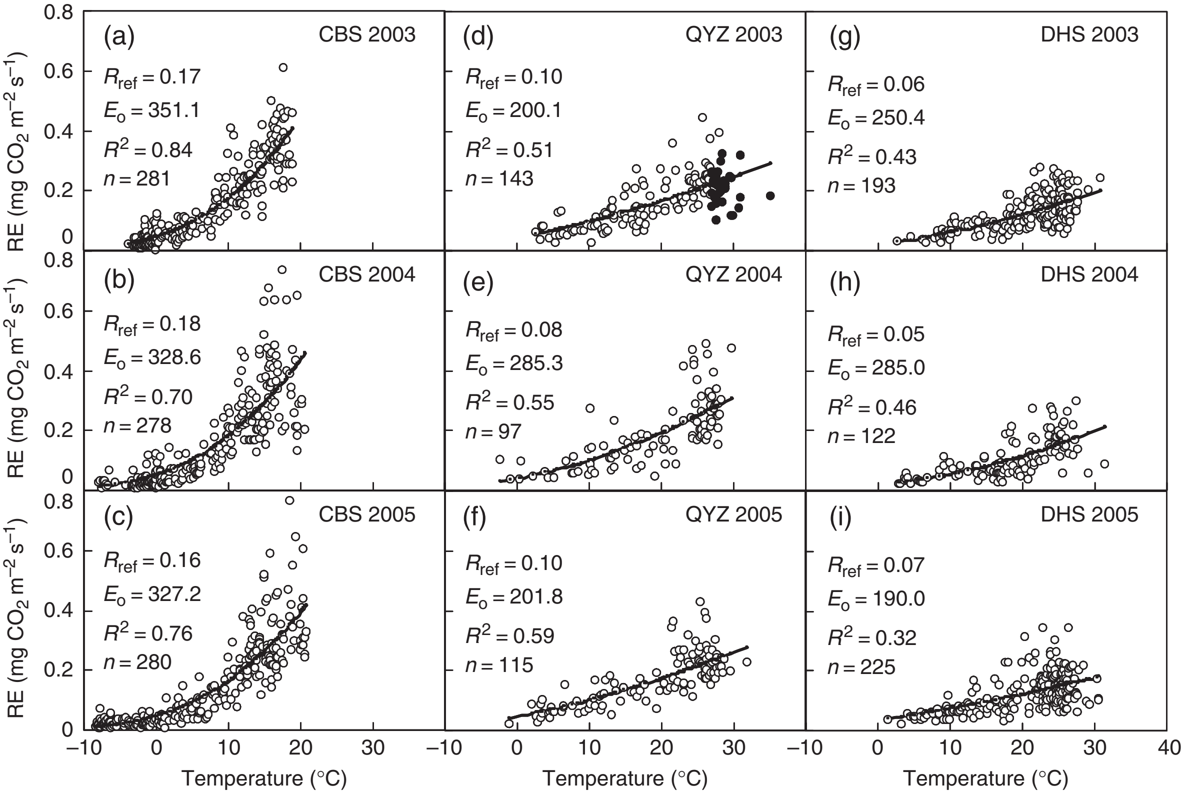

Fig. 3 Relationships between ecosystem respiration (RE) and temperature at the CBS, QYZ, and DHS sites. A bin width of 1 day with a minimum bin size of $n = 5$ was applied to reduce the influence of heteroscedasticity and to provide equal weighting in the parameter estimate ($n = 48$). The fill circle in (d) indicates the depression of RE under drought stress in 2003 at QYZ.

was most sensitive to the change in temperature in 2003 but least in 2005. This interannual variation probably resulted from the occurrence of lower monthly mean air temperature in 2005, especially in May (10.4 °C) relative to the same month in 2003 (13.8 °C) and in 2004 (12.2 °C). Although most variation of GEP at CBS could be explained by temperature, two critical temperature thresholds for GEP were derived. Figure 4 shows that when the daily mean air temperature exceeded 0 °C in spring, GEP began to increase at a slow rate as a result of the gradual sprouting of new branches and leaves. Rapid increase in GEP occurred when the daily mean air temperature was higher than 5 °C.

Responses of the daily GEP at QYZ and DHS forests to Q_p are presented in Fig. 5. The relationships can be well described with a rectangular hyperbola model, such as the modified Michaelis–Menten equation:

$$\mathrm{GEP} = \frac{\alpha' Q_p \mathrm{GEP}'_{sat}}{\alpha' Q_p + \mathrm{GEP}'_{sat}}, \qquad (10)$$

where α' is the daily ecosystem apparent quantum yield (g C mol^{-1} quantum), and Q_p is the daily accumulative photosynthetic photon flux density (mol quantum m^{-2} day^{-1}). GEP'_{sat} is the asymptotic daily GEP at saturating light (g C m^{-2} day^{-1}). GEP'_{sat} and α' were also fitted with the data of the whole year.

The parameters derived from the modified Michaelis–Menten equation for the QYZ and DHS forests in different years are presented in Fig. 5. The average GEP'_{sat} at QYZ during the 3 years was 3.825 g C m^{-2} day^{-1} higher than that at DHS, indicating a larger potential photosynthesis of the young plantation at QYZ relative to the old forest at DHS.

The magnitude of ecosystem carbon exchange of boreal and temperate ecosystems is essentially determined by temperature, while water availability greatly influences the carbon exchange of subtropical and tropical ecosystems (Malhi *et al*., 1999). Our results agreed well with this conclusion. Response of the GEP at QYZ to increasing Q_p was significantly depressed by the drought stress in 2003 (Fig. 5a).

Figure 6 shows the relationships between GEP and RE from 2003 to 2005 at CBS, QYZ, and DHS sites. RE was influenced not only by environmental factors but also by biological activities. The RE of the three forest ecosystems linearly depended on the GEP, although the correlation was relatively weak for the forest of DHS ($R^2 = 0.24$, $P < 0.01$) compared with that of CBS

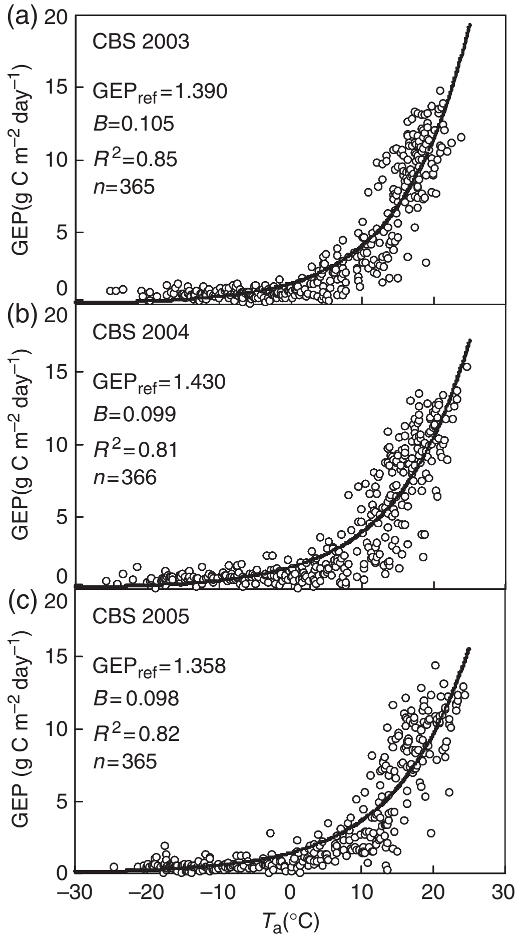

Fig. 4 Relationship between daily GEP and temperature at CBS. The trend lines and parameters were derived from the Van't Hoff model [$\mathrm{GEP} = \mathrm{GEP}_{\mathrm{ref}} e^{B(T_{\mathrm{K}}-T_{\mathrm{ref}})}$, Eqn (9)]. The number of sample is 365, 366, and 365 in 2003, 2004, and 2005, respectively.

($R^2 = 0.88$, $P < 0.01$) and QYZ ($R^2 = 0.70$, $P < 0.01$). This result is consistent with the previous study for 18 forest ecosystems across the European continent (Janssens *et al.*, 2001). Figure 6 also shows that the slope of RE vs. GEP decreased from the temperate forest to the subtropical forests, which probably resulted from the different seasonal variations in RE and GEP between the temperate forest and the subtropical forest (see next section for further discussion).

Seasonal and interannual variations of ecosystem carbon exchange

Apparent seasonal and interannual variations of monthly RE, GEP, and NEP of the three forests during the period from 2003 to 2005 are illustrated in Fig. 7. Site-specific annual carbon budgets are summarized in Table 2. At CBS, seasonal variations of RE, GEP, and NEP generally followed the seasonal trend of temperature. The peak value of NEP occurred in June, 1 month earlier than that of GEP. Different temperature sensitivities of RE and GEP led to higher annual NEP in 2005 than that in 2003 and in 2004 at CBS. This is mostly because the average temperature in 2003 and 2004 was higher than that in 2005, especially in spring and early summer (from January to June). Although both GEP and RE decreased with decreasing temperature, the larger decrease in RE relative to GEP resulted in an increase in NEP. Compared with the annual GEP in 2003 and 2004, GEP decreased by $190\,\mathrm{g\,C\,m^{-2}}$ in 2005, and 61% of the decrease occurred during the periods of spring and early summer. As a result of the combined effect of lower temperature and decreased GEP, RE decreased by $219\,\mathrm{g\,C\,m^{-2}}$ in 2005, which was larger than that of GEP. Overall, the reduction in RE compensated for the decrease in GEP in 2005. These results indicate that temperature played an important role in controlling the seasonal and interannual variations of ecosystem carbon exchange, and RE was more sensitive to temperature than GEP at CBS.

At QYZ, ecosystem carbon fluxes showed similar seasonal trend with regard to air temperature, except for an apparent decrease during the drought period in the summer of 2003. The short-term drought-induced decrease in RE, GEP, and NEP (Fig. 7d–f), however, did not cause significant difference in annual NEP in 2003 compared with 2004 and 2005 (Table 2), which was ascribed to the larger NEP in the first half year of 2003 than during the same period of 2004 and 2005. The cumulative precipitation during the period from October to December in 2002 was 406 mm, 300 mm larger than the average cumulative precipitation during the same period of the following 3 years. High soil water content resulting from the abundant rainfall in late 2002 was presumed to be mainly responsible for the relative larger NEP during the spring and early summer of 2003. This result suggests that soil water availability accounted for the interannual variations of ecosystem carbon fluxes at QYZ, and that the environmental conditions in antecedent years were also important for influencing subsequent variations of ecosystem carbon processes. In addition, the results observed in 2005 suggested the possible effect of solar radiation on the interannual variations of NEP and GEP. The mean daily cumulative Q_{p} in 2005 was 6.9 and $3.6\,\mathrm{mol\,photon\,m^{-2}\,day^{-1}}$ lower than the values in 2003 and in 2004, respectively. Reduction in solar radiation might partly be responsible for the decrease in GEP in 2005.

The seasonal trends of RE, NEP, and GEP at DHS markedly differed from those at CBS and at QYZ. RE and GEP at DHS did not experience synchronous seasonal courses. RE had a trend similar to air temperature, attaining the highest values in July, and decreased

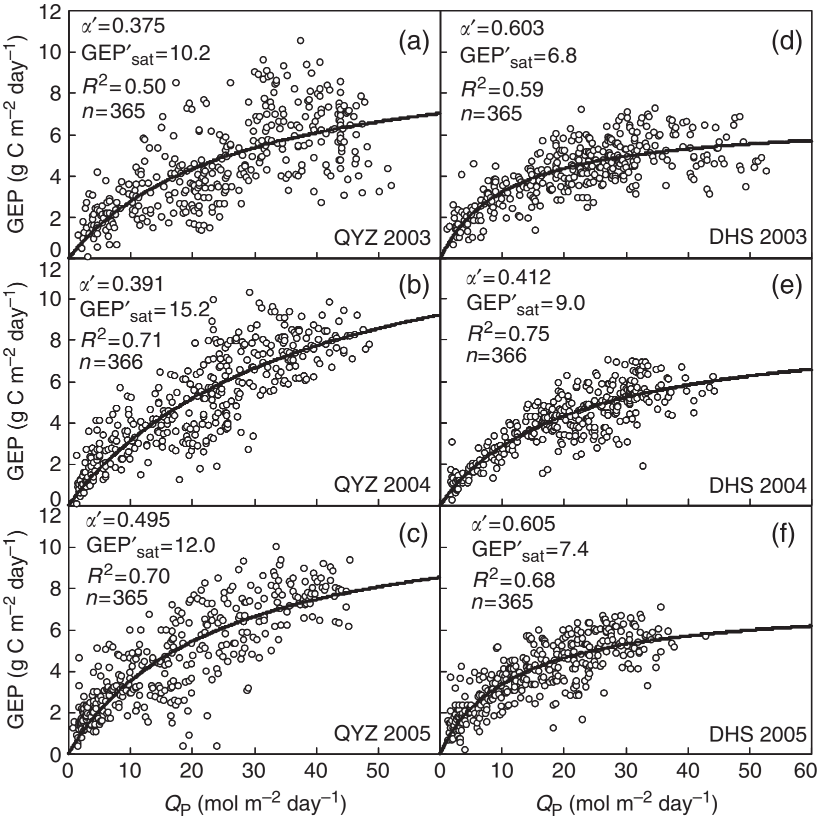

Fig. 5 Relationship of daily GEP and daily incident photosynthetic photon flux density (Q_P) at QYZ (a–c) and DHS (d–f). The trend lines and parameters were derived from the modified Michaelis–Menten equation ($\mathrm{GEP} = \frac{\alpha' Q_\mathrm{P}\mathrm{GEP}'_\mathrm{sat}}{\alpha' Q_\mathrm{P}+\mathrm{GEP}'_\mathrm{sat}}$) [Eqn (10)]. The number of samples is 365, 366, and 365 in 2003, 2004, and 2005, respectively.

with temperature in other months. Seasonal variation of GEP was similar to that of Q_p, with smaller GEP during the winter, and larger values from July to October, especially in October at the beginning of the dry season. The difference in seasonal variations between RE and GEP partly resulted in the weak relationship between RE and GEP (Fig. 6). Higher radiation and less fog during the beginning of dry season were probably responsible for the largest GEP in October. After October, the GEP declined with decreasing Q_p and temperature. The lower GEP in 2005, especially during the first half of the year, mainly resulted from the lower solar radiation compared with the 2 previous years. Because of the different responses of GEP and RE to environmental conditions, the highest value of NEP occurred in October at the beginning of the dry season.

Discussion

Carbon sequestration of forests

Although significant difference in NEP existed among the three forests along the NSTEC, the three forest ecosystems appeared to behave as carbon sinks during the study period, including the two old-growth forests (CBS and DHS) (Fig. 8, Table 2). Old-growth forests have traditionally been considered negligible as carbon sinks and were underestimated in global carbon cycle because their carbon uptake has been thought to be balanced by respiration (Odum, 1969). However, based on long-term measurement (1979–2003) of soil organic carbon stock, Zhou *et al.* (2006) found that the old-growth forest at DHS can still accumulate carbon in the soil. Our continuous EC measurement also confirmed that the two old-growth forests (i.e. temperate mixed forest and the subtropical evergreen broad-leaved forest) in eastern China can still act as significant carbon sinks, but the driving forces for the observed high rate of carbon uptake in the old-growth forests are not clear at present and deserve further study.

Annual NEP at CBS fell within the range of NEP of other temperate mixed or boreal forest ecosystems (Table 3). As an old-growth forest, annual NEP of the mixed forest at CBS was comparable with that of Howland, Harvard, and Camp Borden mixed forests, while it was lower than that of Vielsalm and Duck mixed

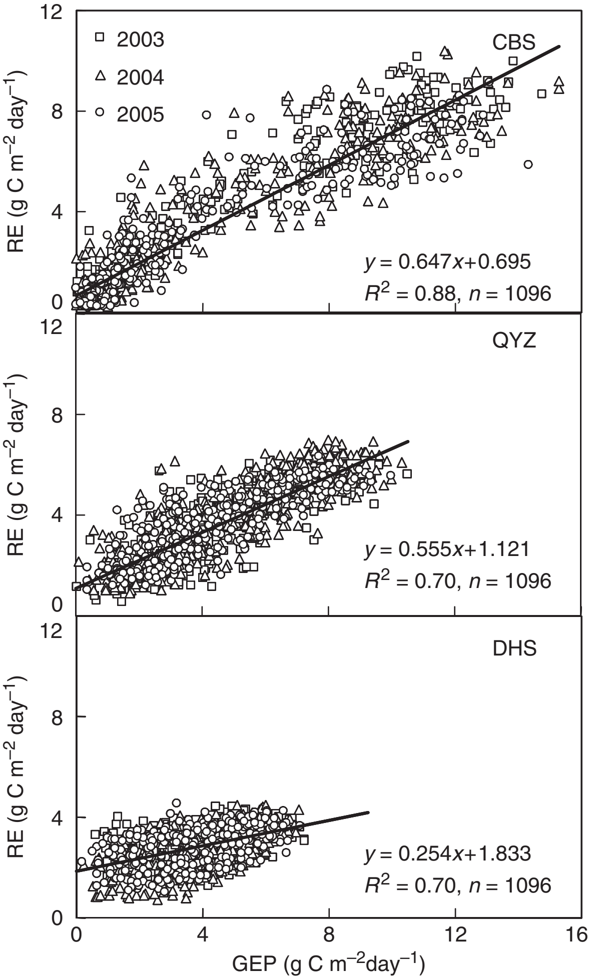

Fig. 6 Relationships between ecosystem respiration (RE) and gross ecosystem productivity (GEP) from 2003 to 2005 at CBS, QYZ, and DHS sites. The square, circle, and triangle denote 2003, 2004, and 2005, respectively. The trend lines are derived with the whole data.

forests. Ecosystem carbon sequestration of the subtropical evergreen needleleaf forest at QYZ was similar to that of the temperate evergreen needleleaf forest at Fujiyoshida, and it was higher than that of other temperate needleleaf forests except Kiryu plantation. Annual NEP of the DHS forest was slightly lower than the maximum annual NEP of tropical forest at La Selva, but was larger than that at other tropical forest ecosystems. This difference might be related to climate type, ages, structure, and plant ecophysiological characteristics of different forests (Malhi *et al.*, 1999; Law *et al.*, 2002; Griffis *et al.*, 2003), which also suggested the complexity and uncertainty in the evaluation of ecosystem carbon balance. Table 3 also indicates that there are few measurements operated at subtropical forests, which should be emphasized in the future.

There was much uncertainty in estimating ecosystem carbon exchange. Guan *et al.* (2006) and Zhang *et al.* (2006a, b) reported that NEP of CBS forest in 2003 ranged from 187 to 317 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. Such uncertainty could be resulted from the different methods of data processing, such as the different u_* thresholds used in night-time data screening and the correction to advective fluxes. Advective fluxes, including horizontal and vertical advective fluxes that were neglected in this study, were assumed to be important to eddy flux, especially to the night-time flux (Aubinet *et al.*, 2000; Baldocchi *et al.*, 2000). Increasing attempts have been made to measure advective flows caused by topography and/or heterogeneity (e.g. Lee, 1998; Baldocchi *et al.*, 2000; Aubinet *et al.*, 2003, 2005). These studies indicated that both horizontal and vertical advective fluxes mainly occurred during night-time, with the same order of magnitude as turbulent flux, and may cause the increases in night source of CO_2 (Feigenwinter *et al.*, 2008). The uncertainty in the estimation of ecosystem carbon flux in this study might be partly ascribed to the negligence of advective fluxes, which need further measurement and study to be quantitatively explained.

Latitudinal trend of NEP

Spatial patterns of NEP and the ratio of RE to GEP along the NSTEC indicate that subtropical forests (e.g. DHS and QYZ forests) had larger potential for carbon sequestration than temperate forest (e.g. CBS forest) (Fig. 9a). The NEP pronouncedly decreased with increasing latitude along the NSTEC (Fig. 9a), which probably results from the latitudinal gradients of temperature and precipitation along the NSTEC. Analyses also show that the NEP at three forest sites can be described as a function of mean annual air temperature (T_a) and annual precipitation (P), $\mathrm{NEP} = 216.17 + 9.39T_a - 0.002P$ ($R^2 = 0.70$, $P < 0.05$, $n = 9$). However, neither RE nor GEP showed such a latitudinal trend along the NSTEC (Fig. 8). This latitudinal trend of NEP was consistent with that of European forests (Valentini *et al.*, 2000).

Valentini *et al.* (2000) reported that annual NEP decreased with increasing latitude across the EUROFLUX sites (40–70°), and they suggested that RE was the main determinant of this relationship because there was no latitudinal trend in GEP. Janssens *et al.* (2001) analyzed the relationship between RE and GEP of 18 forest ecosystems across the European continent. The results indicated that RE strongly depends on GEP across different forest ecosystems, and the average ratio of annual RE to annual GEP was around 0.80. Similar results were found along the NSTEC, and ratio of RE to GEP was 0.82, 0.79, and 0.71 at CBS, QYZ, and DHS,

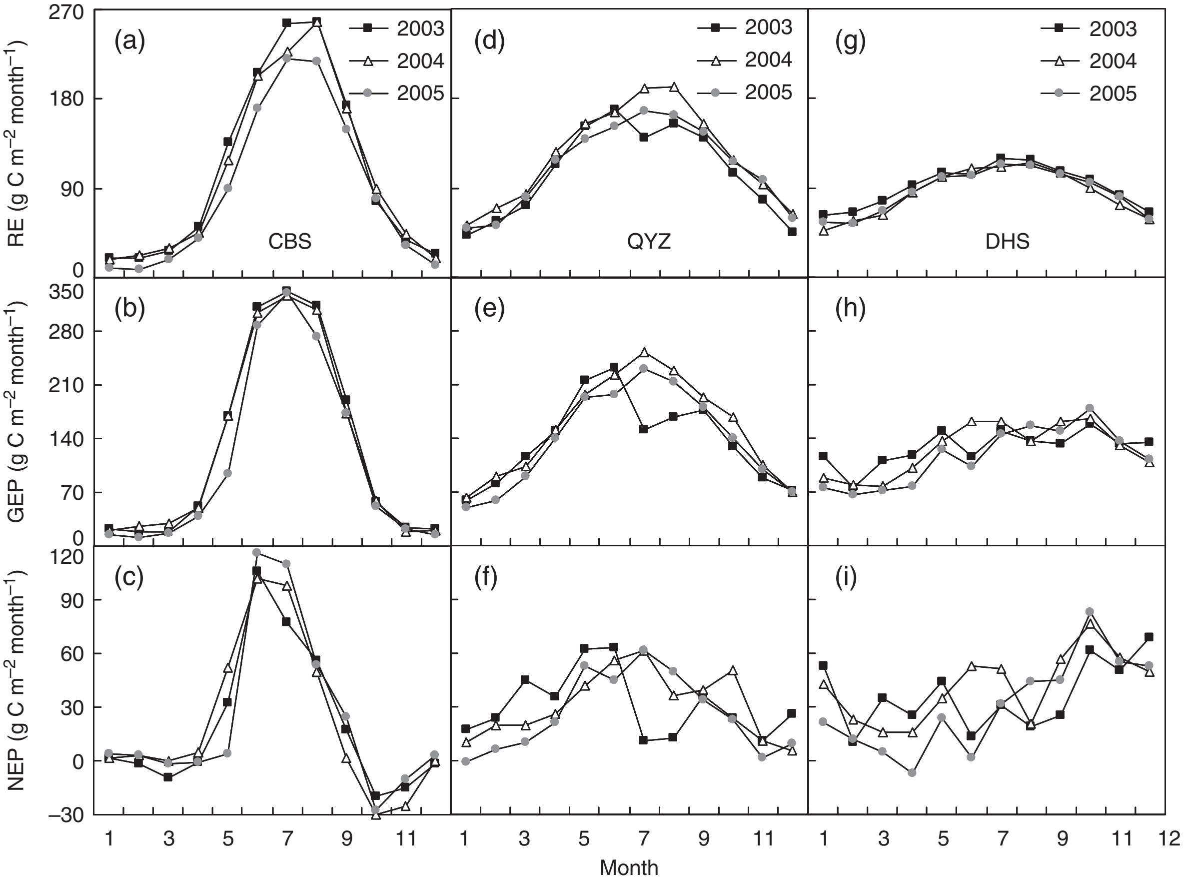

Fig. 7 Seasonal variations of ecosystem respiration (RE), gross ecosystem production (GEP), and net ecosystem production (NEP) at CBS (a–c), QYZ (d–f), and DHS (g–i) sites from 2003 to 2005. The lines with filled squares, open triangles, and gray circles denote 2003, 2004, and 2005, respectively.

Table 2 Annual sums of ecosystem respiration (RE), gross ecosystem productivity (GEP) and net ecosystem productivity (NEP) at the three forest ecosystems from 2003 to 2005

Site	Year	RE ($\mathrm{g\,C\,m^{-2}\,yr^{-1}}$)	GEP ($\mathrm{g\,C\,m^{-2}\,yr^{-1}}$)	NEP ($\mathrm{g\,C\,m^{-2}\,yr^{-1}}$)
CBS	2003	1286	1528	242
	2004	1248	1505	257
	2005	1048	1327	279
	Average	1194 ± 128	1453 ± 110	259 ± 19
QYZ	2003	1272	1641	369
	2004	1466	1844	378
	2005	1345	1661	316
	Average	1361 ± 98	1715 ± 112	354 ± 34
DHS	2003	1094	1530	436
	2004	1012	1512	499
	2005	1030	1398	368
	Average	1046 ± 43	1480 ± 71	434 ± 66

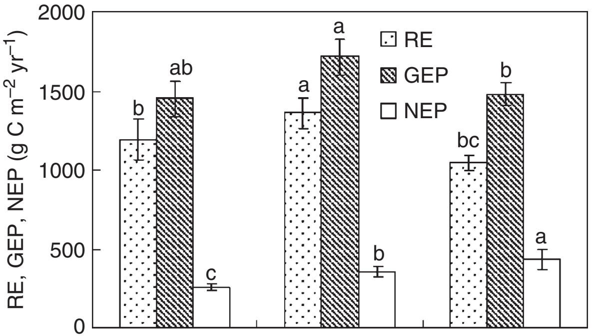

Fig. 8 Comparison of mean values of annual sums of RE, GEP, and NEP at CBS, QYZ, and DHS sites. Different letters denote significant differences (LSD comparison, $P < 0.05$) among the sites.

respectively. The average ratio of annual RE to annual GEP was about 0.77 ± 0.06 along the NSTEC. This result suggested that both RE and GEP determined the relationship between latitude and NEP in eastern China (Fig. 9b).

The difference in the relationship of latitude and NEP between the European forests and the NSTEC forests

Table 3 Comparison of net ecosystem productivity (NEP) among different forest ecosystems

Site	Latitude	Vegetation	Temperature (°C)	Precipitation (mm)	Age (years)	NEP ($g\,C\,m^{-2}\,yr^{-1}$)	Period
Soroe	55°29′N	Mixed forest	8.3	730	–	22.4–227*	1997–1999
Sask-SSA Old Aspen	53°37′N	Deciduous broadleaf forest	0.1	390	70	70–290*	1994–2000
Brasschaat	51°18′N	Mixed forest	9.8	750	–	−255–157*	1997–2001
Vielsalm	50°18′N	Mixed forest	7.5	1000	75	430–600*	1996–1998
Hesse	48°40′N	Deciduous broadleaf forest	9.9	975	–	68–501*	1996–2000
Wind River Crane	45°48′N	Mixed forest	5.1	995	70	476.2*	1999
Laoshan	45°20′N	Deciduous needleleaf forest (larch plantation)	4.8	639	35	10†	2004
Howland	45°12′N	Mixed forest	6.7	1040	140	210–321.9*	1996–1997
Camp Borden	44°19′N	Mixed forest	6.4	858	100	60–240*	1996–1998
Tomakomai	42°44N	Deciduous needleleaf forest (larch plantation)	7.0	1030	45	240–320†	2001–2003
Harvard	42°32′N	Mixed forest	6.5	1071	70	120–303.1*	1991–2000
Changbaishan	**42°24′N**	**Mixed forest**	**3.6**	**738**	**200**	**242–279**	**2003–2005**
Niwot Ridge	40°02′N	Evergreen needleleaf forest	1.5	800	100	49.7–295.2*	1999–2003
Takayama	36°09′N	Deciduous broadleaf forest	7.3	1732	40	56–346‡	1994–2002
Duke	35°59′N	Mixed forest	14.4	1140	17	580–760*	1998–2000
Fujiyoshida	35°27′N	Evergreen needleleaf forest	9.6	2055	90	250–460†	2000–2004
Kiryu	34°58′N	Deciduous needleleaf forest (plantation)	15.1	1596	45	430–540†	2001–2004
Qianyanzhou	**26°44′N**	**Evergreen needleleaf forest (plantation)**	**17.9**	**1485**	**21**	**316–378**	**2003–2005**
Dinghushan	**23°10′N**	**Evergreen broadleaf forest**	**21.0**	**1956**	**100**	**368–499**	**2003–2005**
Sakaerat	14°29′N	Tropical Rainforest	24.4	1483	–	−180–90†	2002–2003
La Selva	10°26′N	Tropical Rainforest	25.0	4000	–	−50–610§	1998–2000
Rond-Rebio Jaru Ji Parana	10°05′S	Tropical Rainforest	27.0	2152	–	102*	1992–1993

*Data source: http://www.fluxnet.ornl.gov/fluxnet/nee.cfm

†Data source: Hirata *et al.* (2008).

‡Data source: Saigusa *et al.* (2005).

§Data source: Loescher *et al.* (2003).

The negative (positive) values mean CO_2 release (uptake) of the ecosystem.

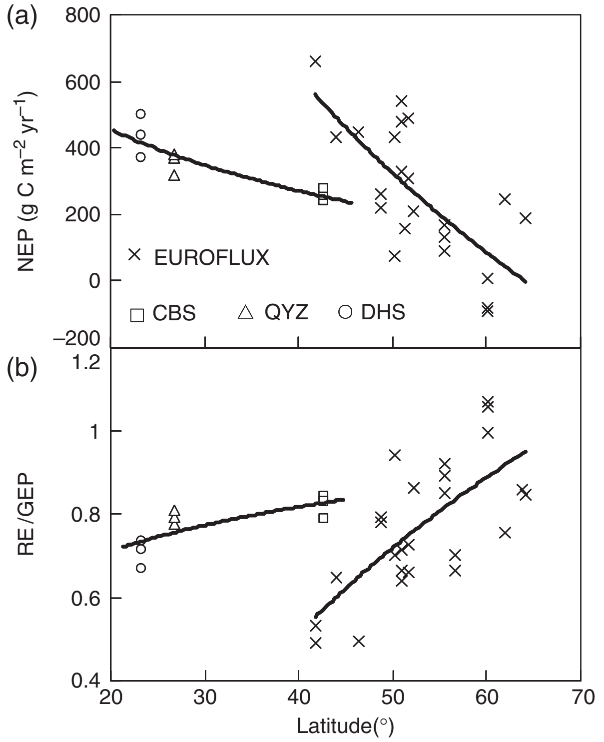

Fig. 9 Spatial patterns of (a) net ecosystem productivity (NEP) and (b) RE/GEP. RE/GEP indicates the ratio of ecosystem respiration to gross ecosystem productivity (GEP). The EUROFLUX data was obtained from Valentini *et al.* (2000). The open squares, triangles, and circles indicate CBS, QYZ, and DHS, respectively. The crosses indicate the EUROFLUX data from Valentini *et al.* (2000). The trend lines are fitted with logarithmic function.

was probably attributable to the following reasons. Firstly, the latitude spanning from CBS to DHS includes forest types from subtropical evergreen broad-leaved forest to temperate mixed forest. In comparison, most forest ecosystems in the European continent are temperate and boreal forests (Valentini *et al.*, 2000). In terms of NEP, the subtropical forest is not so sensitive to the increase in temperature as temperate and boreal forests (Figs 4 and 5). Secondly, forest age may also play an important role in determining the magnitude of ecosystem carbon sink (Chen *et al.*, 2003; Pan *et al.*, 2004). The stand ages of the CBS, QYZ, and DHS forests were about 200, 23, and 100 years, respectively, while the age of most forests in Europe was less than 100 years. Therefore, the net carbon sequestration potential at CBS and DHS might be lower than the forests in the European continent, although they all appeared to be carbon sinks during the study period. Thirdly, the climatic difference between the two continents also causes the difference in NEP between eastern China and Europe, which are mainly influenced by continental climate and oceanic climate, respectively. This continental difference in ecosystem carbon fluxes also suggests that long-term measurements are necessary for examining the biogeographical mechanisms that are responsible for the spatial pattern for NEP at regional and global scales.

Response of net ecosystem production to changing climate

The results outlined earlier demonstrated that the seasonal and interannual variations of RE, GEP, and NEP at CBS were mainly determined by temperature, while the variations of GEP and NEP at QYZ were more sensitive to moisture condition; and the GEP and NEP at DHS were mainly affected by radiation condition. Based on the scenarios of greenhouse gas and aerosol emissions as described in the report of IPCC in 2001 (IPCC, 2001), Qin *et al.* (2005) predicted that by the end of the 21st century, the air temperature and precipitation in China will be, respectively, 3.9–6.0 °C and 14% higher than the average level of 1961–1990. Temperature will increase more significantly in winter than in summer, and this increase is predicted larger in the north of China than in the south of China (Qin *et al.*, 2005). Chen *et al.* (2005) indicated that the northern China is a region that is sensitive to the global warming, and the increase in precipitation is usually less than the increase in evaporation resulting from the global warming, while the increase in precipitation in the south of China will probably exceed the increase of evaporation. Enrichment of atmospheric CO_2 concentration may also cause more increase in precipitation in the southern China compared with the northern China (Yu *et al.*, 2002), whereas the spatial pattern of temperature change is contrary to the change of the spatial pattern of precipitation.

Earlier studies have shown that NEP in China decreased from the 1980s to 1990s because of a stronger warming than the global average (Cao *et al.*, 2003). Our results indicate that both GEP and RE of temperate forests in the NSTEC would increase with increasing temperature (e.g. CBS), while the variation of NEP would depend on the relative contributions from GEP and RE, which differed between regions. As for the subtropical forest ecosystem, GEP might increase with the alleviation of drought stress due to the increase in precipitation (e.g. QYZ) or decrease with the reduction of radiation (e.g. QYZ and DHS). Because of the complexity of structure and function of forest ecosystems and the uncertainty in future climate change, long-term measurement and further analyses are needed to understand and predict the response of different ecosystems to climate change.

Conclusions

This study presents the carbon fluxes from 2003 to 2005 measured with the EC technique at three forest ecosystems in eastern China. The sites were selected along the NSTEC, including CBS, QYZ, and DHS. The seasonal and interannual patterns of RE, GEP, and NEP of the three forest ecosystems and their responses to the variation of climatic variables were investigated.

1. RE of three forests were mainly controlled by temperature. Soil water availability had significant effect on RE during the drought period. Daily RE was highly dependent on GEP, and the dependence of RE on GEP at CBS was more remarkable than at DHS.
2. Daily GEP at CBS was mainly controlled by temperature. The temperature thresholds for initiation and rapid increase of ecosystem carbon exchange at CBS were 0 and 5 °C, respectively. The daily GEP at QYZ and at DHS was mainly controlled by radiation.
3. The seasonal and interannual variations of RE, GEP, and NEP at CBS were mainly determined by temperature, and the response of RE to change in temperature was more sensitive than that of GEP. The seasonal and interannual variations of GEP and NEP at QYZ were the results of combined effects of temperature, soil water, and solar radiation. At DHS, both GEP and NEP attained the highest values at the beginning of autumn probably due to the relative higher radiation and less fog in dry season.
4. Precipitation in the previous year affected the carbon budget in the following year at QYZ. In spite of significant decrease in NEP during the drought stress in summer of 2003, the annual NEP in 2003 was comparable with that in both 2004 and in 2005 because abundant rainfall in 2002 increased its NEP in the spring and early summer of 2003.
5. From 2003 to 2005, all the three forest ecosystems acted as carbon sink. The annual total NEP of CBS, QYZ, and DHS forests were 259 ± 19, 354 ± 34, and $434 \pm 66\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, respectively. Driven by temperature and precipitation gradients along the NSTEC, the annual NEP showed a declining trend with increasing latitude. The result was consistent with that observed for the European continent. However, the slopes of the relationship between latitude and NEP in the NSTEC was different from that in the European continent.

Acknowledgements

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