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Temperature and precipitation control of the spatial variation of terrestrial ecosystem carbon exchange in the Asian region

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ABSTRACT

Carbon exchange between terrestrial ecosystems and the atmosphere is one of the most important processes in the global carbon cycle. Understanding the spatial variation and controlling factors of carbon exchange fluxes is helpful for accurately predicting and evaluating the global carbon budget. In this study, we quantified the carbon exchange fluxes of different terrestrial ecosystems in the Asian region, and analyzed their spatial variation and controlling factors based on long-term observation data from ChinaFLUX (19 sites) and published data from AsiaFlux (37 sites) and 32 other sites in Asia. The results indicated that the majority of Asian terrestrial ecosystems are currently large carbon sinks. The average net ecosystem production (NEP) values were 325 ± 187, 274 ± 207, 236 ± 260, $89 \pm 134\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in cropland, forest, wetland and grassland ecosystems, respectively. The spatial variation of gross primary production (GPP) and ecosystem respiration (Re) were mainly controlled by the mean annual temperature (MAT) and the mean annual precipitation (MAP) in the Asian region. There was a clear linear relationship between GPP and MAT, and a strong sigmoid relationship between GPP and MAP. Re was exponentially related to MAT and linearly related to MAP. Interestingly, those response modes were consistent across different ecosystem types. The different responses of GPP and Re to MAT and MAP determined the spatial variation of NEP. The combined effects of MAT and MAP contributed 85%, 81% and 36% to the spatial variations of GPP, Re and NEP, respectively. Our findings confirmed that the spatial variation of carbon exchange fluxes was mainly controlled by climatic factors, which further strongly supports the use of the climate-driven theory in the Asian region.

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1. Introduction

The global land biosphere has been estimated to be a carbon sink with strong carbon uptake rate at mid-to-high latitudes in the northern hemisphere over the last two decades (Ciais et al., 1995; Tans et al., 1990). However, the sink magnitude and spatial distribution are still uncertain, due to the influence of natural and human factors such as climate, vegetation and land-use change (Crevoisier et al., 2010; Pan et al., 2011; Stephens et al., 2007). Therefore, understanding the spatial variation and controlling mechanisms of carbon exchange fluxes between different carbon pools at global and regional scales is helpful for accurately predicting future climate change (Yu et al., 2011).

Based on global net primary production (NPP) observation data, Lieth (1973) built the 'Miami' model to successfully describe the spatial pattern of global NPP using temperature and precipitation, which implied that the spatial pattern of ecosystem production was mainly controlled by climatic factors. Nemani et al. (2003) and

Yi et al. (2010) further proved ecosystem production was largely controlled by temperature at mid-to-high latitudes, and by precipitation at low latitudes. However, soil, vegetation and land use were also believed to influence the carbon pools (Chapin et al., 2002), and multiple factors were thought to control the carbon exchange fluxes at regional scales (Granier et al., 2007; Thornton et al., 2002). Considering more confounding factors will expect to more accurately assess the carbon balance, but it also may trade off by leading to more complicated and greater uncertainty to the global carbon budget assessment.

The spatial variation of net ecosystem production (NEP) and ecosystem respiration (Re) were weakly related to climatic factors in the European and North-American regions (Law et al., 2002; Luyssaert et al., 2007). Conversely, in the Asian region the spatial variations of gross primary production (GPP), Re and NEP were primarily related to climatic factors based on previous Asi-aFlux sites (Hirata et al., 2008; Kato and Tang, 2008). In China, it was demonstrated that the spatial patterns of GPP, Re and NEP were determined by mean annual temperature and precipitation, and those response modes were consistent in different ecosystem types; this result further developed the climate-driven theory (Yu et al., 2013). With the development of the ChinaFLUX and AsiaFlux network of in situ and continuous measurements in recent decades, the regional analysis of spatial variation in carbon exchange fluxes and the controlling factors behind this are becoming available for the Asian region.

Therefore, this study integrated long-term continuous observation data from ChinaFLUX and published data from AsiaFlux and other affiliated sites, to (1) explore the spatial variation of terrestrial ecosystem carbon exchange fluxes in the Asian region, (2) explore the controlling factors of that spatial variation, and (3) test the applicability of a climate-driven theory in Asia. This study is expected to improve our understanding of the biogeographic mechanism of the spatial variation of ecosystem carbon exchange fluxes and to provide a theoretical basis for developing an assessment model of the carbon budget in terrestrial ecosystems on regional and global scales.

2. Materials and methods

2.1. Observation method

The eddy covariance technique provided a direct and continuous measure of the net carbon and water fluxes between the biosphere and atmosphere (Baldocchi et al., 1996), which consisted of a 3D ultrasonic anemometer to measure three-dimensional wind speed and temperature fluctuations, and an infrared gas analyzer to measure CO_2 and water vapor densities. The eddy covariance technique is closely related to physiological and ecological processes and can reflect seasonal and interannual variability of carbon fluxes (Baldocchi et al., 2001). Globally, there are currently more than 400 sites, spanning forest, grassland, cropland, wetland, tundra, and desert ecosystems (Baldocchi, 2008).

2.2. Data observation and process of ChinaFLUX

Since 2002, ChinaFLUX has grown into a regional observation and research network, covering four main ecosystem types: forest, grassland, cropland and wetland. The open-path eddy covariance (OPEC) system was used to measure carbon and water vapor fluxes at ChinaFLUX sites. All signals were sampled at 10 Hz frequency and the CO_2 and H_2O fluxes were calculated and recorded at 30 min intervals by a CR5000 datalogger (Model CR5000, Campbell Scientific, Logan, UT, USA). At each site, the meteorological variables were measured simultaneously, including solar radiation, air

temperature, rainfall, soil temperature and soil moisture, which were sampled at a 2 s frequency and recorded at 30 min intervals (Yu et al., 2013).

To ensure the reliable processing of flux data, ChinaFLUX has developed a series of proven methodologies for assessing the performance of the observation system and flux data quality control (Yu et al., 2006), including the three-dimensional coordinate rotation (Zhu et al., 2004), WPL correction (Webb et al., 1980), storage flux calculation, outlier filter, nighttime CO_2 flux (Reichstein et al., 2005), gap filling (Falge et al., 2001) and net ecosystem exchange (NEE) flux partitioning (Reichstein et al., 2005). For details of data quality control and gap-filling refer to Yu et al. (2006).

2.3. Collection and integration of carbon flux observation data in Asia

Published carbon flux data from other sites in Asia during the past two decades (1995–2010) were collected. We adopted the following methods to screen these data:

Carbon flux data were uniformly measured by the eddy covariance technique, and subsequently passed a series of processes performed by the individual site researchers, including the three-dimensional coordinate rotation, WPL correction, storage flux calculation, outlier filter, nighttime CO_2 flux, gap filling and flux partitioning. In the dataset, the OPEC was applied in more than 80% of the sites. Although there remain several sites that applied the closed-path eddy covariance (CPEC), the error of these two system results was less than 5% (Baldocchi et al., 2001). The u* threshold varied among different ecosystems because it was identified according to the local topography, vegetation and weather. High canopy vegetation (forests) tend to have larger u* than low canopy vegetation (croplands and grasslands). The smallest u* threshold is 0.1 m/s in forests, and is 0.01 m/s in low canopy ecosystems (Papale et al., 2006). In general, the u* threshold is usually between 0.1 and 0.4 m/s (Reichstein et al., 2005) and the u* threshold in our dataset fall into this range. For gap filling, Mean Diurnal Variation (MDV), Look-Up Tables (LookUp) and Nonlinear Regression (NLR) are used (Falge et al., 2001). More than 57% of sites applied the NLR approach in the dataset. Although these three approaches were adapted to different time scales and gap lengths, there was no significant difference between the interpolated results according to statistical analysis (Falge et al., 2001). For flux partitioning, two approaches were used in our dataset: (1) nighttime data-based (NB): respiration measurements made at night were extrapolated to the daytime based on the relationship between respiration and T_{air} or T_{soil} (Lloyd and Taylor, 1994; Reichstein et al., 2005); (2) daytime data-based (DB): light-response curves were fit to daytime NEE measurements and respiration was estimated from the intercept, then respiration was extrapolated into the nighttime using T_{air} or T_{soil} measured during the night (Falge et al., 2002; Lasslop et al., 2010). The NB approach was overwhelmingly applied in the dataset. Both methods were effective, and no obvious differences were reported between the partitioning results under the condition of no existing large soil carbon storage (Falge et al., 2002). Measurement systems and approaches applied for each site are explicitly shown in Table S2.

2.4. Additional selection criteria

Because the aim of this study was to analyze the spatial variation of carbon fluxes at an annual scale, all data were required to be continuous for longer than 1 year. Except for certain ecosystems in the boreal and subarctic zones, only continuous data collected during the growing season are available, including the Tura, Huzhong, Yichun and Zotino sites. At the Tura site, the annual NEP was estimated based on measurements during the growing seasons
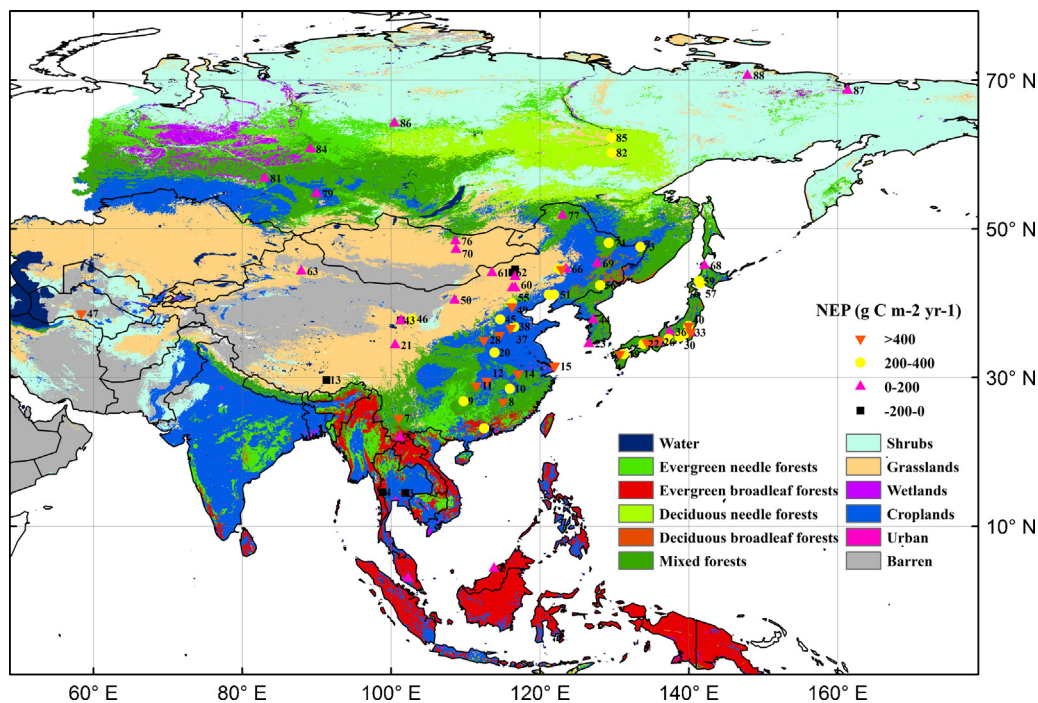
Fig. 1. Location and spatial distribution of the flux sites used in this study. The base map is the reclassified 2008 MODIS land-cover map. Symbols indicate the location of the flux sites. The number of each site refer to the information in Table S1.

(June–September), since GPP can be ignored because the larch forests were leafless, and winter respiration estimated by chamber measurements was negligibly small for scaling to whole-year fluxes (Matsuura et al., 2007). At the Zotino site, eddy covariance measurements were continuously conducted from April to October, but average fluxes measured during 14 continuous days in the non-growing season were applied to the days of the year not covered by measurements in order to give an annual NEP estimate (Arneth et al., 2002). At the Huzhong site, the *Dahurian Larch* forests were leafless during the dormant season, and winter CO_2 efflux from October to April was shown to be small (Cui, 2007; Wang et al., 2010); at the Yichun site, there might be an overestimate of annual NEP. Considering that such ecosystems represent the unique eco-regions that play an important role in spatial variation analysis, these sites were accepted in our study. However, the annual value at these sites might be overestimated NEP due to underestimation of Re in the dormant season. Natural and human disturbances, such as fire, logging, and harvesting, directly or indirectly affect ecosystem photosynthesis, respiration and other carbon exchange processes (Chapin et al., 2002). Ecosystems usually rapidly convert to carbon emissions after a disturbance, while gradually becoming carbon sinks after 2–7 years (Thornton et al., 2002). Therefore, ecosystems were required to have not suffered from natural or human disturbances for longer than 10 years so as to eliminate the effects of recent disturbances on ecosystem carbon exchange fluxes. Cropland ecosystems are different from other natural ecosystems, and can experience large carbon imbalances as a result of tremendous changes in cultivation systems or management practices. Therefore, in this study we only selected croplands that grow typical native crops with relatively long-term cultivation history, and keep constant cultivation systems and management practices.

2.5. Data selection results

A total of 88 flux sites were included in this study, in which 19 sites from ChinaFLUX, 37 sites from AsiaFlux and 32 other sites. These sites are distributed across the East Asia, Far East Asia,

Southeast Asia and Asian Russia region, spanning from 2.97°N to 70.62°N in latitude, and from 58.4°E to 161.34°E in longitude (Fig. 1). These sites are in six climate zones: tropical, subtropical, temperate, boreal, subarctic and alpine. The distribution of these sites in the mean annual climate space (Fig. 2) indicates that they cover typical Asian climate types. These ecosystems were grouped into eight biome types: evergreen broadleaf forests (6 sites), evergreen needle forests (7 sites), deciduous broadleaf forests (9 sites), deciduous needle forests (6 sites), mixed forests (9 sites), grasslands (22 sites), croplands (15 sites) and wetlands (14 sites) (Table S1).

For sites with longer than 2 years of data records, the average values for carbon fluxes and climatic variables were calculated to eliminate the temporal variability in the analysis. For some sites with missing climatic data, that was initially filled by observation from neighboring meteorological stations, and the climate research unit (CRU) database was used further fill in the missing data. The 30-year MAT and MAP from the CRU database showed good agreement with MAT ($R^2 = 0.96$) and MAP ($R^2 = 0.88$) measured at the flux tower site (Fig. 3).

Net ecosystem exchange as NEE was directly measured by eddy covariance, which was shown as negative NEP in most studies. Therefore, we similarly use NEP to represent NEE and the sign of NEP is positive when CO_2 is transported from the atmosphere down to the ecosystem and negative for the opposite case.

2.6. Uncertainty analysis

During the eddy covariance measurements, errors often occurred, such as random errors caused by sensor noise and instantaneous change in atmospheric turbulence, systematic bias caused by sensor drift, limited response of instruments, and selective systematic deviation caused when advection or storage occurred during stable night-time conditions (Aubinet et al., 2000; Baldocchi et al., 2001). Overall, the annual NEE measurement error was within $30–100 \, g \, C \, m^{-2} \, yr^{-1}$ (Baldocchi, 2008), and an approximate $30–50 \, g \, C \, m^{-2} \, yr^{-1}$ error would be introduced during
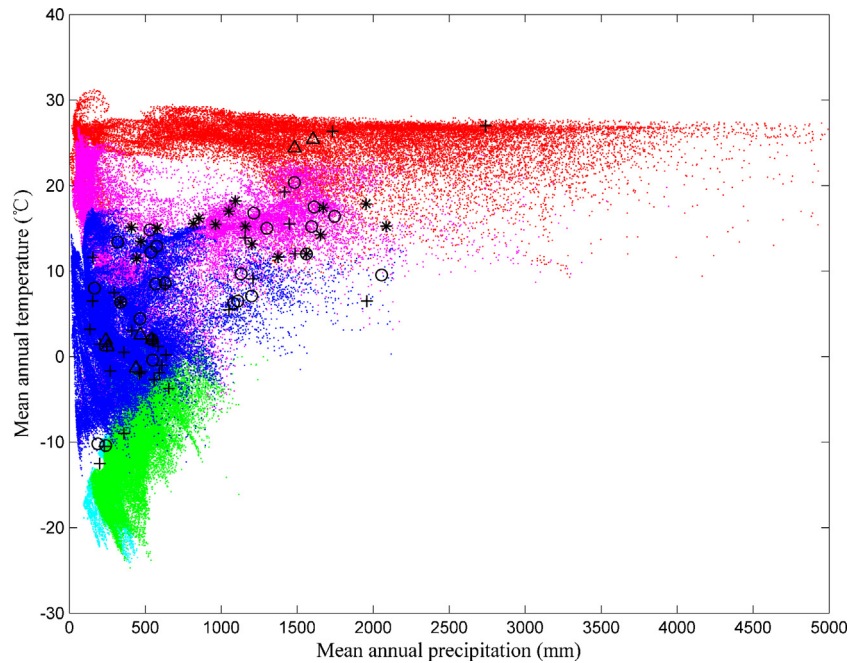
Fig. 2. Distribution of the 88 sites in mean annual climate space. Climate parameters are the mean annual precipitation (*x*-axis) and mean annual temperature (*y*-axis) taken over a 50-year period of record (1950–2000) from the WorldClim database (http://www.worldclim.org/current). Points indicate the climate space distribution within the Asia region at 10 arc-minutes resolution. Red, magenta, blue, green, cyan points indicate tropical zone, subtropical zone, temperate zone, boreal zone, and arctic zone respectively; Symbols show the location of each Flux site in the climate space. Triangle, cross, circle and star symbols indicate the site NEP within −200 to 0, 0–200, 200–400, >400 Pg C m^{-2} yr^{-1} respectively. (For interpretation of the reference to the color in this figure legend, the reader is referred to the web version of the article.)

the data correction. In the regression analysis, several errors were introduced. To test these regression errors, we referred to Reichstein et al. (2007) using the Monte-Carlo simulation method. The results showed that the error was within 200 g C m^{-2} yr^{-1}. First, to the annual flux data of each site a ±200 g C m^{-2} yr^{-1} random error was added using the Monte-Carlo simulation method, which guaranteed that each error direction was random and independent. Valid probability distribution of variance of regression analysis can be obtained after carrying out these simulations 1000 times. The results showed that the expected real error was much less than the set error. Therefore, we can conservatively believe that the error was within 200 g C m^{-2} yr^{-1}.

2.7. Data statistic analysis

All data were analyzed by SPSS 16.0 statistical software, using Linear Regression Analysis and Dynamic Curve Fit to analyze the
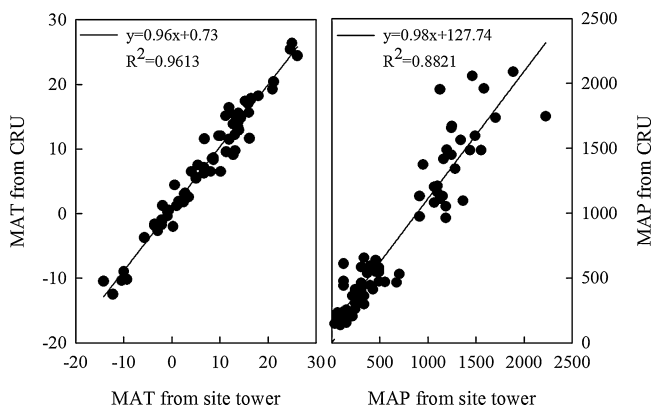
Fig. 3. Correlations of MAT and MAP abstracted from CRU database to MAT and MAP measured at flux tower site.

relationships between (GPP, Re, NEP) and (MAT, MAP) respectively. The correlation figures of (GPP, Re, NEP) to (MAT, MAP) respectively were drawn by Sigma Plot 10.0 software. The spatial distribution figure of sites was plotted by ArcGIS 10.0 software.

3. Results

3.1. Asian terrestrial ecosystem carbon sink strength

As a whole, NEP of Asian terrestrial ecosystems ranged from −150 to 1000 g C m^{-2} yr^{-1}. Most terrestrial ecosystems in Asia were large carbon sinks, giving an overall mean and median NEP of 232 ± 213 g C m^{-2} yr^{-1} (Table 1) and 195 g C m^{-2} yr^{-1}, respectively. The largest carbon source was in Inner Mongolia grasslands, with an NEP of −158 g C m^{-2} yr^{-1}, and the largest carbon sink was found in the Ailaoshan subtropical forest, with an NEP of 976 g C m^{-2} yr^{-1}. The GPP of Asian terrestrial ecosystems ranged widely, from 130 to 3800 g C m^{-2} yr^{-1}, and averaged of 1182 ± 878 g C m^{-2} yr^{-1}. The GPP was less than 200 g C m^{-2} yr^{-1} in the Damxung alpine meadow, Xilinhot arid and semi-arid steppe and Kherlenbayan boreal meadow. In contrast, in tropical forests (Pasoh, Lambir, Sakaerat, Mae Klong), the GPP was larger than 3000 g C m^{-2} yr^{-1}. Especially in the Sakaerat tropical forest, the GPP was up to 3760 g C m^{-2} yr^{-1}. The average Re of Asian terrestrial ecosystems was 990 ± 827 g C m^{-2} yr^{-1}. Similar to GPP, the Re in arid (Fukang) and cold (Kherlenbayan, Tura, Cherskii) regions was low, less than 200 g C m^{-2} yr^{-1}. However, in tropical regions (Pasoh, Lambir, Sakaerat, Mae Klong), the Re was higher than 3000 g C m^{-2} yr^{-1}.

The carbon sink strength differed greatly among ecosystem types in the Asian region (Table 1). The cropland ecosystems had the highest carbon sink strength with an average NEP of 325 ± 187 g C m^{-2} yr^{-1}. The average NEP of forest ecosystems was 274 ± 207 g C m^{-2} yr^{-1}. In forest ecosystems, the GPP and Re was highest, averaging 1691 ± 884 g C m^{-2} yr^{-1} and

Table 1
GPP, Re and NEP of different ecosystems in the Asian region (mean ± STD).

	Grassland	Cropland	Forest	Wetland	Average
NEP (g C m^{-2} yr^{-1})	89.2 ± 134.5 (n = 21)	325.0 ± 187.4 (n = 15)	273.7 ± 207.2 (n = 37)	236.1 ± 259.7 (n = 14)	232.0 ± 212.9 (n = 87)
GPP (g C m^{-2} yr^{-1})	458.5 ± 548.7 (n = 15)	1209.3 ± 670.5 (n = 6)	1690.8 ± 883.6 (n = 24)	1052.8 ± 639.6 (n = 12)	1181.5 ± 878.2 (n = 57)
Re (g C m^{-2} yr^{-1})	447.4 ± 561.0 (n = 14)	902.6 ± 503.2 (n = 6)	1428.4 ± 952.8 (n = 24)	789.5 ± 437.0 (n = 12)	989.9 ± 826.8 (n = 56)

1428 ± 953 g C m^{-2} yr^{-1} respectively. The average NEP of wetland ecosystems was 236 g C m^{-2} yr^{-1} equivalent to forest ecosystems, but large variability existed in wetlands, reaching 260 g C m^{-2} yr^{-1}. The NEP, GPP and Re of grassland ecosystems tended to be the lowest. The average NEP of grassland was 89 ± 134 g C m^{-2} yr^{-1}, shown as the smallest carbon sink but with the largest spatial variability.

### 3.2. The effect of temperature on the spatial variation of GPP, Re and NEP

Temperature is an important factor driving the ecosystem carbon budget. As is clearly shown in Fig. 4a–c, the site-average annual GPP, Re and NEP were correlated to the mean annual temperature (MAT). MAT contributed 73%, 75% and 41% to the spatial variation of GPP, Re and NEP ($P < 0.001$), respectively. In the regression analysis, two outliers are excluded, Karrykul and KBQ, where the carbon fluxes are already limited by low MAP (<200 mm) that do not benefit from high MAT ($>10\,°C$) in line with the basic ecological principle (Liebig's 'Law of the Minimum').

GPP, Re and NEP responded to MAT differently. There was a clear linear relationship between GPP and MAT ($R^2 = 0.7310$; $P < 0.001$) (Table 2). For every 1 °C increase in MAT, GPP increased by 84.55 g C m^{-2} yr^{-1} spatially. Re was strong exponentially related to MAT ($R^2 = 0.7529$; $P < 0.001$), better than a linear relationship ($R^2 = 0.6133$; $P < 0.001$) (Table 2). The temperature sensitivity (Q_{10}) of the site-average annual Re was about 2.17. The spatial variation of NEP was significantly related to MAT in the Asian region ($P < 0.001$), and MAT can explain 41% of the spatial variation of NEP. At the low temperature range (0–$10\,°C$), GPP tended to grow faster than Re with an increase in MAT, leading to an initial increase in NEP. At about 12 °C, the increase in the rate of Re was equivalent to that of GPP. As the temperature continuously increased, ecosystem respiration consumption (Re) exceeded ecosystem productivity (GPP). Therefore, NEP was no longer increasing but declining when the annual air temperature was higher than approximately 20 °C (Fig. 4c). The relationship between NEP and MAT was expressed as the different responses of GPP and Re to MAT, rather than a linear or quadratic relationship (Table 2).

3.3. The effect of precipitation on the spatial variation of GPP, Re and NEP

Water is the basic material required for maintenance of ecosystem structure and function. Water shortage can severely limit ecosystem carbon sequestration capacity, especially in arid areas. As is clearly shown in Fig. 5a–c, the site-average annual GPP, Re and NEP were significantly correlated to mean annual precipitation (MAP). MAP contributed 62%, 52% and 22% to the spatial variation of GPP, Re and NEP ($P < 0.001$).

GPP, Re and NEP also responded differently to MAP. There was a clear sigmoid relationship between GPP and MAP ($R^2 = 0.6192$; $P < 0.001$), which was stronger than a linear relationship ($R^2 = 0.5892$; $P < 0.001$) (Table 2). GPP grew rapidly with an increase in MAP when MAP was below 1500 mm. As the water situation improved, the growth rate of GPP was reduced, and GPP remained relatively stable when precipitation reached approximately 2000 mm (Fig. 5a). There was a linear relationship between Re and MAP ($R^2 = 0.5248$; $P < 0.001$) (Table 2). When MAP increased
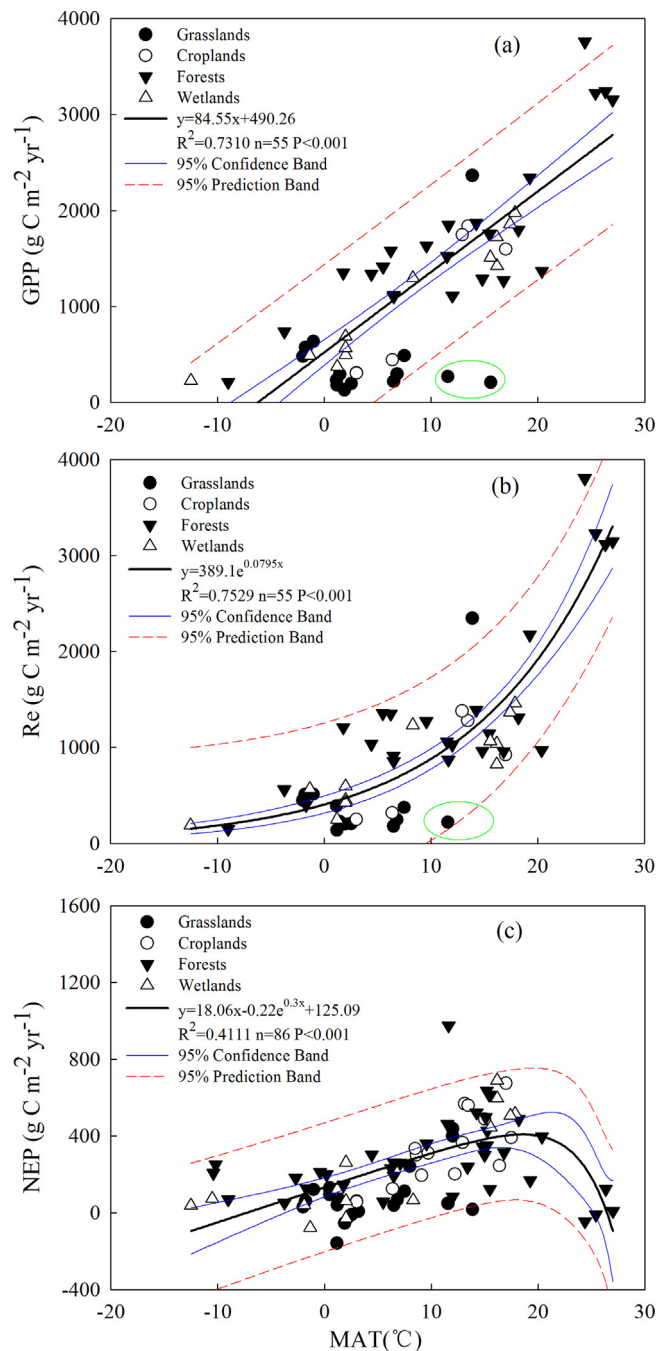
Fig. 4. The influence of MAT on the spatial pattern of NEP, GPP and Re in the Asian region. Notes: According to Liebig's 'Law of the Minimum' as Lieth (1973) and Luyssaert et al. (2007), two sites: Karrykul (MAT:15.6 °C, MAP:148 mm) and KBQ (MAT:11.6 °C, MAP:155 mm) were excluded in the green circles. NEP: Net Ecosystem Production; GPP: Gross Primary Production; Re: Ecosystem Respiration; MAT: Mean Annual Temperature. (For interpretation of the reference to the color in this figure legend, the reader is referred to the web version of the article.)

Table 2
Univariate regression models between carbon fluxes (GPP, Re, NEP) and climatic factors (MAT, MAP) in the Asian region.

CO_2 fluxes	Variable	Model type	Regression coefficients				Determination coefficient R^2	P
			a	b	c	d		
GPP	MAT	Linear	84.55	490.20			0.7310	<0.0001
	MAP	Linear	1.14	220.44			0.5892	<0.0001
		Sigmoid	3552	0.0005			0.6192	<0.0001
Re	MAT	Linear	73.20	372.72			0.6133	<0.0001
		Exponential	389.1	0.0795			0.7529	<0.0001
	MAP	Linear	1.014	120.20			0.5248	<0.0001
NEP	MAT	Linear	11.21	145.86			0.2105	<0.0001
		Quadratic	16.63	−0.37	153.82		0.2376	<0.0001
		Combined	18.06	−0.22	0.3	125.09	0.4111	<0.0001
	MAP	Linear	0.12	128.44			0.1084	0.0018
		Quadratic	0.53	−0.0002	−20.48		0.2156	<0.0001
		Combined	2530	−0.0005	−0.66	−59	0.2176	0.0001

by 100 mm, Re correspondingly increased by 101 g C m^{-2} yr^{-1} spatially. GPP and Re increased along MAP at different rate. When precipitation was below 1000 mm, GPP tended to grow faster than Re as MAP increased, and the difference between GPP and Re was maximized at approximately 1500 mm, at which point NEP showed the highest value. As MAP continuously increased, Re exceeded GPP, which resulted in NEP decreasing when MAP was above 2500 mm (Fig. 5c). The results showed that spatial variation of NEP due to MAP was significant in the Asian region ($P < 0.001$), and MAP could explain 22% of the spatial variation of NEP. The effect of MAP on the spatial variation of NEP was also determined by the different responses of GPP and Re to MAP, rather than by a linear or quadratic relationship (Table 2).

3.4. The combined effect of temperature and precipitation on the spatial variation of GPP, Re and NEP

GPP, Re and NEP were all significantly related to MAT and MAP. The single factor of MAT or MAP contributed 62–73% of the spatial variability of GPP, 52–75% of Re and 22–41% of NEP in the Asian region.

Subsequently, we analyzed the combined effect of temperature and precipitation on the spatial variation of GPP, Re and NEP. The results showed that MAT and MAP combined contributed 85% of the spatial variation of GPP, 81% of the spatial variation of Re and 36% of the spatial variation of NEP in the Asian region (Eqs. (1)–(3)). Compared to linear and quadratic equations, the combined equation not only had a higher determination coefficient (Table 3), but also followed the fact that NEP is a combined result of ecosystem photosynthetic and respiratory fluxes which respond to climatic variables linearly or exponentially (Figs. 4 and 5). This result indicated that temperature and precipitation were the two main factors regulating the spatial variation of GPP and Re. The contribution of MAT and MAP to the spatial variation of NEP is approximately 36% which was relatively low compared to GPP and Re.

$$\text{GPP} = 6.2\text{MAT} - 0.6\text{MAP} + 2067 \log \text{MAP} + 164.6e^{0.1\text{MAT}}$$
$$- 4750; \quad R^2 = 0.853, \quad n = 55, \quad P < 0.001; \tag{1}$$

$$Re = -18.2\text{MAT} - 0.4\text{MAP} + 1399 \log \text{MAP} + 223.1e^{0.1\text{MAT}}$$
$$- 3252; \quad R^2 = 0.805, \quad n = 54, \quad P < 0.001; \tag{2}$$

$$\text{NEP} = 21.4\text{MAT} - 0.1\text{MAP} + 322 \log \text{MAP} - 47.7e^{0.1\text{MAT}}$$
$$- 608; \quad R^2 = 0.358, \quad n = 85, \quad P < 0.001; \tag{3}$$

4. Discussion

4.1. Carbon sink/source strength of Asian terrestrial ecosystems

The results showed that the NEP of Asian terrestrial ecosystems ranged between −150 and 1000 g C m^{-2} yr^{-1} with an average of 232 ± 213 g C m^{-2} yr^{-1}, which indicated that the majority of ecosystems studied functions as a net carbon sink. The NEP of global terrestrial ecosystems ranged widely between −1000 and 1300 g C m^{-2} yr^{-1} (Baldocchi, 2008), hence the NEP of Asian terrestrial ecosystems varied within a reasonable range.

The carbon sink strength differed greatly in Asian terrestrial ecosystems. NEP tended to be higher in warm environments compared to cold environments, and in humid areas compared to arid areas, which was consistent with the results of Kato and Tang (2008) and Luyssaert et al. (2007). However, we found that the largest NEP did not appear in the warmest and moistest tropical ecosystems. Sufficient light, moisture and temperature maximized GPP in the tropical ecosystems, such as the Pasoh, Lambir and Sakaerat sites, in which GPP was larger than 3000 g C m^{-2} yr^{-1}. However, ecosystems with the largest GPP do not take the maximum NEP for granted (Baldocchi, 2008). It was reported that NEP would not keep increasing when GPP was over 2200 g C m^{-2} yr^{-1} (Luyssaert et al., 2007). Our results further confirmed that NEP was not only affected by GPP but also constrained by Re. Hot and humid environments in tropical ecosystems promoted decomposition of abundant litterfall substrates. Additionally, dry topsoil caused by a lowering of groundwater levels due to human drainage activities in tropical ecosystems accelerated the decomposition of soil organic matter (Hirano et al., 2007). Therefore, high Re made NEP lower in hot and humid tropical ecosystems, even though they had the maximum GPP.

4.2. Carbon sink strength of different ecosystem types in the Asian region

The carbon sink strength differed greatly among ecosystem types in the Asian region. Forest ecosystems usually are strong carbon sinks (Unger et al., 2009). Global forest ecosystems had a net uptake of $1.1 + 0.8$ Pg C yr^{-1} from the atmosphere during 1990–2007 (Pan et al., 2011), which accounted for 70–80% of the global terrestrial carbon sinks. The study found that the NEP of Asian forest ecosystems averaged 274 ± 207 g C m^{-2} yr^{-1}, which was consistent with the results of Kato and Tang (2008). Yuan et al. (2009) noted that the NEP of global evergreen coniferous forests and deciduous broadleaf forests averaged between 190 and 250 g C m^{-2} yr^{-1}, and the NEP of global forests averaged approximately 247 g C m^{-2} yr^{-1} (geometric average value of the results

Table 3
Multivariate regression models between carbon fluxes (GPP, Re, NEP) and climatic factors (MAT, MAP) in the Asian region.

| CO_2 fluxes	Linear		Quadratic		Combined	
	Determination coefficient R^2	P	Determination coefficient R^2	P	Determination coefficient R^2	P
GPP	0.752	<0.0001	0.827	<0.0001	0.853	<0.0001
Re	0.664	<0.0001	0.758	<0.0001	0.805	<0.0001
NEP	0.206	<0.0001	0.299	<0.0001	0.358	<0.0001

by Luyssaert et al., 2007), indicating that Asian forest ecosystems generally function as net carbon sinks and play an important role in the global carbon balance. The large strength of the carbon sink was closely related to national afforestation-reforestation programs of Asian countries in the past few decades (Fang et al.,

Fig. 5. The influence of MAP on the spatial pattern of NEP, GPP and Re in the Asian region. NEP: Net Ecosystem Production; GPP: Gross Primary Production; Re: Ecosystem Respiration; MAP: Mean Annual Precipitation.

2001). Especially in China, since the 1960s and 1970s, plantation forest areas have increased to 61.69ɤMha, while large areas of secondary natural forest were restored. The area of natural forests in China increased 3.93ɤMha from 2004 to 2008 (State Forestry Bureau, 2010). Most of these young plantations and secondary natural forests were in a rapid growth period with strong carbon absorption ability (Stoy et al., 2008; Goulden et al., 2011). Thus, the forest carbon sink of China has increased 34% from 1990–1999 to 2000–2007 (Pan et al., 2011). However, on an area basis, the accumulation of carbon in Asian forests was still relatively lower than that of European forest ecosystems (Janssens et al., 2003; Piao et al., 2009a,b, 2012), which was related to forest ecosystem management methods and intensity. In Europe, large areas of temperate and boreal forests are maintained with intensive forest management such as thinning and harvesting. Under human management and protection, the litterfall was removed through harvesting and was subsequently consumed off-site; therefore, litter decomposition and soil heterotrophic respiration in situ tended to be lower in managed ecosystems compared to non-managed ecosystems (Wilkinson et al., 2012). It is suggested that the future development of forest ecosystems in Asia requires a continuous increase in forest coverage, and an intensification of forest ecosystem management as well.

Asian cropland ecosystems had the highest carbon sink strength (NEP: $325 \pm 187\,g\,C\,m^{-2}\,yr^{-1}$), which was consistent with the previous report of Kato and Tang (2008) on Asian cropland ecosystems. This result indicated that Asian cropland ecosystems have a net uptake of atmospheric CO_2. The carbon sink function of Asian cropland ecosystems was likely related to Asian cropland management practices and cropping systems. In Asia, croplands are usually under fertilization, irrigation and other intensive managements, and straw returning and no-tillage systems are widely utilized (Shen, 1998). These management systems supply adequate nutrient to croplands, and also allow abundant residues and organic matter to return to the soil, which were most likely increases the carbon absorption of the croplands (Huang and Sun, 2006; Lal, 2004).

Generally limited by water supply, grassland ecosystems are often weak carbon sinks, or even carbon sources. Kato and Tang (2008) noted that the NEP of Asian grasslands was approximately $116 \pm 167\,g\,C\,m^{-2}\,yr^{-1}$. Janssens et al. (2003) reported that the NEP of European grasslands was approximately $142\,g\,C\,m^{-2}\,yr^{-1}$. We consistently found that Asian grassland ecosystems were weak carbon sinks with an average NEP of $89 \pm 134\,g\,C\,m^{-2}\,yr^{-1}$. However, Asian grasslands tended to have larger variation compared to cropland and forest ecosystems. The grassland sites were distributed over a wide longitudinal scale and were often vulnerable, either restricted by temperature or moisture or both. In addition, the grassland ecosystems were often subjected to different management practices, such as grazing, harvesting, irrigation and drainage (Cao et al., 2004; Fu et al., 2009), which resulted in large differences in the carbon uptake or release of grassland ecosystems.

The Asian wetland ecosystems were strong carbon sinks, with an average NEP of $236\,g\,C\,m^{-2}\,yr^{-1}$, which was equivalent to forest ecosystems. Kato and Tang (2008) previously found that the typical Asian wetland was a weak carbon source with carbon emissions of $42 \pm 76\,g\,C\,m^{-2}\,yr^{-1}$. As the number and coverage of the
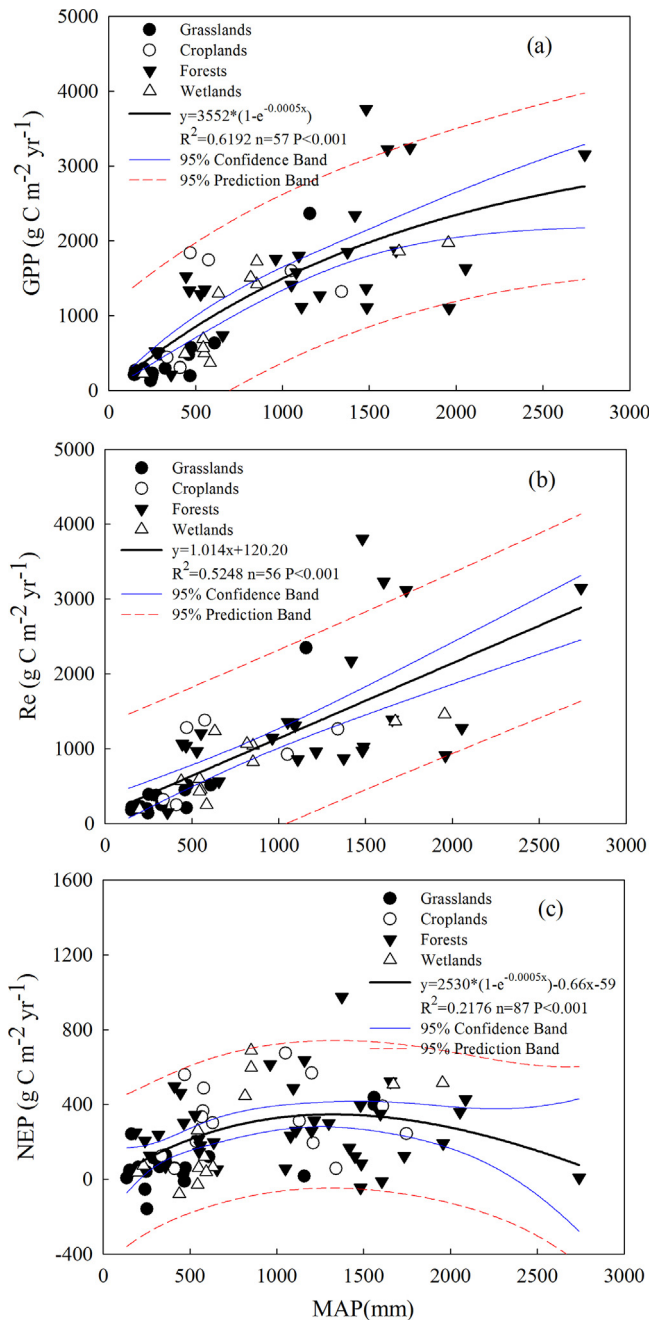
wetland sites were greatly improved in our study, the results tended to be more credible. However, it is still important to note that there was a large variability of NEP among wetland ecosystems, reaching $260\,g\,C\,m^{-2}\,yr^{-1}$. This variation was largely due to the large influence of different management schemes on wetlands. Natural wetlands provided weak uptake of carbon at $71\,g\,C\,m^{-2}\,yr^{-1}$, while carbon was released intensively at $399\,g\,C\,m^{-2}\,yr^{-1}$ when the wetlands were under disturbance (Janssens et al., 2003). Thus, although the coverage of the wetlands in our statistical analysis has expanded compared to previous studies, we were still limited in determining the source or sink function of wetlands and their strength due to the modest number of sites in our study. It is suggested that wetland site construction and research should be strengthened to allow a better regional and global terrestrial ecosystem carbon budge analysis.

4.3. Environmental control on the spatial variation of carbon exchange fluxes in the Asian region

4.3.1. GPP

Numerous studies have indicated that the spatial variation of GPP is mainly determined by temperature, and GPP increases with an increase in temperature (Hirata et al., 2008; Kato and Tang, 2008; Law et al., 2002; Luyssaert et al., 2007; Wang et al., 2008; Sasai et al., 2011). The spatial variation of GPP in Asia consistently showed a strong linear relationship with MAT ($R^2 = 0.73$), and this linear relationship was uniform in single ecosystems (forest, cropland, grassland and wetland) (Figs. S1 and S2) and in combined ecosystems (Figs. 4a and 5a). This result indicated that the decisive effect of temperature on the spatial variation of GPP did not vary across different ecosystem types. Temperature was the most important factor regulating the potential photosynthetic activity of vegetation as well as the length of the growing season (Hirata et al., 2008; Saigusa et al., 2008), which both directly determined ecosystem productivity (Chapin et al., 2002). In addition to temperature, precipitation was another determinant of the spatial variation of GPP, and MAP contributed 60% of the spatial variation of GPP. However, there was a strong sigmoid relationship between GPP and MAP in the Asian ecosystems which was consistent with the classic expression of the 'Miami' model (Lieth, 1973) rather than a linear relationship (Kato and Tang, 2008). GPP grew rapidly along with an increase in MAP when MAP was lower than 1500 mm, but GPP remained relatively stable when precipitation reached approximately 2000 mm (Fig. 5a). This result was partially supported by the finding, in a global forest study, that GPP was saturated at annual precipitation above 1500 mm (Luyssaert et al., 2007; Wang et al., 2008). This saturation occurred because abundant rainfall would flow away as runoff when the soil and vegetation were saturated; hence, soil moisture and vegetation evapotranspiration and production remained relatively constant (Luyssaert et al., 2007). Furthermore, a lack of radiation originating from numerous rainy days in high precipitation sites likely limited the increase in GPP.

4.3.2. Re

The spatial variation of Re was significantly exponentially and linearly correlated to MAT and MAP, respectively ($R^2 = 0.75$; $R^2 = 0.52$), indicating that temperature and precipitation were the major determining factors of the spatial variation of Re in the Asian region. Similarly, the relationship of Re to MAT and MAP was uniform in a single ecosystem (forest, grassland and wetland, cropland excluded due to a scarcity of sites) (Figs. S3 and S4) and in combined ecosystems (Figs. 4b and 5b). This result indicated that the decisive effect of temperature and precipitation on the spatial variation of Re did not vary across different ecosystem types. More than 75% of ecosystem respiration is derived from soil autotrophic and heterotrophic respiration (Janssens et al., 2003), which is mainly controlled by temperature and moisture at an individual site scale (Reichstein et al., 2003). At a large spatial scale in Asia, the decisive role of temperature and moisture on Re still exists (Hirata et al., 2008).

4.3.3. NEP

The spatial variation of NEP in Asia was correlated to MAT and MAP, especially with MAT, contributing 41% of the spatial variation of NEP. However, our study found that the dependency of NEP on MAT at the Asian region was expressed as the difference response function of GPP and Re to MAT ($R^2 = 0.41$), rather than a linear (Kato and Tang, 2008) or quadratic function relationship (Wang et al., 2008). That is because NEP is not determined by a single physiological process but rather is a result of the combined responses of ecosystem photosynthetic and respiratory fluxes to environmental conditions (Piao et al., 2009a,b). The NEP of the Asian ecosystems gradually increased as GPP linearly increased with an increase in MAT. As MAT continuously increased, the ecosystem respiration consumption eventually exceeded ecosystem productivity. Therefore, under the combined effects of GPP and Re, NEP showed an increasing than decreasing trend with an increase in MAT (Fig. 4c). The dependency of NEP on the combined effects of GPP and Re has also been confirmed within the relationship between NEP and MAP ($R^2 = 0.22$). This new function of the dependency of NEP on combined climatic factors (MAT, MAP) provides a new approach for the analysis of spatial patterning of NEP at regional and global scales.

In summary, the spatial variation of GPP, Re and NEP was strongly regulated by MAT and MAP in the Asian region. This result was consistent with the results of previous studies on Asian ecosystems (Hirata et al., 2008; Kato and Tang, 2008) and global forests (Wang et al., 2008; Yi et al., 2010). The result also further proved the applicability of the spatial variation of ecosystem carbon exchange fluxes by climate-driven theory (Lieth, 1973; Nemani et al., 2003; Yi et al., 2010). The spatial variation of GPP, Re and NEP in the Asian region tended to be more strongly determined by climatic factors (temperature and precipitation) compared to European and North American regions. This result was most likely due to the fact that ecosystems in Asia are less exposed to severe water stresses compared to ecosystems of Europe and North America. Especially in the 20–35°N subtropical regions, the MAP (1200 mm) in Asia was much higher than that of Europe and North America (300–500 mm). Precipitation largely influenced the spatial pattern of the carbon fluxes (Reichstein et al., 2007) in Europe, and summer droughts or heat waves severely suppressed the carbon uptake of European and North American ecosystems (Ciais et al., 2005). The slope and correlation coefficients of the regression between GPP and temperature in Europe and North America ($47\,g\,C\,m^{-2}\,yr^{-1}\,°C^{-1}$; 0.50) (Law et al., 2002) were comparatively lower than those in Asia ($84\,g\,C\,m^{-2}\,yr^{-1}\,°C^{-1}$; 0.75). Another potential origin of the differences in spatial variation between Europe/North America and Asian ecosystems is that ecosystems in the Asian region were relatively less disturbed by human activities. Most Asian ecosystems are in the natural and primary state, especially for forest and wetland ecosystems. In Europe and North America, forest ecosystems are maintained in a long-term intensive management system with such practices as thinning, harvesting, irrigation and drainage, which would weaken the climate regulation on ecosystem carbon uptake to a certain extent.

4.4. Uncertainty analysis

This study used rigorous data screening and quality control. With wide coverage and a reasonable range, hence the results of this study provide a robust estimate of carbon fluxes in the Asian region. It is important to note that the results of the analyses are based on current limited sampling, across certain biomes

and measurement spans, hence several sources of uncertainties still existed that mainly derived from the following aspects: (1) Errors of eddy covariance measurement. Systematic errors are caused by the influences of complex topography, atmospheric stability, frequency response of data acquisition, advection or storage under stable nighttime conditions during the eddy covariance measurements (Aubinet et al., 2005; Finnigan et al., 2003; Loescher et al., 2006; Massman, 2000). (2) Errors of statistical analysis of data. Several systematic errors were likely to be introduced in the process of outlier removal, gap-filling, flux partitioning and integrated analysis. (3) Uneven site distribution. In this study, sites tended to be more concentrated in the eastern than the western part of Asia, and more concentrated in the temperate than the tropical and subarctic zone. Therefore, limitations in the analysis of results are introduced by this uneven site distribution. (4) Limited and uneven time scale. When analyzing the spatial variation of carbon fluxes at an annual scale, errors were likely to be produced by the use of different time spans of data collection and the effects of inter-annual variability. There is a clear need to strengthen the construction of flux sites in the western Asian and tropical and subarctic zones, and it is necessary to maintain long-term continuous monitoring. In the future, these measures would provide a sufficient data base and a higher certainty in the Asian and global carbon budget studies.

It is also important to note that although temperature and precipitation were the important decisive factors in the spatial variation of NEP in Asia, there were still amounts of spatial variation of NEP that could not be explained. We inferred that under the main effect of climatic variables, the spatial variation of NEP was additionally influenced by other factors in the Asian region, such as age, nitrogen deposition (Magnani et al., 2007), disturbance (Thornton et al., 2002) and soils. Therefore, an intensive study on this aspect in the future are expect to conduct.

5. Conclusions

Based on long-term observation data of ChinaFLUX (19 sites) and published data from AsiaFlux (37 sites) and 32 other sites in Asia, we quantified the carbon exchange fluxes of different terrestrial ecosystems in the Asian region and analyzed their spatial variation and controlling factors. The results indicated that:

(1) The majority of Asian terrestrial ecosystems currently are large carbon sinks. NEP tended to be higher in warm environments compared to cold environments, and higher in humid areas compared to arid areas. Since the NEP was restricted by Re, the ecosystems with the largest GPP was not shown the maximum NEP.
(2) The carbon sink strength differed greatly among ecosystem types in the Asian region. Cropland ecosystems had the highest net carbon sink strength. Forest and wetland ecosystems followed with equivalent carbon sink strength, and grassland ecosystems were weak carbon sinks with the largest spatial variability. The NEP was 325 ± 187, 274 ± 207, 236 ± 260, $89 \pm 134\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in cropland, forest, wetland and grassland ecosystems, respectively.
(3) Temperature and precipitation were the main controlling factors in the spatial variation of terrestrial ecosystem carbon exchange fluxes in the Asian region. The combined effects of MAT and MAP contributed 85%, 81% and 36% to the spatial variations of GPP, Re and NEP, respectively.
(4) Spatially, GPP and Re were significantly linearly and exponentially correlated to MAT, and were sigmoidally and linearly correlated to MAP respectively, and those response modes did not vary across different ecosystem types.

(5) The different responses of GPP and Re to MAT and MAP determined the spatial variation of NEP.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2013.04.026.

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