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Carbon exchange in a freshwater marsh in the Sanjiang Plain, northeastern China

Changchun Song[a,**], Li Sun[a,*], Yao Huang[b], Yuesi Wang[b], Zhongmei Wan[c]

[a] Key Laboratory of Wetland Ecology and Environment, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Weishan Road 3195, Changchun 130012, China
[b] Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing 100029, China
[c] College of Earth Sciences, Jilin University, Changchun 130061, China

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ABSTRACT

Northern wetlands are critically important to global change because of their role in modulating atmospheric concentrations of greenhouse gases, especially CO_2 and CH_4. At present, continuous observations for CO_2 and CH_4 fluxes from northern wetlands in Asia are still very limited. In this paper, two growing season measurements for CO_2 flux by eddy covariance technique and CH_4 flux by static chamber technique were conducted in 2004 and 2005, at a permanently inundated marsh in the Sanjiang Plain, northeastern China. The seasonal variations of CO_2 exchange and CH_4 flux and the environmental controls on them were investigated. During the growing seasons, large variations in net ecosystem CO_2 exchange (NEE) and gross ecosystem productivity (GEP) were observed with the range of −4.0 to 2.2 (where negative exchange is a gain of carbon from the atmosphere) and 0–7.6 $g\,C\,m^{-2}\,d^{-1}$, respectively. Ecosystem respiration (RE) displayed relatively smooth seasonal pattern with the range of 0.8–4.2 $g\,C\,m^{-2}\,d^{-1}$. More than 70% of the total GEP was consumed by respiration, which resulted in a net CO_2 uptake of 143 ± 9.8 and $100 \pm 9.2\,g\,C\,m^{-2}$ for the marsh over the growing seasons of 2004 and 2005, respectively. A significant portion of the accumulated NEE-C was lost by CH_4 emission during the growing seasons, indicating the great potential of CH_4 emission from the inundated marsh. Air temperature and leaf area index jointly affected the seasonal variation of GEP and the seasonal dynamic of RE was mainly controlled by soil temperature and leaf area index. Soil temperature also exerted the dominant influence over variation of CH_4 flux while no significant relationship was found between CH_4 emission and water table level. The close relationships between carbon fluxes and temperature can provide insights into the response of marsh carbon exchange to a changing climate. Future long term flux measurements over the freshwater marsh ecosystems are undoubtedly necessary.

1. Introduction

Natural wetlands in mid-high latitudes are significant contributors to the global carbon (C) cycle through the exchange of greenhouse gases, especially CO_2 and CH_4, because their soils store large amount of carbon (Post et al., 1982; Chapin et al., 2002) and because of the high temperature sensitivity of the biogeochemical processes associated with cool local environments (Davidson and Janssens, 2006; Zimov et al., 2006; Koch et al., 2007).

Compared to upland ecosystems, such as forests and grasslands, northern wetlands tend to have relatively small CO_2 exchange rates (Schimel, 1995; Frolking et al., 1998), however, the fate of the large C store in northern wetlands is of concern given the spatial pattern and magnitude of current and anticipated changes in climate (Schlesinger, 1997; IPCC, 2007). Wetlands are among the primary sources of atmospheric CH_4, as they release about 20–39% of the annual global CH_4 budget (IPCC, 2007). Neglecting CH_4 in the estimation of wetland C balance prohibits determining whether the balance is significantly different from zero (Roulet et al., 2007).

Although many studies have been conducted on greenhouse gas emissions from natural freshwater wetlands around the world (Aselmann and Crutzen, 1989; Martikainen et al., 1993; Melloh and Crill, 1996; Alm et al., 1999; Arnold et al., 2005; Bonneville et al., 2008), few measurements have been carried out for the wetlands in Asia, especially in China (Ding and Cai, 2007). While several observations have been reported in the past decades on natural wetlands in China, using the chamber method (e.g. Ding et al., 2004a,b; Wang et al., 2006; Yang et al., 2006), long-term continuous observations of CO_2 and CH_4 fluxes are still lacking.

The eddy covariance (EC) technique allows near continuous measurements of net ecosystem CO_2 exchange (NEE) to be made during diurnal, seasonal and annual variation in weather (Aubinet et al., 2000; Baldocchi, 2003). NEE measured by EC technique can

* Corresponding author. Fax: +86 431 85542298.
** Co-corresponding author.
E-mail addresses: songcc@neigae.ac.cn (C. Song), sunli@neigae.ac.cn (L. Sun).

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be erroneous under stable atmospheric conditions (especially during the nighttime) or when the precipitation events occur (as far as the open path gas analyzers are concerned). Thus the data measured must be carefully quality controlled and gap filled to obtain acceptable time series. In spite of the limitations of EC technique, analysis of the NEE data can provide important information for the assessment and improvement of mechanistic ecosystem models and also for providing empirical information about the potential responses of ecosystems to future environmental changes (Aubinet et al., 2000; Baldocchi, 2003).

In this paper, we report EC measurements of CO_2 flux and the static chamber/gas chromatography measurements of CH_4 flux for the growing seasons of 2004 and 2005 in a freshwater marsh in the Sanjiang Plain in northeastern China. The objectives of this study are: (1) to determine the magnitude and seasonal pattern of gross ecosystem productivity (GEP), ecosystem respiration (RE) and NEE; (2) to investigate the magnitude and seasonal variation of CH_4 emission from the marsh and (3) to explore the major environmental controls on these carbon exchange terms.

2. Materials and methods

2.1. Site description

The study site is located at Sanjiang Experimental Station of Wetland Ecology, Chinese Academy of Sciences (47°35′N, 133°31′E) at an altitude representative of the natural freshwater wetland in the Sanjiang Plain (56 m a.s.l.), northeastern China. The Sanjiang Plain inhabits the largest freshwater wetland area in China, approximately 10,400 km^2 (Zhao, 1999). Covered continuously by a clay layer, the Sanjiang Plain has a slope of about 1:5000–1:10,000, which is favorable for wetland formation. Wetland initiation in the Sanjiang Plain started during late-Pleistocene epoch due to convergence of the water from Helongjiang River, Songhuajiang River and Wusulijiang River and blockage of water seepage by the clayey soil. Generally, the long term accumulation and decomposition rates of plant residues are approximate and there is little peat accumulation for most of the wetlands in the Sanjiang Plain (Zhao, 1999). The three types of wetland present are: permanently inundated wetland, seasonally inundated wetland, and shrub swamp, account 56.9%, 22.6% and 20.5%, respectively, for the wetland area in the Sanjiang Plain (Zhao, 1999; Liu, 2005). Freshwater sedge marshes are the major form of wetland in this area.

In this research, the EC flux tower was set at a permanently inundated and eutrophic freshwater marsh. The vertical profile of the marsh is composed of standing water (0–50 cm), live and dead root layer saturated with water (20–40 cm), humus layer (5–10 cm) and gley soil layer whose soil parent material is impermeable clay and sub-clay. The topography of the marsh is flat with homogeneous herbaceous vegetation dominated by *Carex lasiocarpa*. Other plants in the marsh include *Carex pseudocuraica*, *Glyceria spiculosa* and *Carex meyeriama*.

The climate is a temperate continental monsoon type with annual mean temperature 2.5 °C. The mean temperature in July and January is 22 and −21 °C, respectively. The mean annual precipitation is approximately 552 mm with approximately 80% occurring during the growing season from May to September. Precipitation is the main water source in freshwater marshes in normal years. Water and soil in marshes are completely frozen from late October to next April and begin to melt from late April till July.

2.2. Eddy covariance and meteorological measurements

CO_2 flux was measured with EC system from June to September 2004 and during the growing season (May to September) of 2005. The EC system includes a three-dimensional ultrasonic anemometer (CSAT-3, Campbell, Scientific, USA), used to measure wind velocity and direction, as well as sonic temperature fluctuation, and a fast response open-path infrared gas analyzer (IRGA, Li-7500, Li-Cor Inc., USA), used to simultaneously measure changes in CO_2 and H_2O molar densities. The spatial separation distance between the mid-points of these two neighboring sensors was about 15 cm to minimize underestimation of fluxes (Lee and Black, 1994). All signals for the sensors were sampled at 10 Hz by a datalogger (CR5000, Campbell Scientific, USA) and then block-averaged over 30-min intervals for analyses and archiving. CO_2 flux data were corrected for the variation of air density caused by the transfer of heat and water vapor (Webb et al., 1980). Instruments were mounted on the tower approximately 2.5 m above the ground and 2 m above the fully grown vegetation.

Parallel to the flux measurements, meteorological data such as net radiation (R_n) and photosynthetically active radiation (PAR) at a height of 2 m, air temperature and relative humidity at 2 and 3 m, wind speed and direction at 0.5, 1, 2, and 3 m, soil temperature at 5, 10, 15, 20, 30, 40 and 70 cm depth below the surface and precipitation were obtained from a long-term automatic weather station about 200 m away from the EC system in the marsh. Vapor pressure deficit (VPD) was calculated as the difference between the saturation and actual vapor pressures at the given temperature based on the measured relative humidity and air temperature.

Site visits every 6–10 days were conducted for maintenance and collection of the most recent data. Water level above the marsh surface was recorded manually at each site visit.

Phenology observation and measurements of leaf area index (LAI) were done every ten days for the two growing seasons. By destructive sampling three 0.25 m^2 quadrates within a radius of 200 m around the EC system, the total leaf area in each quadrate was measured using the area meter (CI 203, CID Inc., USA). LAI was calculated as the mean value of the measured data in each measurement. Linear interpolation was applied between measurements.

2.3. Chamber measurement

A site with three replicated measurement plots was set up for chamber measurements at locations about 150 m southeast (prevailing wind direction) of the EC tower. Boardwalks were constructed around the sample plots to minimize disturbance. CH_4 emissions were measured at weekly to biweekly intervals using opaque static chambers (stainless steel made, 50 cm × 50 cm × 50 cm) during the growing seasons of 2004 and 2005 (Song et al., 2008). There was only one sample site with three replicates for CH_4 measurements in the current study because of the limitation in manpower to carry out the labor intensive chamber measurements. However, the spatial variability of CH_4 emissions can be generally considered small since the microrelief of the marsh is flat with evenly distributed vegetation. During each observation, the chambers were placed into the collars (also stainless steel made) with water to prevent leakage, and the vegetation was included within the chambers. Inside each chamber, a small fan that was used to stir the air, and a thermometer sensor and a trinal-venthole were installed. Gas sampling lasted half an hour and four gas samples were took in 10-min intervals. Measurements were usually carried out around 9:00 AM at local time.

The gas samples were stored in syringes less than 12 h before being measured. Gas chromatography (Agilent 4890D, Agilent Co., Santa Clara, CA, USA) was used to measure the gas concentrations; then the gradient of gas concentration during sampling was used to calculate the CH_4 flux. Sample sets were rejected unless they yielded a linear regression of R^2 greater than 0.9. Average CH_4 flux and standard error were calculated from the three replicates for each observation.

At the same time the chamber measurements were conducted, the air temperature inside and outside the chambers and the soil temperature at 0, 5, and 10 cm depth at the sample plots were measured.

2.4. Data quality control

On average, 33% of the half-hour CO_2 flux measurements by EC system were removed from each year's data set due to instrument malfunction or quality control procedures described by Lafleur et al. (2003). Of the removed data, 24% were due to calm conditions when friction velocity (u^*) fell below the threshold of 0.1 m s^{-1} at night; 73% were due to concerns over data quality and instrument malfunction, and 3% were due to a C uptake at night.

The variation of CO_2 storage in the air column beneath the EC instrumentation in our case was neglected since the height of the micrometeorological sensors at 2.5 m above ground corresponded to the low (<0.5 m) and sparse (LAI < 2.0) vegetation and flat microtopography of the footprint. Further, the long-term sum of the storage flux was assumed to be zero (Baldocchi et al., 2000).

The footprint routine used in this study is the flux source area model FSAM by Schmid (1994, 1997). According to the calculation of FSAM, the footprint was estimated between 40 and 180 m from the EC tower (representing 90% of the total flux), depending on the atmospheric conditions during the time the footprint prediction was calculated. The footprint analysis indicated that most EC fluxes originated from within the marsh over the two growing seasons.

Since soil and water heat fluxes were not measured in this study, the energy balance was calculated on a daily basis to minimize the influence of these fluxes. The energy balance closure was estimated by regressing the daily mean of the convective heat fluxes (latent heat flux LE plus sensible heat flux H) against net radiation R_n over the two growing seasons, giving the linear equations $H + LE = 0.71 \times R_n + 12.46$ ($R^2 = 0.93$, $n = 122$, $P < 0.001$) in 2004 and $H + LE = 0.66 \times R_n + 11.54$ ($R^2 = 0.91$, $n = 150$, $P < 0.001$) in 2005. Li et al. (2005) reported that the energy balance closure generally varied from 0.49 to 0.81 for the flux sites of ChinaFLUX. The energy closure of 0.66–0.71 in this study is within the range. We think that most of the deficit of R_n is mainly due to soil and water warming of the permanently inundated marsh during the growing seasons, and the energy balance closure without including the two terms can be considered reasonable.

2.5. Gap filling

Following the micrometeorological convention, negative NEE values represent a net uptake of CO_2 by the marsh while positive values indicate a net release to the atmosphere. However, we discuss "photosynthesis" and "uptake" as processes with positive signs. In order to integrate the seasonal NEE budgets, missing CO_2 flux data from the EC system had to be replaced. Missing NEE was filled via a combination of linear interpolation and empirical modelling (Lasslop et al., 2010b). Small gaps of fewer than 2 h were filled by linear interpolation. Longer gaps were filled via modelling, as follows:

$$\mathrm{NEE} = R_{ref}\ \exp\left[E_0\left(\frac{1}{T_{ref}-T_0} - \frac{1}{T-T_0}\right)\right] - \frac{\alpha \mathrm{PAR}\, A_m}{\alpha \mathrm{PAR} + A_m} \quad (1)$$

$$\mathrm{RE} = R_{ref}\ \exp\left[E_0\left(\frac{1}{T_{ref}-T_0} - \frac{1}{T-T_0}\right)\right] \quad (2)$$

$$\mathrm{GEP} = \frac{\alpha \mathrm{PAR}\ A_m}{\alpha \mathrm{PAR} + A_m} \quad (3)$$

the first term on the right-hand side of Eq. (1) describes the exponential relationship between RE and temperature (Eq. (2)). The second term describes the rectangular hyperbolic relationship between GEP and PAR (Eq. (3)). T_{ref} is the reference temperature set to 283.15 K and T_0 is kept constant at 227.13 K as in Lloyd and Taylor (1994). R_{ref} and E_0 are the free estimated parameters representing the ecosystem respiration rate at reference temperature and the activation energy that represents the response of respiration to a temperature variation. A_m is the maximum gross productivity (mg CO_2 m^{-2} s^{-1}), and α is the initial slope of the GEP–PAR relationship (quantum yield, mg CO_2 μmol^{-1} quantum).

The first step in gap filling was to determine the relationship between nighttime ($R_n \le 10$ W m^{-2}) NEE with $u^* > 0.1$ m s^{-1} and temperature. Since there is greater variability for the observed nighttime NEE at higher temperature because of intermittent turbulence (Morgenstern et al., 2004), a logarithmic transformation was used to reduce the variation of the original nighttime data and stabilize the variance of errors (Chatterjee and Hadi, 2006). Then linear ordinary least square regression was used to find the best fit and estimate the parameter of E_0. After E_0 was fixed for the whole growing season, the parameters R_{ref}, α and A_m were derived from daytime ($R_n > 10$ W m^2) data. As the GEP–PAR relationship varies in time, due to seasonal changes in plant biomass and microbial activity (Lafleur et al., 2003), separate relationships in Eq. (1) were derived for every 15 days during the growing seasons. Parameters R_{ref}, α and A_m were estimated using the nonlinear regression of SPSS 13.0.

Of the temperature monitored in this study, soil temperature at a depth of 10 cm (T_{s10}) demonstrated the best correlation with nighttime respiration, thus hourly RE was calculated using Eq. (2) and known T_{s10}. Similarly, Eq. (3) and PAR were used to estimate hourly GEP. Daily and monthly GEP and RE were obtained by summing all the half-hourly values.

Continuous EC measurements at the study site for the growing seasons of 2005–2007 have proved that the monthly NEE is almost equal to the monthly RE in May due to the low photosynthesis of the sedges during this period. In this study, since the EC measurement began in June 2004 and the monthly NEE in May was absent, we used the monthly RE in May 2004 as a substitute.

For EC measurements, a random error corresponding to a SD of 20% was applied on 30 min fluxes (Morgenstern et al., 2004; Humphreys et al., 2006; Nilsson et al., 2008), both on measured and gap-filled 30 min values. The total seasonal uncertainty (SD) was then calculated as the square root of the sum of the respective variances. As to the CH_4 measurements, standard error was calculated from the three replicates from each observation.

3. Results and discussion

3.1. Climate variation

The study site is characterized by strong variation in air temperature, with the highest average (±SD) temperature of 21.6 ± 0.9 °C occurring in July and the lowest average temperature of −20.8 ± 2.1 °C observed in January (Fig. 1a). The annual mean temperatures in 2004 and 2005 were 2.14 and 2.25 °C, respectively, close to the long-term average of 2.52 ± 0.9 °C.

Monthly average precipitation also showed large seasonal variation, with nearly half of the annual precipitation occurring in July and August (Fig. 1b). The precipitation was lower in 2004 (449 mm), compared with the long-term average of 552 ± 94 mm, mainly due to decrease during August; 31 mm falling in August 2004, compared with the long-term average of 136 ± 57 mm during this month. The precipitation was near normal in 2005 (544 mm).

The water table level (WTL), which was always above the marsh surface during the growing seasons generally increased with rainfall and decreased with evapotranspiration. The growing season

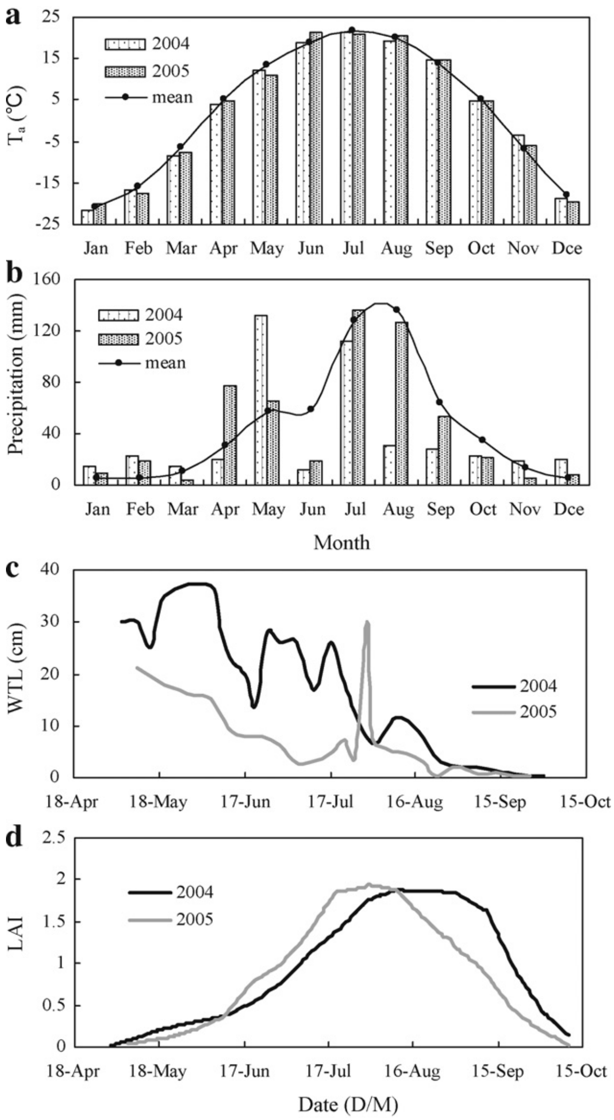

Fig. 1. Seasonal pattern of (a) monthly mean air temperature (T_a), (b) monthly cumulative precipitation, (c) water table level (WTL) and (d) leaf area index (LAI) from 2004 to 2005 at the study site (mean represents the average for 1990–2005).

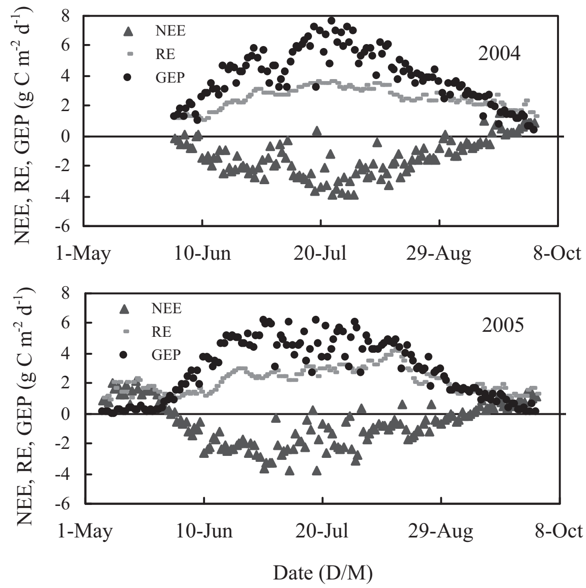

Fig. 2. Seasonal variation of daily NEE, GEP and RE during the growing seasons of 2004 and 2005. NEE, GEP and RE are net ecosystem CO_2 exchange, gross ecosystem productivity and ecosystem respiration, respectively. Negative values of NEE indicate net carbon uptake from the atmosphere.

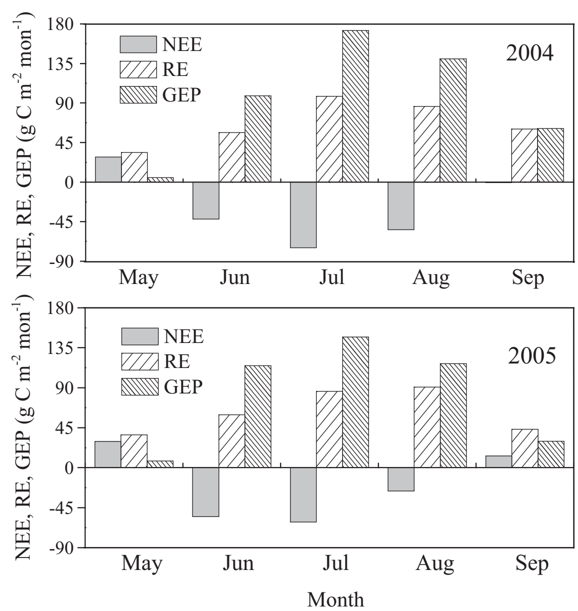

Fig. 3. Seasonal variation of monthly NEE, GEP and RE during the growing seasons of 2004 and 2005.

WTL was generally higher in 2004 than 2005 (Fig. 1c), with an average of 19 cm and 7 cm, respectively, although the growing season precipitation was lower in 2004 (315 mm) than that of 2005 (399 mm). We did not find significant difference between the precipitation amount during October 2003 to April 2004 and that during October 2004 to April 2005. Therefore, the relatively higher WTL in the growing season of 2004 could be attributed to the especially high rainfall in May 2004 (131.4 mm) compared to 65 mm in May 2005 and the long-term average of 57.7 ± 38.8 mm during this month.

The vegetation in the marsh began to leaf-out in May and reached the maximum LAI around 2 in late July and early August (Fig. 1d). The plants showed visible signs of senescence in late August. Senescence accelerated in September and there was almost no green leaves remaining by late September.

3.2. Daily and seasonal variation of ecosystem CO_2 exchange

Daily RE displayed relatively smooth seasonal pattern with the range 1.1–3.6 and 0.8–4.2 $g\,C\,m^{-2}\,d^{-1}$ during the growing seasons of 2004 and 2005, respectively, while daily NEE and GEP showed a similar overall pattern with noticeable variations with season (Fig. 3). Daily NEE gradually switched from positive values in May to a maximum daily net uptake rate of 3.8–4.0 $g\,C\,m^{-2}\,d^{-1}$ in July (24 July in 2004 and 18 July in 2005) when the marsh canopy fully developed and the monthly average temperature reached its peak in 2004 or approached its peak in 2005. Daily NEE gradually declined after August and net CO_2 release was observed on 16 September 2004 and 9 September 2005, respectively. Similar to NEE, maximum daily GEP also occurred in July 2004 and 2005 with the rate of 7.6 and 6.2 $g\,C\,m^{-2}\,d^{-1}$, respectively.

Although net uptake of CO_2 occurred for most days during the growing seasons, there were some close to zero or minor positive NEE peaks (low GEP peaks) in July and August (Fig. 2). For example, the PAR during the rainy or heavily overcast days of 19 July and

8 August 2004 deceased by about 75% compared with that of the adjacent sunny days, while GEP decreased by about 45% and 68%, respectively, and the NEE for these two days was positive or close to zero, accordingly. Similar patterns could also be found in the measurement period of 2005. This pattern suggests that low photosynthetic activity is responsible for the observed low net absorption rates during the vigorous growing period. The large variation in daily NEE and GEP indicates that the marsh at the study site has the potential to respond to a changing climate, within certain limits.

During the measurement periods, both monthly GEP and NEE reached maximum value in July while monthly RE was highest in July or August (Fig. 3). The cumulative CO_2 uptake (GEP) was 472 g C m^{-2}, 71% of which was lost through ecosystem respiration, which resulted in a net CO_2 uptake of 143 ± 9.8 g C m^{-2} for the marsh during growing season of 2004. The cumulative CO_2 uptake was 416 g C m^{-2}, 76% of which was lost by ecosystem respiration, which resulted in a net CO_2 uptake of 100 ± 9.2 g C m^{-2} during the growing season of 2005.

Although many studies have examined the growing season CO_2 fluxes in northern wetlands based on eddy covariance measurements, large variability exists in the findings due to the diverse vegetation and climate types or the different definition of the growing season length. Here, we selected the very limited studies that have similar vegetation and climate types or growing season length with our site for comparison.

In this research, the cumulative growing season NEE was −143 ± 9.8 and −100 ± 9.2 g C m^{-2} in 2004 and 2005, respectively. In the study of Glenn et al. (2006), the net CO_2 uptake at an extreme rich fen dominated by *C. lasiocarpa* in northern Alberta Canada was about −43 g C m^{-2} for the period of May to September 2004. Roulet et al. (2007) reported the cumulative growing season (mid-April to mid-October) NEE-C ranged from −164.8 to −76 g C m^{-2} with an average of −97.1 ± 38.7 g C m^{-2} from a northern ombrotrophic bog of Mer Bleue during 6 years of continuous observation. Nilsson et al. (2008) reported the accumulative net CO_2 uptake in the Degerö Stormyr mire was 92 and 86 g C m^{-2} during the net uptake season (157 ± 7 days) of 2004 and 2005, respectively. Suyker et al. (1997) estimated that a boreal minerotrophic fen in Central Saskatchewan was a net sink of approximately 88 g C m^{-2}, during mid May to early October. Our results of the growing season NEE were similar to or higher than the above mentioned results but lower than the cumulative NEE of about −355 g C m^{-2} from May to September 2004 at a cattail marsh east of Ottawa, Ontario, Canada (Bonneville et al., 2008), mainly because the cattail marsh has much higher plant productivity.

According to Eq. (1), the seasonal average of R_{ref} (ecosystem respiration rate at 10 °C) was 0.07 mg CO_2 m^{-2} s^{-1} in 2004 and 0.06 mg CO_2 m^{-2} s^{-1} in 2005, which was within the range 0.04–0.10 mg CO_2 m^{-2} s^{-1} of R_{10} (ecosystem respiration rate at 10 °C) for the sedge-dominated peatland in north-central Alberta, Canada (Glenn et al., 2006), and the R_{10} value 0.02–0.11 mg CO_2 m^{-2} s^{-1} determined for three grassland ecosystems in China (Fu et al., 2009). Compared with R_{10} (0.16–0.18 mg CO_2 m^{-2} s^{-1}) from the temperate forest in eastern China (Yu et al., 2008), the R_{10} values determined in the current study were low. This difference was likely due to lower live biomass and decomposition rates under water saturated conditions of the marsh substrate.

3.3. Environmental controls over gross ecosystem productivity and ecosystem respiration

Since NEE is the difference between RE and GEP, environmental variables affect NEE indirectly through their controls on RE and GEP. On a daily timescale, a simple regression (Pearson correlation, 2-tailed test for significance) showed that of all the environmental and biological variables measured or calculated in this research, variables that correlated significantly with GEP included T_a, LAI, PAR, and VPD ($P < 0.01$), whereas those that correlated significantly with RE included T_{s10}, LAI and GEP ($P < 0.01$).

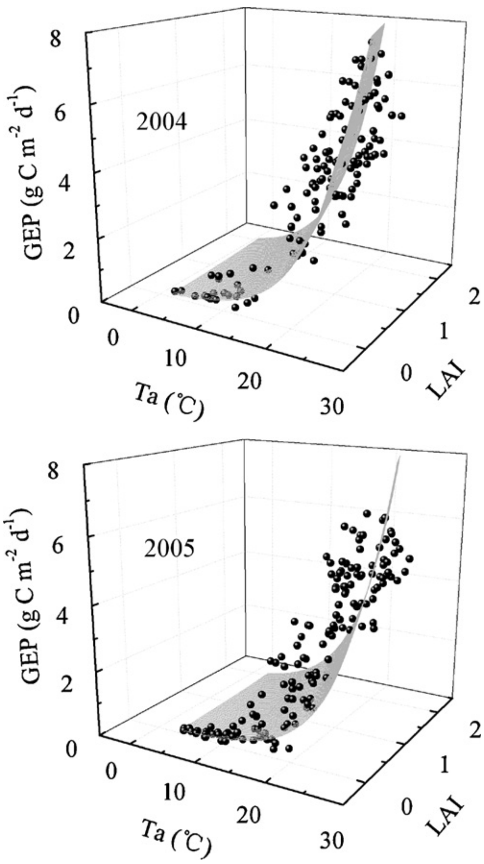

Fig. 4. Illustration of the influence of air temperature and LAI on GEP during the growing seasons of 2004 and 2005. The regression equations of the curved surface shown are given in Table 2.

We performed a multiple regression analysis to differentiate variables of particular importance for GEP and RE. These analyses were performed between GEP or RE and the variables that significantly correlated with them in simple regressions. The analyses performed were step-wise regression where a condition index (CI) greater than 15 was used to indicate potential multicolinearity problems (Chatterjee and Hadi, 2006).

Results showed that the multiple variable model of daily GEP included air temperature and leaf area index (Table 1). Variable of PAR or VPD had to be removed from the multivariable model due to CI > 15 which indicated a colinearity problem.

Daily GEP increased exponentially with air temperature and leaf area index during the two growing seasons (Fig. 4, Table 2). To use the multiple stepwise regressions, the relationships between the explained variable and the explanatory variables are assumed to be linear while actually more appropriate relationships may be nonlinear. The exponential models shown in Table 2 reduced the specification bias efficiently and thus R^2 increased. Air temperature and leaf area index expressed about 80–84% of the variations of GEP during the growing seasons. Although most variation of GEP can be explained by temperature, GEP did not increase obviously when daily mean air temperature increased from 0 to 10 °C (Fig. 4), which mainly happened in May. This was because it took a long time for *C. lasiocarpa* to develop leaf tissue in spring (May) that their photosynthetic capacity was correspondingly low. After daily mean air temperature exceeded 15 °C, GEP increased rapidly with

Table 1
The multiple regression results between carbon fluxes (GEP or RE) and the main controlling factors during the growing seasons of 2004 and 2005.

	Factor	Year	F	P	ΔR^2	Year	F	P	ΔR^2
GEP	T_a	2004	277.94	**	0.685	2005	302.74	**	0.661
	LAI		27.38	*	0.056		58.32	*	0.094
	PAR		21.83	*	0.040		18.05	*	0.026
	VPD		14.03	*	0.007		6.40	*	0.002
RE	T_{s10}		700.18	**	0.834		377.73	**	0.709
	LAI	2004	38.64	*	0.053	2005	25.09	*	0.051
	GEP		25.73	*	0.028		5.71	*	0.009

GEP, gross ecosystem productivity; RE, ecosystem respiration; T_a, air temperature; T_{s10}, soil temperature at 10 cm depth; T_{s5}, soil temperature at 5 cm depth; LAI, leaf area index; PAR, photosynthetically active radiation and VPD, vapor pressure deficit.
* Significant at $P < 0.01$.
** Significant at $P < 0.001$.

Table 2
The regression results of the curved surface GEP = a_1 exp(a_2 T_a + a_3 LAI).

	Year	a_1	a_2	a_3	R^2	F
GEP	2004	0.05**	0.18**	0.65**	0.84	318.6
	2005	0.02**	0.19**	0.81**	0.80	300.5

The parameters a_1, a_2 and a_3 were estimated by linear ordinary least square regression after the equation was logarithmically transformed.
** Significant at $P < 0.001$.

the increase of temperature and the vigorous growth of *Carex* in the marsh.

As showed in Table 1, soil temperature at 10 cm depth and leaf area index explained about 76–89% of the variability in daily RE. Although there existed close relationship between RE and GEP in bivariate correlation analysis (R^2 0.80 in 2004 and 0.65 in 2005, $P < 0.001$), GEP had to be removed from the multivariable model due to CI > 15 and an indication of multicolinearity. The close relationship between ecosystem respiration and photosynthesis in bivariate correlation could be mainly ascribed to their dependence on similar environmental variables and the possible spurious correlation between them, which was caused by the calculation of GEP as RE minus NEE in this study (Vickers et al., 2009; Lasslop et al., 2010a,b).

Although water table position may be an important controlling factor over wetland ecosystem respiration (Bubier et al., 1998; Syed et al., 2006), we found no significant relationship between respiration rates and water table levels in this study. We consider this lack of influence of water table level on respiration may be due to the fact that the marsh soil and vegetation roots layer are permanently inundated during the growing seasons, thus the fluctuations of water level above marsh surface have minor effects on soil respiration and decomposition processes which largely depend on oxygen availability and microbial activity. Similar result can also be seen in the research of Bonneville et al. (2008).

3.4. Seasonal dynamic and environmental controls on CH_4 flux

The seasonal dynamics of CH_4 emission over the marsh ecosystem during the two growing seasons are shown in Fig. 5. Increasing emissions were noticeable from the beginning of May, and maximum CH_4 flux was observed on 24 July (30.5 ± 23.5 mg C m^{-2} h^{-1}) and 5 August (28.3 ± 16.4 mg C m^{-2} h^{-1}) in 2004 and 2005, respectively. CH_4 emission decreased gradually since mid August, however, by the end of September, CH_4 flux kept relatively high (5–13 mg C m^{-2} h^{-1}) compared with the beginning of the growing season (0.1–0.2 mg C m^{-2} h^{-1}).

By bivariate correlation analyses between measured CH_4 flux and variables including T_a, soil temperature at 5 cm depth (T_{s5}), T_{s10} and WTL, we found that the seasonal variation of CH_4 fluxes was significantly correlated with temperature ($P < 0.01$) but barely

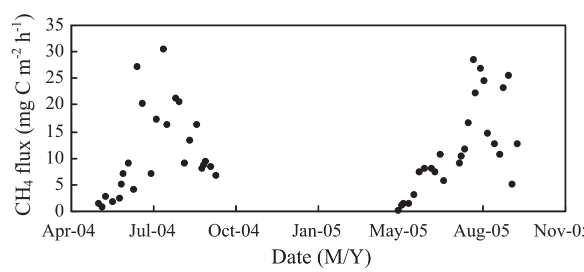

Fig. 5. Instantaneous CH_4 emission rate from the marsh during the growing seasons of 2004 and 2005.

correlated with water table level ($P > 0.1$). Of the temperature mentioned above, T_{s5} demonstrated better correlation with CH_4 flux compared with T_a and T_{s10}. CH_4 emission increased exponentially with the increase of T_{s5} which could explain about 74–77% of the seasonal variation of CH_4 fluxes during the measurement periods (Fig. 6).

Since methanogenesis occurs across a range of soil depths which have different soil temperatures and diurnal temperature lags, determining the relationship between short-term soil temperature patterns and CH_4 flux may not be straight forward (Zona et al., 2009). The close relationship between CH_4 emission and T_{s5} in this research could be ascribed to that soil temperature around 5 cm depth represented the average temperature condition conducive to methanogenesis.

Water table level is generally considered to be a physical parameter of major importance for CH_4 emissions from wetlands (Kettunen et al., 1999; Frenzel and Karfeld, 2000; Updegraff et al., 2001; Treat et al., 2007). In this study, the bivariate correlation analysis showed that WTL was not significant in predicting CH_4 fluxes. This relationship is probably due to the fact that the water table was always above the marsh surface (Fig. 1c) and thus the anaerobic environment for methanogenesis was kept relatively stable during the growing seasons.

CH_4 transport through vascular plants is frequently mentioned as one of the major pathways for CH_4 emissions from wetlands (Kelker and Chanton, 1997; Greenup et al., 2000; Kutzbach et al., 2004). At the study site, more than 3/4 of the biomass of *C. lasiocarpa* was belowground and root biomass was therefore correspondingly

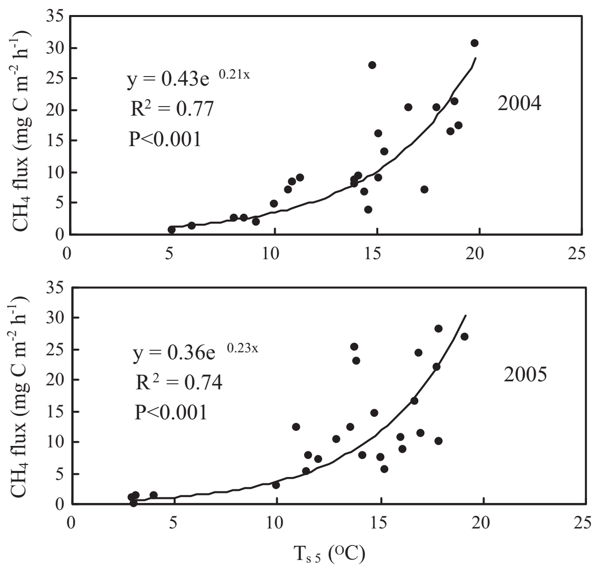

Fig. 6. Relationship between CH_4 flux and 5 cm depth soil temperature (T_{s5}) during the growing seasons of 2004 and 2005.

high within the marsh (Yang et al., 2002). The root aerenchyma of *Carex* could serve as conduits for CH_4 transport to the atmosphere and the effect of plant-mediated CH_4 transport could be maximized by the high water level and the bulk of the roots growing in anoxic soil horizons (Waddington et al., 1996). In contrast to the slow development of plant tissues in spring, the gradual senescence of the aboveground parts of *Carex* coincides with the translocation of resources to the rhizomes in autumn. Further, the average 5 cm depth soil temperature in September was 5.5 °C higher than that in May. Therefore, the higher soil temperature and the more active belowground biological activities in September could explain the relatively higher CH_4 emission in this period compared with the beginning of the growing season (Fig. 5).

Using the exponential regression equations (showed in Fig. 6) and continuous soil temperature data, the seasonal CH_4 flux could be determined. The main period for CH_4 emission was from July to September, during which about 80% of the growing season emission occurred. The cumulative CH_4 release from May to September was 41.7 ± 16.8 and 42.9 ± 29.6 g C m^{-2} in 2004 and 2005, respectively.

It is difficult to provide enough manually operated chambers for precise flux measurement because of the complicated microrelief and the heterogeneous vegetation covers for many wetland ecosystems. As a general rule, increasing the number of chambers will enhance the precision in the measured fluxes (Loescher et al., 2006). In this research, we conducted CH_4 emission measurements using static chamber method at only one sample site (with three replicates) within the footprint of the EC measurements. It should be pointed out that, the measured fluxes by these three chambers could not necessarily provide a good statistical representation for the spatial variability of CH_4 emission from the marsh. However, considering the flat microtopography of the marsh and the evenly distributed sedge-dominated plant community, we assumed that the estimated CH_4 emissions were to some extent representative of CH_4 emissions of the marsh ecosystem. In this case, about 29% of the growing season NEE-C in 2004 and 43% in 2005 were consumed as CH_4 emission. Thus CH_4 emission was significant not only for the greenhouse warming potential balance, but also as an important component of the carbon balance of the inundated marsh.

4. Conclusions

This study investigated the CO_2 fluxes (NEE, GEP and RE) and CH_4 flux over a permanently inundated marsh in northeastern China, and analyzed the relevant factors influencing them. The net CO_2 uptake was 143 ± 9.8 and 100 ± 9.2 g C m^{-2} for the marsh during the growing seasons of 2004 and 2005, respectively. Ecosystem respiration consumed more than 70% of the total GEP. Meanwhile, a significant portion of the accumulated NEE-C was lost through CH_4 emission during the growing seasons, which indicated the great potential of CH_4 emission from the inundated marsh. The seasonal variations of GEP and RE were jointly affected by temperature and LAI, of which, temperature acted as the primary controlling factor. Soil temperature exerted the dominated influence over the seasonal variation of CH_4 flux.

As the chamber measurement for CH_4 flux was made at plot scale (<1 m^2), to determine CH_4 emission from the marsh ecosystem, more sample sites within the marsh should be included and more attention should be paid on the upscaling of the plot-scale chamber measurements. To estimate the carbon budget of the marsh ecosystem, measurements of fluxes of dissolved organic and inorganic carbon are also necessary. Future work should focus on the long-term and complete observations of all terms of carbon fluxes and the associated environmental factors to determine the carbon balance of the marsh ecosystem and its response to a changing climate.

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