

TITLE: Seasonal variations in carbon dioxide exchange in an alpine wetland meadow on the
Qinghai-Tibetan Plateau

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Abstract

The unique climate of the alpine wetland meadow is characterized by long cold winters and short cool summers with relatively high precipitation. These factors shorten the growing season for vegetation to approximately 150 to 165 days and prolong the dormant period to almost 7 months. Understanding how environmental variables affect the processes that regulate carbon flux in alpine wetland meadow on the Qinghai-Tibetan plateau is critical because alpine wetland meadow plays a key role in the carbon cycle of the entire plateau. To address this issue, Gross Primary Production (*GPP*), Ecosystem Respiration (R_{eco}), and Net Ecosystem CO₂ Exchange (*NEE*) were examined for an alpine wetland meadow at the Haibei Research Station of the Chinese Academy of Sciences. The measurement was used the eddy covariance approach during October 2003 to December 2006. Seasonal patterns of *GPP* and R_{eco} were closely associated with that of leaf area index (*LAI*). R_{eco} exhibited the same exponential variation as soil temperature with seasonally-dependent on R_{10} (R_{10} is the ecosystem respiration rate when the soil temperature reach 283.16 K (10°C)). Annual total *GPP* were 575.7, 682.9, and 630.97 gCm⁻² in 2004, 2005, 2006, respectively, similar to the R_{eco} were 676.8, 726.4, 808.2 gCm⁻², and the *NEE* were 101.1, 44.0 and 173.2 gCm⁻². It indicated that the alpine wetland meadow was a moderately important source of CO₂. The observed carbon dioxide fluxes in the alpine wetland meadow plateau were higher than other alpine meadow environments such as *Kobresia humilis* meadow and shrubland meadow which located in similar areas. Furthermore, relatively low R_{eco} levels occurred during the non-growing season after a rain event. This result is inconsistent with the result observed in alpine shrubland meadow. The timing of rain events had more impact on ecosystem *GPP* and *NEE*.

1. Introduction

Estimates of global wetland area vary between 5.3 and 6.4Mkm² (Matthews and Fung, 1987; Lappalainen, 1996). Northern wetlands play an important role in the global carbon cycle. Development of such wetlands has reduced atmospheric CO₂ concentrations and impacted the global climate system by reducing the greenhouse effect (Moore et al., 1998). It is estimated that northern peatlands cover 346 million hectares of the Earth's surface and represent a soil carbon sink of 455 Pg (Gorham, 1991). The deep organic soils stored in wetlands have been accumulating carbon for 4000–5000 years. Temperature increase due to climate change and drainage of wetlands may provide conditions to reverse this trend, leading to overall carbon loss.

The Qinghai-Tibetan Plateau (4000 m above sea level on average) is the largest grassland unit on the Eurasian continent, and its lakes and wetlands occupy a considerable area (ca. 50,000 km²; Zhao and K, 1999). Field studies have shown that alpine *Kobresia humilis* meadow or *Potentilla fruticosa* shrubland ecosystems sequester carbon on the Qinghai-Tibetan Plateau, at least under normal climatic conditions (Zhao et al., 2006; Kato et al., 2006; Zhao et al., 2007). However, little evidence is available to assess the carbon budget in alpine wetland ecosystems.

On the Qinghai-Tibetan Plateau, alpine wetland ecosystems are unique because they are typically underlain by permafrost, maintain a water table near the surface, and have a diverse vegetation cover consisting of both vascular and nonvascular plants (Zhao and Zhou, 1999). Climatic change is expected to have pronounced effects on these landscapes. On the plateau, future warming is expected to shorten the frozen period, increase precipitation, enhance evaporation, promote surface drying, increase the length of the growing season, advance active layer deepening, and have a significant impact on photosynthesis, plant respiration, and organic decomposition rates. Alpine wetland meadow ecosystems contain a large amount of soil organic

carbon, estimated 2.5% of the global pool of soil carbon. Moreover, 8% of the soil organic carbon is stored in plateau wetlands (Wang et al., 2002). The organic content of the wetlands soil is extremely high because of its low decomposition rate. The unique climate of the region is characterized by long cold winters, a short growing season, and cool summers with relatively high precipitation. In summer, the relatively humid climate supports high productivity and induces input of organic carbon to the soil. In winter, the rate of decomposition of organic carbon is low because of the cold. However, most recent carbon-budget studies of meadow ecosystems have conducted in alpine *K. humilis* meadow or *P. fruticosa* shrubland ecosystems (Kato et al., 2006; Zhao et al., 2005a, 2005b; Zhao et al., 2006). Much less attention has been given to CO₂ exchange in high-elevation alpine wetland ecosystems (Zhao et al., 2005b). Therefore, a discussion of their carbon cycle is very important for understanding the plateau's entire ecosystem, as well as the carbon cycle of other high-altitude grassland ecosystems in the world.

Eddy covariance technology provides a reliable way to measure the net CO₂ exchange of an ecosystem. Using this method, it is possible to use knowledge of leaf and whole-plant physiology to interpret whole-system variability (Amthor et al., 1994; Hollinger et al., 1994). This micrometeorological approach has been used widely in various terrestrial ecosystems (Aubinet et al., 2000; Baldocchi et al., 2001; Yamamoto et al., 2001). The authors used the eddy covariance method and measured the CO₂ exchange between the atmosphere and the ecosystem from January 2004 to December 2006 in an alpine wetland meadow on the Qinghai–Tibetan Plateau. The aims of this study are to (1) understand more fully the complex interrelationship between climate and phenology and their influence on CO₂ flux; (2) explore the causes of interannual variability of CO₂ flux; (3) examine how CO₂ cycle will change under different climatic conditions.

2. Materials and Methodology

2.1 *Site Description*

The experimental site was located in the vicinity of the Haibei Research Station, Chinese Academy of Sciences, in Qinghai, China (37°35'N, 101°20'E, 3250 m above sea level), and the measurement were conducted during October 2003 to December 2006. The eddy covariance (EC) method was used to examine carbon dynamics and variability. This wetland is characterized by nonpatterned, hummock-hollow terrain, with hummocks representing 40%, hollows 55%, and other features 5% of the landscape, it covers about 6 kilometers. The catchment is flooded at an average water depth of 30 cm during the growing season. Wetland vegetation is dominated by four species (*K. tibetica*, *Carex pamirensis*, *Hippuris vulgaris*, *Blysmus sinocompressus*) in different zones along a gradient of water depth reaching maximum values of 25–30 cm (Zhao et al., 2005b). The soil is a silty clay loam of Mat-Cryic Cambisols with heavy clay starting at depths between 0.1 and 1.0 m. The local climate is characterized by strong solar radiation with long cold winters and short cool summers. The annual mean air temperature recorded at the station is -1.7°C ; the coldest month is January (mean -15°C), and the warmest month is July (mean 10°C). Annual mean precipitation is 570 mm; more than 80% of the precipitation is concentrated in the growing season from May to September. The grassland turns green at the end of April or the beginning of May, depending on the year. The study site is grazed by yaks and Tibetan sheep from June to September with a low stocking rate of about one animal per hectare.

2.2 *Eddy Covariance, Meteorological, and Soil Measurements*

CO_2 and H_2O flux were measured at a height of 2.2 m in the center of an open area of at least 1 km in all directions using the open-path eddy covariance method from October 1, 2003, to December 31, 2006. Further details are described in Zhao et al. (2005a). The eddy covariance

sensor array included a three-dimensional sonic anemometer (CSAT-3, Campbell Scientific Inc., Logan, Utah, United States) and an open-path infrared gas analyzer (CS7500, Campbell Scientific Inc.). Wind speed, sonic virtual temperature, and CO₂ and H₂O concentrations were sampled at rate of 10 Hz. Their mean, variance, and covariance values were calculated and logged every 30 min using a CR5000 data logger (Campbell Scientific Inc., Logan, Utah, United States). The collected data were adjusted using the WPL (Webb, Pearman, and Leuning) density adjustment (Webb et al., 1980). In this study, three common flux data corrections (coordinate rotation, trend removal, and water vapor correlation) were not performed. However, the effect of lacking of these corrections on the calculated flux was examined for 10 days in July 2004 by using flux data sampled at the frequency of 10 Hz, and the implicit estimation error in the flux data was evaluated by comparing corrected and uncorrected fluxes in CO₂ flux calculations. The regression line slopes (slope=0.99, r²=0.53) showed small differences, within 1%, between corrected and uncorrected fluxes. This result indicated that the small negative bias resulting from the omission of these corrections is likely to be negligible in the study. The CO₂/H₂O analyzer system was calibrated on May 10, 2004, May 15, 2005 and May 11, 2006, respectively. Zero points were established using 99.999 % N₂ gas, the CO₂ span was calibrated using a standard gas bottle of CO₂, and the water vapor measurement was calibrated using a dewpoint generator (model Li-610; LiCor, Lincoln, NE). Calibration results showed that the cumulative deviations for zero drift and span change for both CO₂ and water vapor channels over a period of one full year were less than 2 and 0.5%, respectively. Thus, shift of zero and span over a month period can be considered insignificant.

Mean air temperature (Ta), humidity, wind speed, Photosynthetic Photon Flux Density (*PPFD*), net radiation (R_n), soil heat flux (G), and soil temperature (Ts) were also measured. Soil

moisture was monitored using time-domain reflectometry (TDR). These data were sampled and logged every 30 min using a digital micrologger (CR23X, Campbell Scientific, Inc.) equipped with an analog multiplexer (AM25T).

2.3 Green Leaf Area Index (LAI) and Biomass

Green and total *LAI* and biomass were measured by harvesting the vegetation approximately every two weeks during the growing season.

2.4 Data quality control, gap filling, Calculation of Ecosystem Respiration (R_{eco}) and Gross Primary Production (GPP)

All flux and meteorological data were quality controlled after data collection. Overall flux recovery was 82%, which is typical of flux recovery rates for most Fluxnet sites reported by Wilson et al. (2002). Ground heat flux, G , was calculated as the average of the three soil heat flux plates, and was corrected for heat storage above the plates. Rate of H and LE were stored in the air column below EC sensors. An examination of the energy budget closure indicated: $(H + LE) = 0.74 * (R_n + G) - 22.45, r^2 = 0.94$, where H and LE are the flux of sensible heat and latent heat, respectively. The slope fell in the median region of reported energy closures, which range from 0.55 to 0.99 (Wilson et al., 2002). The lack of energy balance closure has also been reported many times (Aubinet et al., 2000; Gu et al., 1999), and energy balance closure has accepted as an important new test of eddy covariance (Mahrt, 1998).

When daytime half-hourly values were missing, the net flux density of CO_2 (F_c) flux was estimated as a hyperbolic function of incident *PPFD* (adjacent days were included to establish the relationship, as shown in Eq. 1. Missing R_{eco} values were extrapolated by exponential regression Eq. 2) between measured nighttime R_{eco} under well-mixed conditions ($u^* > 0.1 \text{ms}^{-1}$, Aubinet et al., 2000; Lloyd 2006), with soil temperature at -5cm depth. Nighttime eddy

covariance flux data under low-turbulence conditions, that is, below the u^* threshold (Aubinet et al., 2000; 0.1 ms^{-1} in this study), were also corrected by the regression equation (Eq. 2). Daytime estimates of ecosystem respiration (R_{eco}) were obtained from the nighttime F_c -temperature relationship Eq. 2 (Lloyd and Taylor, 1994):

$$F_c = \frac{F_{\max} \cdot \alpha \cdot Q_p}{F_{\max} + \alpha \cdot Q_p} + R_{eco} \quad , \quad (1)$$

where Q_p ($\mu\text{molm}^{-2} \text{ s}^{-1}$) is incident photosynthetically active radiation, F_{\max} ($\mu\text{molm}^{-2} \text{ s}^{-1}$) the maximum CO_2 flux at infinite light, and α the apparent quantum yield. R_{eco} can be calculated as:

$$R_{eco} = R_{e,T_{ref}} \exp \left[\left(E_a / R \right) \left(\frac{1}{T_{ref}} - \frac{1}{T_s} \right) \right] \quad , \quad (2)$$

where R_{eco} is the nighttime ecosystem respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), $R_{e,T_{ref}}$ is the ecosystem respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at the reference temperature T_{ref} (K), and E_a is the activation energy (J mol^{-1}). These latter two parameters are site-specific. R is a gas constant ($8.134 \text{ J K}^{-1} \text{ mol}^{-1}$), and T_s is the soil temperature at a depth of 5 cm. $R_{e,T_{ref}}$ was set equal to R_{10} , the respiration rate at a T_{ref} of 283.16 K (10°C), and evaluated for every month during the study period. E_a was evaluated using a regression of all R_{eco} data in reference year against T_s as a constant value throughout each year (for 2004, 2005, and 2006, the values were 50093.43, 61084.73, and 44743.55 Jmol^{-1} respectively).

NEE (net ecosystem production as CO_2 uptake, i.e., NEE) was calculated from the sum of the eddy covariance flux, F_c and the storage term (F_s). As mentioned above, the F_c is sum of EC-measured flux and F_s is the flux associated with the change in storage in CO_2 in the layer below the level of CO_2 flux measurement and the values of F_s were obtained by integrating the change in CO_2 concentration through the air layer up to the heights of the eddy

covariance sensors (Suyker and Verma, 2001). For in the study site the storage term F_s was smaller more than F_c , and the daily calculate values tend to zero so the F_s was neglected in the calculated of NEE .

GPP was calculated as the sum of NEE and R_{eco} , as follows:

$$GPP = -NEE + R_{eco} \quad , \quad (3)$$

The monthly and annual average values (\pm SD) of GPP , NEE and R_{eco} are listed in the table.3.

2.5 Data analysis

We preformed the regression analyses to investigate the relationship of GPP , NEE , or R_{eco} with concurrent changes in environmental variables (T_a , T_s , $PPFD$) using the monthly and annual data in SAS V8 software, as well as the stepwise multi-linear analysis of those variable. The statistical information for the relationship between GPP , NEE , or R_{eco} and T_a , T_s , $PPFD$ is listed in Table.4 and Table.5, respectively. The multiple linear analyses at annual step are listed in Table.6.

3. Results

3.1 Information on weather conditions, biomass, and leaf area

Fig.1 shows daily $PPFD$, average air temperatures at a height of 2.2 m, average soil temperatures at depths of 3cm, 40 cm, daytime average Vapor Pressure Deficits (VPD) at a height of 2.2 m, and daily total precipitation. The daily average temperatures ranged from -23.6 to 14.3°C (air temperature), -6.2 to 12.0°C (soil temperature at 5cm depth), and 0 to 8.5°C (soil temperature at 40cm depth), with maximum temperatures recorded from the late of July to the early of August. $PPFD$ reached its annual maximum in the beginning of July and then decreased gradually. There were no significant differences in $PPFD$ or VPD among the years 2004, 2005,

and 2006 (years differences did not exceed 5%, $PPFD: F_{(2, 1071)} = 1.07, P > 0.05$; $VPD: F_{(2, 1071)} = 1.26, P > 0.05$), as shown in Table 1. It was slightly cooler in 2004 than 2005 and 2006. Precipitation was concentrated in the period from May to August (Fig. 1e). Total annual precipitation in 2004 was similar to 2005, but slightly less than 2006 (Table 1). Above-ground biomass increased from mid-April (DOY100) each year and reached maximum of 305.3 ~ 335.6 g m⁻² during late August. Maximum Leaf Area Index (LAI) followed the similar trend of green biomass and reached 3.9 m²m⁻² in 2005.

3.2 Response of R_{eco} to temperature

Fig.2 shows the specific response curve of the growing period at monthly step (Fig. 2) for 2004, 2005, and 2006. The exponential function given in Eq. (2) described very well the relationship between R_{eco} and soil temperature at 5-cm depth. From Eq. (2), R_{10} was estimated to be 2.3–5.5 during the growing period (Fig. 2). Meanwhile, high R_{10} values were observed in the initial stage of growth (May and June, Fig. 2), whereas low R_{10} values occurred mostly in the wet season when grass grown vigorously (July and August, Fig. 2). Fig.3 shows the relationship between R_{eco} and soil temperature (at 5 cm) in the non-growing season. R_{10} values were estimated to be 2.7, 2.7, and 2.6 in 2004, 2005, and 2006 respectively, it was clearly lower than the R_{10} values observed during the growing season (Fig. 2), which is consisted with the result of Zhao et al. (2006). The annual averaged R_{10} were 3.05, 2.98, and 3.24 $\mu\text{mol Cm}^{-2}\text{s}^{-1}$ for 2004, 2005, and 2006, whereas the values for annual active energy (E_a) were 50093.43, 61084.73, and 44743.5 J mol⁻¹ respectively. Thus, the temperature dependence of R_{10} was higher in 2004 and 2006 than in 2005.

3.3 GPP in relation to PPFD

Fig. 4 shows the relationship between *GPP* and *PPFD* from May to September. The values of *GPP* responded exponentially to *PPFD* during July and August, but the light response was linear in May, June, and September. The dependence of these fluxes on *PPFD*, however, changed with the seasons. In May, as shown in Fig. 4, the values of *GPP* were very low in the alpine wetland, and even in day time, the *GPP* slightly decreased as *PPFD* increased. The values of *GPP* increased from June to August under the constant *PPFD* condition. In September, although the increase in *LAI*, the dependence of *GPP* on *PPFD* did not change greatly

Based on statistical analysis using Eq. (1), GPP_{SAT} values in July and August were 14.30 and 16.21 $\mu\text{molm}^{-2}\text{s}^{-1}$ respectively, and α was 0.084 and 0.070. The quantum yield was not within the range of published data for C_3 grasses (Ruimy et al., 1995; Flanagan et al., 2002; Xu and Baldocchi, 2004), and was very higher than the values from other eddy covariance studies in temperate C_3 grassland (Flanagan et al., 2002). Quantum yield values of the alpine wetland were higher than the values of the alpine shrubland meadow, which is located in the vicinity of the study site (0.0056 and 0.0082 for July and August respectively) (Zhao et al. (2006). However, the photosynthetic capacity of the alpine shrubland meadow was smaller than the alpine shrubland meadow (17.93 and 20.54 $\mu\text{molm}^{-2}\text{s}^{-1}$ for July and August respectively), probably due to larger canopy size, more vascular plants, and the presence of enough moisture.

Before 13:00 (Beijing Standard Time, BST) at the study site, light response increased with increasing *PPFD* values, jumped to 830 $\mu\text{molm}^{-2}\text{s}^{-1}$ (Fig. 4), and then declined. These results indicate the light-use efficiency decreased while *PPFD* rised. In the afternoon, the values of *GPP* responded linearly to *PPFD* ($GPP=b+a\times PPFD$) during all months, with small a (Fig. 5).

3.4 *GPP* in relation to *LAI*, and Depth of Water table (D_{WT})

The maximum value of *GPP* occurred during the period of greatest *LAI* in all years, and *GPP* decreased with decreasing *LAI*. Fig. 6 illustrates the effect of *LAI* at controlling *GPP*. In general, *GPP* increased about 2.23 gCm^{-2} per day for *LAI* increased pre unit.

R_{eco} from peat soils is commonly dependent on D_{WT} since aerobic microbial activity increases with decreasing D_{WT} (Andreis, 1976; Stephens et al., 1984; Hodge, 2002; Lloyd 2006). Unexpectedly, the authors did not observe decreases in nighttime R_{eco} with increasing D_{WT} . Linear relationships between R_{10} and D_{WT} were insignificant ($R^2=0.02$, $n= 38$, $P>0.05$) for alpine wetland meadow.

3.5 Influence of rain events on non growing R_{eco}

Small pulses of R_{eco} were observed immediately after individual rain events during the non-growing period, when herbage was senescent. Data from October 5, 2004, to February 1, 2005, are presented in Fig. 7. The I rain event occurred on October 9, 2004, with total precipitation of only 1.7 mm/day (Fig.7). On October 11, R_{eco} suddenly decreased to 4.74 gCm^{-2} per day from the background level of 8.70 gCm^{-2} per day which was observed a few days ago. Then after two days, R_{eco} increased to 7.25 gCm^{-2} per day, as observed on October 13. After the II rain event (6.5 mm rainfall), R_{eco} again greatly decreased from 8.98 gCm^{-2} per day on October 30 to 4.40 gCm^{-2} per day on November 1. After the X rain event (1.1 mm) on January 8, 2005, R_{eco} decreased from 2.77 gCm^{-2} per day to 1.99 gCm^{-2} per day. After this, R_{eco} showed an exponential decrease with time (Fig. 7).

3.6 Diurnal variations in *NEE*

Seasonal variations in the diurnal patterns of *NEE* can provide insights into how *PPFD* and *LAI* interact to control photosynthesis and respiration. Diurnal sequences of mean *NEE* and *PPFD* values at different growth periods are presented in Figs. 9 and 10 try to illustrate this; data

from ten consecutive days were combined to reduce the sampling error. Four examples were from sunny days: one from the non-growing season during DOY 101–110 (before the growing season) and one from DOY 301–310 (the senescent period) in 2005, and the other two from the growing season, DOY 151–160 (with *LAI* of 2.2) and DOY 206–215 (*LAI* of 3.2) in 2005. This chart shows that during the non-growing season, diurnal variation is not obvious or consistent, and was very small at any time (Fig. 8). During the two periods, the releases of CO₂ were visibly. Obverse, the differences in amplitude of the diurnal variations in *NEE* between periods were very small by comparing the release rates of both periods. It can also be noted from Fig. 8 that *NEE* from 13:00 to 17:00 BST was much higher in the senescent period than that in the pre-growing period, probably due to higher soil temperature. During the growing season, the diurnal variations in *NEE* showed a similar temporal pattern to the *PPFD* curves. The diurnal *NEE* patterns of daytime uptake and nighttime release are clear. After dawn, *NEE* moved from a positive value (release) to a negative value (uptake). The highest uptake rate arised around noon and began to decrease afterwards. At dusk, *NEE* moved from a negative value to a positive value. However, positive and negative value changes are also clearly affected by seasonal variations. The highest diurnal uptake rate and highest diurnal release rate occur between 11:00–12:00 and 16:00–17:00 ,respectively. The maximum net CO₂ uptake for the two growing periods, 2.5 and 11.5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ respectively, indicated that the diurnal variations in *NEE* depended mainly on *LAI*. Fig. 9 shows that nighttime *R_{eco}* was much higher in the peak growth stage (DOY206-215) than in the early season (DOY151-160), reflecting the importance of photosynthetic activity for ecosystem respiration (Xu et al., 2004). We compared the observed maximum values of CO₂ uptake with those at other sites located in similar latitudes. The maximum CO₂ uptake observed in this research was slightly larger than that for alpine *K. humilis* meadow ($-10.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$;

Kato et al., 2004a) and for alpine shrubland meadow ($-10.87 \mu\text{mol m}^{-2}\text{s}^{-1}$; Zhao et al., 2005) in the same latitudes. The values fell within the range of those reported from other grassland studying sites. For example, Valentini et al. (1995) observed maximum rates of CO_2 uptake between -6 and $-8 \mu\text{mol m}^{-2}\text{s}^{-1}$ in serpentine grassland in California. By contrast, much higher maximum rates of CO_2 uptake (between -30 and $-40 \mu\text{mol m}^{-2}\text{s}^{-1}$) have been reported from more productive perennial grasslands which contain C_4 species (Kim and Verma, 1990; Dugas et al., 1999; Suyker and Verma, 2001; Li et al., 2003).

3.7 Seasonal variations of cumulative GPP , R_{eco} , and NEE

Fig. 10 illustrates the seasonal variations in daily GPP , R_{eco} , and NEE over the course of this study. In the growing season, the three years showed similar patterns of seasonal variation in GPP , R_{eco} , and NEE . The seasonal distributions of daily GPP , R_{eco} , and NEE follow that of green leaf area for all years. Both GPP and R_{eco} gradually increased in April and May, and NEE became slightly negative in the end of May. Then as the temperature warmed up, meanwhile, LAI and day length increased, GPP and R_{eco} present a rapidly rising trend in June, July, and August, and it would make a strong carbon sink of the ecosystem. The daily maximum net CO_2 uptake (-3.9gCm^{-2} per day), was within the observed range for other alpine meadow ecosystems at similar latitudes (-1.7 to -5gCm^{-2} per day; Kato et al., 2004a; Zhao et al., 2006). The maximum net CO_2 uptake observed in this research was 20–55% less than values observed for tallgrass prairies in Kansas, California, and Oklahoma, United States (-4.8 to -8.4gCm^{-2} per day; Kim et al., 1992; Ham and Knapp, 1998; Suyker and Verma, 2001; Xu and Baldocchi, 2004). However, the seasonal maximum observed in this research was almost four times greater than values observed for subalpine conifer forest in Colorado (-1.0gCm^{-2} per day) at similar altitude (3050 m). GPP and R_{eco} plummeted to near-zero about October 26. After grass senescence, the

grassland continuously lost carbon via soil respiration, but crept along at a very low rate (0.3–0.9 gCm^{-2} per day) due to the low soil temperature.

The authors observed slightly difference about the rates of R_{eco} change in the pre-growing period and in the senescence period among the three years. R_{eco} during the pre-growing period in 2004 and 2006 were 0.72Cgm^{-2} per day and 0.76Cgm^{-2} per day, respectively, compared to 0.58Cgm^{-2} per day in 2005 (Fig. 10). This difference in R_{eco} values was probably caused by the difference in rain event times in the three years. As shown in Fig. 1, during the pre-growing period in 2005 there were 26 rain events, which caused the ecosystem to lose less carbon than usual. In the senescence period, the observed R_{eco} were 1.00 gm^{-2} per day in 2004 and 0.95 gm^{-2} per day in 2006. They were higher than the value of 0.83 gm^{-2} per day in 2005, it probably caused by the difference in soil temperature.

GPP reached a maximum value ($7.15\text{--}10.15 \text{ gCm}^{-2}$ per day) during mid-August. Information on cumulative carbon exchange (GPP , R_{eco} , and NEE) for the alpine wetland meadow from January 1, 2004 to December 31, 2006, is shown in Fig. 11. Since the growing season for the grass did not extended across two calendar years, cumulative GPP and NEE values were computed over the calendar year. As shown in Fig. 12, annual total GPP , R_{eco} , and NEE were 575.7 , 676.8 , and 101.1 g Cm^{-2} for 2004, 682.9 , 726.4 and 44.0 g Cm^{-2} for 2005, and 631.0 , 808.2 , and 173.2 gCm^{-2} for 2006 (Table 1). For 2006, the GPP/R_{eco} ratio of the ecosystem (0.78) was smaller than for 2004 (0.85) and 2005 (0.86). This indicates that the ecosystem released more carbon in 2006 than in 2004 and 2005.

4. Discussion

A seasonal variation occurred in NEE . Furthermore, this variation due to large CO_2 fluxes of the release by R_{eco} and CO_2 uptaked by GPP . In general, NEE was slightly positive or almost

zero during pre-growing (January-April), and during senescence (October-December). It became most negative in June-September, the end of the growing season or the beginning of the cold season (Fig. 10). Opposite patterns of R_{eco} and GPP caused this seasonal variation in NEE .

4.1 Gross primary production (GPP)

The pattern of seasonal variation of the daily maximum GPP was similar to the daily mean GPP . The relationship between GPP and $PPFD$ was shown in Fig.4. The fact result from that LAI was so small that the rate of canopy photosynthesis was lower than the CO_2 emission rate from both plant respiration and soil emission. As the $PPFD$ gradually stabilized, the values of GPP increased from June to August. This result was strongly influenced by the LAI . It increased from 0.09 (May 7) to 3.95 (July 16) and rose with the corresponding leaf-level photosynthetic capacity. However, in September, the dependence of GPP on $PPFD$ did not change greatly as the LAI increased. Because the midsummer air temperature might be higher than the optimum temperature for photosynthesis for some species, especially for C_3 plants in this alpine region (Zhao et al., 2005a). Most species flowered and produced seeds before the end of August, whereas NEE decreased under the same conditions of $PPFD$. This decrease may be due to the reduction in the activity of endemic plants. For higher $PPFD$, the GPP seemed to approach saturation, a common phenomenon for C_3 species. For the fluctuation of GPP , the $GPP_{\text{rate, before noon}}$ was greater than $GPP_{\text{rate, afternoon}}$, the results probably due to the appearance of photo-inhibition. At 13:00, the increased $PPFD$ and temperature induced the stomas closed to avoid wasting much water. Although the $PPFD$ increased, the rate of CO_2 became the leading limiting factor. And the vegetation also experience higher heat load, which enhances respiration, and thus lowers their photosynthesis rates (Chen et al.2009).

GPP was positively related to *LAI*, as shown also by Saigusa et al. (2002) and Flanagan et al. (2002). Over the course of the growing season, day-to-day variations in *GPP* on sunny days were highly correlated with variations in *LAI*. For the wetland meadow, over 85% of the variance in *GPP* was explained by changes in *LAI*. The remaining 15% of the variance was due to variations in weather, vapor pressure deficit, temperature, and direct and diffuse radiation. The result suggests that *LAI* determines the ecosystem capacity for assimilation and resource requirements. For example, based on carbon flux data from 18 sites across European forests, Janssens et al. (2001) found that productivity of forests overshadows temperature as a factor determining soil and ecosystem respiration. A study by Högberg et al. (2001) in a boreal pine forest in Sweden showed that a decrease of up to 37% in soil respiration was detected within five days after the stem bark of pine trees were girdled. Therefore, when simulating R_{eco} over the entire season, the impact of canopy photosynthetic activity must be taken into account (Janssens et al., 2001). The linear relationship observed in this study is consistent with other grassland studies (Saigusa et al., 1998; Flanagan et al., 2002; Xu and Baldocchi, 2004). The slope of the *GPP-LAI* relationship obtained from the present data was two-thirds of that reported by Xu and Baldocchi (2004), but 30–40% less than that reported by Flanagan et al. (2002) for a continental grassland (7–9 gCm⁻² per day per *LAI*). For the period of peak CO₂ uptake, the *GPP/LAI* values calculated from this meadow ecosystem were 2.8–3.6Cm⁻² per day, higher than the values reported in Tappeiner and Cernusca (1996) (1.1–1.5 Cm⁻² per day), but below the range of other reports for temperate grasslands (Ruimy et al., 1995; Flanagan et al., 2002).

For the daily maximum *GPP* value (7.15–10.15 gCm⁻² per day during mid-August), Xu and Baldocchi (2004) reported nearly identical peak daily *GPP* (10.1 gCm⁻² per day) in a temperate C₃ grassland near Alberta, Canada. But the daily maximum *GPP* values obtained here were lower

than a tallgrass prairie and mid-latitude deciduous forest (19 and 16 gCm^{-2} per day respectively; Turner et al., 2003). The daily maximum values of R_{eco} were in the range of 4.65–6.79 gCm^{-2} per day. Seasonal maxima of R_{eco} in a California grassland were approximately 4.0–6.5 gCm^{-2} per day (Flanagan et al., 2002); in a tallgrass prairie, 9–9.5 gCm^{-2} per day (Suyker and Verma, 2001); in a southern boreal forest, 7–12 gCm^{-2} per day (Griffis et al., 2003); and in a tropical peat swamp forest floor, 12 gCm^{-2} per day (Jauhiainen et al., 2005).

In comparison with the cumulative *GPP* of similar latitude ecosystems reported by Kato et al.(2006) and Zhao et al.(2006), that of our study site was close to *K. humilis* meadow (Kato et al., 2004b, 2006), and larger than the alpine shrubland meadow (Zhao et al., 2006). Although alpine wetland meadow ecosystem has a higher annual *GPP* than the near area meadow ecosystem, it has an obvious carbon emission, which attributed to the high soil organic matter. The cumulative *GPP* measured at this site was less than reported values for some grasslands and pastures (Xu and Baldocchi, 2004; Griffis et al., 2003), for temperate deciduous forests (1122–1507 gCm^{-2} , Falge et al., 2002), and for most temperate and boreal coniferous forests (992–1570 gCm^{-2} , Falge et al., 2002). Thus, although the daily CO_2 assimilation of the alpine wetland equal to the California annual grassland ecosystem, it had a lower annual *GPP* because of the short growing period and lower temperature. Lower values have been reported in Sweden (699 gCm^{-2} ; Law et al., 2002) and the United States (454 gCm^{-2} ; Baldocchi et al., 2000; 407 gCm^{-2} ; Zeller and Nikolov, 2000).

4.2 Ecosystem Respiration (R_{eco})

The daily R_{eco} showed similar seasonal patterns in their seasonal variations. And the daily R_{eco} were associated more closely with the seasonal pattern of soil temperature than with that of *PPFD* (Fig. 1). However, R_{eco} even increased with soil temperature decreased during the same

period, according to the variation of R_{10} (Fig.2, 3). In general, climatic factors control the seasonal changes of respiratory processes stronger than biological factors (Falge et al., 2002). However, R_{eco} seemed to be tightly associated with aboveground and belowground biomass in the alpine meadow (Kato et al., 2004b).

The values of R_{10} during the growing season fell in the range (1.8–6.1) of the numerous observations in wetlands reported in literatures (Svensson, 1980; Chapman and Thurlow, 1996; Silvola et al., 1996). These values of R_{10} were based on seasonal changes in soil temperature, and the dependence on temperature was higher in June than in the other months. The measured values of R_{10} (3.4, 3.6, and 3.9 in 2004, 2005, and 2006, respectively) during the growing season were higher than the mean values reported in *Kobresia humilis* meadow (Kato et al. 2006) and *Potentilla fruticosa* shrubland (Zhao et al. 2006); it was caused by different vegetation and soil organic matter. These values outside the range (1.3–3.3) which was reported by Rainch and Schlesinger (1992), but within the range (1.9–5.5) given in other reports for forest (Massman and Lee, 2002). The variation of R_{10} values during the growing season reflected different temperature sensitivities to autotrophic and heterotrophic respiration and the turnover times of the multiple carbon pools. High temperature sensitivity may include the direct physiological effect of temperature on root and microbial activities and the indirect effect related to photosynthetic assimilation and carbon allocation to roots (Davidson et al., 1998). Evidence for the indirect effect of photosynthesis on autotrophic respiration comes from a series of recent studies (Bremer et al., 1998; Bowling et al., 2002; Zhao et al., 2006). In addition, the surface of the frozen soil on the Qinghai-Tibetan plateau thawed during April to June (Fig. 2), resulting in an increase in R_{10} (Zhao et al., 2006). The annual R_{10} values obtained in this research were higher than alpine meadow (1.60–1.89 $\mu\text{mol C m}^{-2}\text{s}^{-1}$) by Kato, et al. (2006) thus manifested that the effects of

temperature change on ecosystem respiration in the wetland meadow were larger than the alpine meadow.

With respect to the effect of Depth of Water table (D_{WT}) on R_{eco} , Nieveen et al. (2005) and Lloyd and Taylor (1994) found no change in soil respiration with water-table location. However, recently Lloyd (2006) used eddy correlation instrumentation found changes in soil respiration with water-table depth. Silvola et al. (1996) observed an increase in CO_2 emissions from peat soil with increases in D_{WT} along the depths of 0.3–0.4m. In this study, as D_{WT} increased, the air-filled porosity also increased, supporting greater aerobic degradation of peat. In the current research, even though D_{WT} varied little at the field site, the site was still waterlogged. Therefore, oxygen availability in peat would be fairly constant, thus D_{WT} had little effect on soil respiration. In a similar vein, a few studies have shown that ecosystem respiration is dependent on peat temperature, but not on water table level (Bubier et al., 2003; Lafleur et al., 2005). These observations might be explained by the fact that the soil moisture content was relatively invariant in the upper layers, and therefore little change in heterotrophic respiration would be expected to result from observed changes in water-table depth. It was assumed that D_{WT} was not a limiting factor at this site.

The authors found the evidence that rain events reduced respiration rates, in contrast to others (Zhao et al., 2006). These different conclusions regarding the coupling between R_{eco} and rain events may explain the different opinion about the effect of soil moisture on R_{eco} . The study site was icebound during the non-growing season, and the soil temperature was relatively steady. Therefore, the authors speculated that oxygen availability in the peat soil was fairly constant, and thus rain events had little effect on increasing aerobic degradation. On the other hand, after continuing rain events (>2mm per day), small pulses of increased R_{eco} (in the range of 0.7–1

gCm⁻² per day) were observed immediately. Similarly, Zhao et al. (2005c) maintained that seasonal snowfall influences the ecosystem respiration in a cool wetland on the Qinghai-Tibetan alpine zone. Net ecosystem CO₂ exchange under snow-covered conditions was significantly greater than under snow-free conditions.

4.3 Ecosystem Carbon Exchange Ability

In comparison with the total annual NEE of similar latitude ecosystems reported by Kato et al. (2006) and Zhao et al. (2006), it is found that the alpine wetland meadow (44.0 – 173.2 gCm⁻²), was a source of atmospheric CO₂. Yet *Kobresia humilis* meadow and alpine shrubland meadow of which climate are similar to our study site were sink (Table 2). Although the annual GPP of the three ecosystems were comparable, the annual R_{eco} of the wetland was higher than *Kobresia humilis* meadow and alpine shrubland meadow 43.5% and 52.1%, respectively. Both higher soil organic carbon content (wetland: 28.06%; shrubland: 7.54%; *Kobresia humilis* meadow: 5.19%, Zhao et al. 2005b) and lower grazing intensity (wetland: 38.8-62.6 %; *Kobresia humilis* meadow: 82.7-87.1 %) may stimulate ecosystem respiration, and thus lead to a large amount of C release. The low grazing intensity in a heavily grazed area near our study site increased both aboveground and belowground biomass, and should have an impact on litter decomposition and soil structure, which affect soil respiration.

The extent of carbon release in this alpine wetland meadow ecosystem was similar to other observed northern ecosystems. The calculated whole-year NEE was similar to those obtained from other wetland sites and fell within the range of reported data (Table 2). For example, a high-Arctic is located in northern Alaska, Coyne and Kelly (1975) observed a net seasonal uptake of 40 g C m⁻²y⁻¹, while Suyker et al. (1997) measured a net uptake of 88 g C m⁻² for a period from mid-May to early October in boreal fen. The most significant carbon loss for wet

Arctic ecosystems through CO₂ exchange has been reported by Oechel et al. (1997) for both tussock (122 g C m⁻²y⁻¹) and wet sedge tundras (25.5 g C m⁻²y⁻¹), and by Oechel et al. (1993), 156 g C m⁻²y⁻¹ for a tussock tundra and 34 g C m⁻²y⁻¹ for a wet sedge tundra. However, wet sedge and tussock tundras have also been recorded to be a carbon sink with uptake rates of 27 and 23 g C m⁻²y⁻¹ respectively by Oechel and Billings (1992), and a sedge-dominated fen at Zackenberg has been observed to be a sink with uptake of 64.4 g C m⁻²y⁻¹ (Soegaard and Nordstroem, 1999).

The single factor linear regression was performed between CO₂ flux and environmental factors (table.4 and table.5). It is indicated that on the annual base the *GPP* and *R_{eco}* were closely associated with *T_a*, *T_s*, (*R*²>0.5). Furthermore, during end of growing season (September to October), *T_s* has greater effect on the *GPP*. The similar phenomenon was happened at *R_{eco}* during the peak of growing stage (June to August). As to *NEE*, it was also well connected with the both temperature (*P*<0.001), but the regress equation is not obvious enough to reach significant level.

To distinguish the factors affecting the seasonal variation in CO₂ fluxes among the three years at the alpine wetland ecosystem, a multiple regression analysis was performed to assess the relationships of *GPP*, *R_{eco}* and *NEE* with the main environmental factors using daily data on annual base (Table 6). Results show that the variability of *GPP*, *R_{eco}*, *NEE* at the study site significantly connected with changed in air temperature, soil temperature, *PPFD*, and *VPD* (*p*<0.001).

5. Conclusions

The conclusions that can be drawn from the current research can be summarized as follows: (i) seasonal trends of *GPP* and *R_{eco}* closely followed the changes of *LAI*. *R_{eco}* followed the exponential variation of soil temperature with seasonally-dependent *R₁₀* values, (ii) carbon

dioxide fluxes in an alpine wetland meadow are larger than *K. humilis* meadow and *P. fruticosa* shrubland meadow which share similar alpine meadow environments and located in cooler seasonal climate areas, (iii) CO₂ emissions rates decrease notably after rain events, especially in the non-growing season, and (iv) the alpine wetland meadow was a moderate source of CO₂.

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References

- Amthor, J.S., Goulden, M.L., Mungeer, J.W., Wofsy, S.C., 1994. Testing a mechanistic model of forest-canopy mass and energy exchange using eddy correlation: carbon dioxide and ozone uptake by a mixed oak-maple stand. *Australian Journal of Plant Physiology*, 21, 623–651.
- Andreis, H.J., 1976. A water table study on an Everglades peat soil: effects on sugarcane and on soil subsidence. *Sugar Journal*, 39, 8–12.
- Aubinet, M., Grelle, A., Ibrom, A. et al., 2000. Estimates of the annual net carbon and water vapor exchange of forests: the EUROFLUX methodology. *Advances in Ecological Research*, 30, 113–175.
- Baldocchi, D., Kelliher, F.M., Black, T.A., 2000. Climate and vegetation controls on boreal zone energy exchange. *Global Change Biol.* 6, 69–83.
- Baldocchi, D., Falge, E., Olson, R. et al., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. *Bulletin of the American Meteorological Society*, 82, 2415–2434.
- Bowling, D.R., McDowell, N., Bond, B., 2002. ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. *Oecologia*, 131, 113–124.
- Bremer, D.J., Ham, J., Owensby, C.E., 1998. Responses of soil respiration to clipping and grazing in a tallgrass prairie. *J. Environ. Qual.*, 27, 1539–1548.
- Bubier, J.L., Bhatia, G., Moore, T.R., Roulet, N.T., Lafleur, P.M., 2003. Spatial and temporal variability in growing season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems*, 6, 353–367.
- Chapman, S.J., Thurlow, M., 1996. The influence of climate on CO_2 and CH_4 emissions from organic soils. *Agric. For. Meteorol.*, 79, 205–217.

- Chen, B., Black, T.A., Coops, N.C., Krishnana, P., Jassal, R., Brümer, C., Nesic, Z., 2009. Seasonal controls on interannual variability in carbon dioxide exchange of a near-end-of-rotation Douglas-fir stand in the Pacific Northwest, 1997-2006. *Global Change Biol.*, 15:1962-1981.
- Coyne, P.I., Kelly, J.J., 1975. CO₂ exchange in the Alaskan tundra: meteorological assessment by the aerodynamical method. *Journal of Applied Ecology*, 12, 587–611.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Glob. Change Biol.*, 4, 217–227.
- Dugas, W.A., Heuer, M.L., Mayeux, H.S., 1999. Carbon dioxide fluxes over Bermuda grass, native prairie, and sorghum. *Agric. For. Meteorol.*, 93, 121–139.
- Falge, E., Baldocchi, D.D., Tenhunen, J., 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agric. For. Meteorol.*, 113, 53–74.
- Flanagan, L.B., Wever, L.A., Carson, P.J., 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology*, 8, 599–615.
- Gu, J., Smith E. A., Merritt J. D., 1999. Remote Sensing of Carbon/Water/Energy Parameters- Testing energy balance closure with GOES-retrieved net radiation and in situ measured eddy correlation fluxes in BOREAS: *Journal of Geophysical Research*, 104, 27881-27894.
- Gorham, E., 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, 1, 182–195.

- Griffis, T.J., Black, T.A., Morgenstern, K., 2003. Ecophysiological controls on the carbon balance of three southern boreal forests and southern boreal aspen forest. *Agric. Forest Meteorol.*, 117, 53–71.
- Ham, J.M., Knapp, A.K., 1998. Fluxes of CO₂, water vapor, and energy from a prairie ecosystem during the seasonal transition from carbon sink to carbon source. *Agric. For. Meteorol.*, 89, 1–14.
- Hollinger, D.Y., Kelliher, F.M., Byers, J.N. et al., 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology*, 75, 134–150.
- Hodge, P.W., 2002. *Respiration processes in Waikato peat bogs*. MSc thesis, University of Waikato, Hamilton, New Zealand.
- Högberg, P., Nordgren, A., Buchmann, N. et al., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, 411, 789–792.
- Janssens, I.A., Lankreijer, H., Matteucci, G. et al., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Glob. Change Biol.*, 7, 269–278.
- Jauhiainen, J., Takajashi, H., Heikkinen, J.E.P. et al., 2005. Carbon fluxes from a tropical peat swamp forest floor. *Glob. Change Biol.*, 11, 1788–1797.
- Kato, T., Tang, Y.H., Gu, S. et al., 2004a. Carbon dioxide exchange between the atmosphere and an alpine meadow ecosystem on the Qinghai–Tibetan Plateau, China. *Agricultural and Forest Meteorology*, 124, 121–134.

- Kato, T., Tang, Y.H., Gu, S. et al., 2004b. Seasonal patterns of gross primary production and ecosystem respiration in an alpine meadow on the Qinghai-Tibetan Plateau. *J. Geophys. Res.*, 109, D12109, doi: 10.12109/ 2003JD003951.
- Kato, T., Tang, Y., Gu, S., Hirota, M., Du, M.Y., Li, Y.N., Zhao, X.Q., 2006. Temperature plays a major role in controlling ecosystem CO₂ exchange in an alpine meadow on the Qinghai-Tibetan Plateau. *Glob. Change Biol.*, 12, 1285–1298.
- Kim, J., Verma, S.B., 1990. Carbon dioxide exchange in a temperate grassland ecosystem. *Bound. Layer Meteorol.*, 52, 135–149.
- Kim, J., Verma, S.B., Clement, R.J., 1992. Carbon dioxide budget in temperate grassland ecosystem. *J. Geophys. Res.*, 97, 6057–6063.
- Lafleur, P.M., Moore, T.R., Roulet, N.T., Frolking, S., 2005. Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. *Ecosystems*, 8, 619–629.
- Lappalainen, E., 1996. *Global Peat Resources*. 368p. International Peat Society, Finland.
- Law, B.E., Falge, E., Gu, L. et al., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agric. For. Meteorol.*, 113, 97–120.
- Li S.G., Lai C.T., Yokoyama T. and Oikawa T., 2003. Seasonal variation in energy budget and net ecosystem CO₂ exchange over a wet C₃/C₄ co-occurring grassland: effects of development of the canopy. *Ecological Research*, 18: 661–675.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Functional Ecology*, 8, 315–323.
- Lloyd, C.R., 2006. Annual carbon balance of a managed wetland meadow in the Somerset Levels, UK. *Agric. For. Meteorol.*, 138, 168–179.

- Mahrt, L., 1998. Flux sampling errors for aircraft and towers. *Journal of Atmospheric and Oceanic technology*, 15, 416-429
- Matthews, E., Fung, I., 1987. Methane emission from natural wetlands: global distribution, area, and environmental characteristics of sources. *Global Biogeochemical Cycles*, 1, 61–86.
- Massman, W.J., Lee, X., 2002. Eddy covariance flux corrections and uncertainties in long-term studies of carbon and energy exchanges. *Agric. For. Meteorol.*, 113, 121–144.
- Moore, T.R., Roulet, N.T., Waddington, J.M., 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change*, 40, 229–245.
- Nieveen, J.P., Campbell, D.I., Schipper, L.A., Blair, I.J., 2005. Carbon exchange of grazed pasture on a drained peat soil. *Global Change Biol.*, 11, 607–618.
- Oechel, W.C., Billings, W.D., 1992. Effects of global change on the carbon balance of Arctic plants and ecosystems. In Chapin, F.S. III, Jefferies, P.L., Reynolds, J.F., Shaver, G.R., Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective*, Academic Press, London, 139–168.
- Oechel, W.C., Hastings, S.J., Vourlitis, G., Jenkins, M., Riechers, G., Grulke, N., 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature*, 361, 520–523.
- Oechel, W.C., Vourlitis, G., Hastings, S.J., 1997. Cold season CO₂ emission from arctic soils. *Global Biochemical Cycles*, 11(2), 163–172.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, 44B, 81–99.

- Ruimy, A., Jarvis, P.G., Baldocchi, D.D. et al., 1995. CO₂ fluxes over plant canopies and solar radiation: a review. *Advances in Ecological Research*, 26, 1–68.
- Saigusa, N., Oikawa, T., Liu, S., 1998. Seasonal variations in the exchange of CO₂ and H₂O between a grassland and the atmosphere: an experimental study. *Agric. For. Meteorol.* 89, 131–139.
- Silvola, J., Alm, J., Ahlholm, U., Nykanen, H., Martikainen, P.J., 1996. CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. *J. Ecol.*, 84, 219–228.
- Soegaard, H., Nordstroem, C., 1999. Carbon dioxide exchange in a high-arctic fen estimated by eddy covariance measurements and modeling. *Glob. Change Biol.*, 5, 547–562.
- Stephens, J.C., Allen, L.H. Jr., Chen, E., 1984. Organic soil subsidence. In Holzer, T.L. (ed.), *Man-induced land subsidence*, Geological Society of America Reviews in Engineering Geology, Boulder, CO, USA, Vol. 6, 107–122.
- Suyker, A.E., Verma, S.B., Arkebauer, T.J., 1997. Season-long measurements of carbon dioxide exchange in a boreal fen. *J. Geophys. Res.*, 102, 29021–29028.
- Suyker, A.E., Verma, S.B., 2001. Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Glob. Change Biol.*, 7, 179–289.
- Svensson, B.H., 1980. Carbon dioxide and methane fluxes from the ombrotrophic parts of a subarctic mire. *Ecol. Bull. Stockholm*, 30, 235–250.
- Tappeiner, U., Cernusca, A., 1996. Microclimate and fluxes of water vapour, sensible heat and carbon dioxide in structurally differing subalpine plant communities in the Central Caucasus. *Plant, Cell and Environment*, 19, 403–417.

- Turner, D.P., Urbanski, U., Bremer, D., Wofsy, S.C., Meyers, T., Gower, S.T., Gregory, M., 2003. A cross-biome comparison of daily light use efficiency for gross primary production. *Global Change Biol.*, 9, 383–395.
- Valentini, R., Gamon, J.A., Field, C.B., 1995. Ecosystem gas exchange in a California grassland: seasonal patterns and implications for scaling. *Ecology*, 76, 1940–1952.
- Wang, G.X., Qian, J., Cheng, G.D., Lai, Y.M., 2002. Soil organic carbon pool of grassland soils on the Qinghai-Tibetan Plateau and its global implication. *The Science of Total Environment*, 291, 207–217.
- Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapor transport. *Quarterly Journal of the Royal Meteorological Society*, 106, 85–100.
- Wilson, K., A. Goldstein, E. Falge, M. Aubinet, D. Baldocchi, P. Berbigier, C. Bernhofer, R. Ceulemans, H. Dolman, and C. Field, 2002, Energy balance closure at FLUXNET sites: *Agricultural and Forest Meteorology*, v. 113, p. 223-243.
- Xu, L., Baldocchi, D.D., 2004. Seasonal variation in carbon dioxide exchange over Mediterranean annual grassland in California. *Agric. For. Meteorol.*, 123, 79–96.
- Xu, L., Baldocchi, D.D., Tang, J., 2004. How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biol. Geo. Chem. Cycles*, 18, GB4002,doi:10.1029/2004GB002281.
- Yamamoto, S., Saigusa, N., Harazono, Y. et al., 2001. Present status of AsiaFlux Network and a view toward the future. *Extended Abstract, Sixth International Carbon Dioxide Conference*, Sendai, Japan, 404–407.

- Zeller, K.F., Nikolov, N.T., 2000. Quantifying simultaneous fluxes of ozone, carbon dioxide and water vapour above a subalpine forest ecosystem. *Environ. Pollution*, 107, 1–20.
- Zhao, K., 1999. *Marshes and Swamps of China: A Compilation*. Science Press of China Beijing.
- Zhao, X., Zhou, X., 1999. Ecological basis of alpine meadow ecosystem management in Tibet: Haibei Alpine Meadow Ecosystem Research Station, *Ambio*, 8, 642–647.
- Zhao, L., Li, Y.N., Gu, S., Zhao, X.Q., Xu, S.X., Yu, G.R., 2005a. Carbon dioxide exchange between the atmosphere and an alpine shrubland meadow during the growing season on the Qinghai-Tibetan plateau. *Journal of Integrative Plant Biology*, 47, 271–282.
- Zhao, L., Li, Y.N., Zhao, X.Q., Xu, S.X., Tang, Y.H., Yu, G.R., Gu, S., Du, M.Y., Wang, Q.X., 2005b. Comparative study of the net exchange of CO₂ in 3 types of vegetation ecosystems on the Qinghai-Tibetan Plateau. *Chinese Science Bulletin*, 50, 1767–1774.
- Zhao, L., Xu, S.X., Fu, Y.L., Gu, S., Li, Y.N., Wang, Q.X., Du, M.Y., Zhao, X.Q., Yu, G.R., 2005c. Effects of snow cover on CO₂ flux of northern alpine meadow on Qinghai-Tibetan plateau. *Acta Agrestia Sinica*, 13(3), 242–247.
- Zhao, L., Li, Y.N., Xu, S.X., Zhou, H.K., Gu, S., Yu, G.R., Zhao, X.Q., 2006. Diurnal, seasonal and annual variation in net ecosystem CO₂ exchange of an alpine shrubland on Qinghai-Tibetan plateau. *Glob. Change Biol.*, 12, 1940–1953.
- Zhao L., Xu S.X., Li Y.N., Tang, Y.H., Zhao, X.Q., Gu, S., Du, M.Y., Yu, G.R., 2007. Relations between carbon dioxide fluxes and environmental factors of *Kobresia humilis* meadows and *Potentilla fruticosa* meadows. *Front. Biol. China* 2007, 2(3), 1–9.

Tables

Table 1. Average daily values of photosynthetically active radiation (*PPFD*), air temperature (*Ta*), vapor pressure deficit (*VPD*), soil temperature (*Ts*:5 cm depth), total precipitation (*PPT*), ecosystem respiration (*R_{eco}*), gross primary production (*GPP*), and net ecosystem carbon exchange(*NEE*) for various periods during each year: Pre-growing period (1January to 20 April), Growing season (21 April to 26 October), Senescence (27 October to 31December), and Annual . Data were from 1January, 2004 to 31 December, 2006.

Period	Year	PPFD molm ⁻² d ⁻¹	Ta °C	Ts °C	VPD kPa	PPT mm	NEE gCm ⁻²	GPP gCm ⁻²	R _{eco} gCm ⁻²
Pre growing	2004	23.98	-9.4	-3.0	0.18	36.9	80.0	-	80.0
	2005	22.58	-8.3	-2.9	0.19	32.5	62.8	-	82.8
	2006	23.53	-9.2	-3.0	0.18	29.2	85.8	-	85.8
Growing	2004	30.51	5.6	6.9	0.66	446.9	-46.3	600.1	529.4
	2005	30.26	6.4	8.1	0.71	438.5	-73.0	710.3	671.9
	2006	29.68	6.4	8.4	0.71	529.0	24.8	631.0	659.9
Senescence	2004	17.88	-9.8	-1.1	0.17	9.8	67.4	-	67.4
	2005	17.36	-10.6	-1.7	0.15	4.2	55.0	-	55.0
	2006	17.05	-9.8	-1.1	0.18	4.2	63.8	-	63.8
Annual	2004	26.32	-1.5	2.34	0.43	493.5	101.1	575.7	676.8
	2005	25.66	-1.0	2.17	0.45	475.2	44.0	682.9	726.9
	2006	25.87	-0.8	3.58	0.47	562.4	173.2	631.0	808.2

Table 2. Published studied sites characteristics, environmental variables and carbon fluxes

Site	Latitude	Longitude	Elevation (m)	LAI m^2m^{-2}	Period	Ta $^{\circ}C$	GPP $\frac{g}{m^2} C y^{-1}$	NEE $\frac{g}{m^2} C m^{-1}$	R _{eco} $\frac{g}{m^2} C m^{-1}$	Reference
Alpine wetland meadow	37°35'	101°20'	3250	3.9	2004	-1.5	575.7	101.1	676.8	This Study
					2005	-1.0	682.9	44.0	726.4	
					2006	-0.8	631.0	173.2	808.2	
Alpine <i>Kobresia humilis</i> meadow	37°36'	101°20'	3250	3.8	2002	-0.7	575.1	-78.5	496.6	Kato et al. (2006)
					2003	-0.9	647.3	-91.7	555.6	
					2004	-1.5	681.1	-192.5	488.5	
Alpine shrubland meadow	37°36'	101°18'	3250	2.2	2003	-1.23	544.0	-58.82	485.2	Zhao et al. (2006)
					2004	-1.9	559.4	-75.46	483.9	
Mediterranean annual grassland	38°24'	120°57'	129	2.5	2000-2001		867	-131	735	Xu and Baldocchi (2004)
					2001-2002	16.2	729	29	758	
Sedge-dominated fen	74°28'N	20°34'W	1500	1.2	1996	-19.5	-	-64.4	-	Soegaard and Nordstroem (1999) Suyker et al. (1997)
Boreal minerotrophic patterned fen	53°57'N	105°57'W		1.3	Mid-day to early October 1994	9.2-28.2	-	-88	-	
Tussock tundra	68°38'	149°35'	732	-	1990	-	-	156	-	Oechel et al. (1993)
Wet sedge tundra	70°22'	148°45'	3	-	1990	-	-	34	-	Oechel et al. (1993)
Flakaliden	64.11	19.46	226	3.4	1997	3.0	699	-193	526	Law et al.(2002)
Glacier lake	41.37	-106.24	3186	2.5	1996	-0.7	407	195	212	Zeller and Nikolov (2000)
Metolius-intemEDIATE	44.45	-121.56	1310	2.96	1996-1997	8.7	454	27	481	Baldocchi et al.(2000)

Table 3. The monthly and annual average values (\pm SD) of *NEE*, *GPP*, and *R_{eco}* ($\text{gCm}^{-2}\text{d}^{-1}$). Data are from data are from January 2004 to December 2006, and the symbol (-) indicate the *GPP* was zero during the no growing season.

	January	February	March	April	May	June	July	August	September	October	November	December	Annual
<i>NEE</i>	0.49 \pm 0.18	0.61 \pm 0.30	0.72 \pm 0.35	1.32 \pm 0.59	1.17 \pm 0.49	0.22 \pm 0.77	-2.31 \pm 0.84	-1.46 \pm 0.85	0.05 \pm 0.76	0.90 \pm 0.62	1.02 \pm 0.27	0.77 \pm 0.32	0.29 \pm 1.20
<i>GPP</i>	-	-	-	0.10 \pm 0.38	0.95 \pm 0.51	3.43 \pm 1.03	5.55 \pm 1.04	5.76 \pm 0.94	3.39 \pm 1.00	1.33 \pm 0.84	-	-	1.72 \pm 2.25
<i>Reco</i>	0.49 \pm 0.18	0.61 \pm 0.30	0.72 \pm 0.35	1.42 \pm 0.60	2.12 \pm 0.48	3.66 \pm 0.81	3.29 \pm 0.54	4.31 \pm 0.92	3.44 \pm 0.58	2.29 \pm 0.97	1.02 \pm 0.27	0.77 \pm 0.32	2.02 \pm 1.43

Table 4. Characteristics of linear regression analysis [$y=ax+b$] of daily mean ecosystem respiration (*R_{eco}*, in $\text{umol m}^{-2}\text{d}^{-1}$) and gross primary productivity (*GPP*, in $\text{umolm}^{-2}\text{d}^{-1}$) vs. monthly mean air temperature (*T_a*, in $^{\circ}\text{C}$), and monthly mean soil temperature at the depth of 5cm for individual month and annual clusters; data are from January 2004 to December 2006.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
<i>GPP</i> vs. <i>T_s</i>													
r	-	-	-	0.181	0.109	0.493	0.382	0.559	0.742	0.785	-	-	0.939
a	-	-	-	0.161	0.032	2.025	0.150	0.369	0.450	0.409	-	-	0.333
b	-	-	-	0.121	0.835	0.228	3.784	0.942	-0.840	-0.427	-	-	0.741
<i>GPP</i> vs. <i>T_a</i>													
r	-	-	-	0.010	-0.059	0.589	0.409	0.525	0.521	0.644	-	-	0.793
a	-	-	-	0.001	-0.001	0.334	0.156	0.220	0.223	0.251	-	-	0.194
b	-	-	-	0.098	0.994	0.912	3.929	3.564	0.278	1.483	-	-	1.976
<i>R_{eco}</i> vs. <i>T_s</i>													
r	0.077	0.447	0.057	0.658	0.419	0.829	0.784	0.714	0.642	0.673	0.573	0.474	0.907
a	0.018	0.137	0.013	0.946	0.119	0.302	0.158	0.460	0.227	0.399	0.328	0.095	0.211
b	0.613	1.124	0.718	1.552	1.684	1.802	1.416	-1.713	1.303	0.575	0.974	1.071	1.407

The bold number indicated those are statistically significant ($P<0.05$) and r is the correlation coefficient. Symbol (-) stand for the value of *GPP* was zero during the non-growing season.

Table 5 Characteristics of linear regression analysis [$y=ax+b$] of daily net CO_2 ecosystem exchange (*NEE*, in $\text{umol m}^{-2}\text{d}^{-1}$) vs. monthly mean air temperature (*T_a*, in $^{\circ}\text{C}$), and monthly

mean soil temperature at the depth of 5cm for different growth stage; data are from January 2004 to December 2006.

Seasonal periods	<i>NEE</i> vs. T_a				<i>NEE</i> vs. T_s			
	r	a	b	p	r	a	b	p
January-April	0.551	0.039	1.112	<0.001	0.600	0.039	1.112	<0.001
May-September	-0.642	-0.263	1.483	<0.001	-0.670	-0.263	1.483	<0.001
October-December	0.206	0.015	1.026	<0.001	0.215	0.015	1.026	<0.001

Table.6 The multi-factor regression analysis of CO₂ flux (*GPP*, *NEE*, *Reco*) vs. T_a , T_s , PPFD, VPD, the data is on the annual base.

	T_a	T_s	VPD	PPFD	intercept	R ²	P
<i>GPP</i>	-0.113	0.212	5.344	0.002	-2.411	0.871	<0.001
<i>NEE</i>	0.119	-0.050	-4.571	-0.002	3.474	0.522	<0.001
<i>R_{eco}</i>	0.013	0.170	0.530	0.0004	1.312	0.828	<0.001

Figure Legends

Fig. 1 Seasonal variability of (a) photosynthetically active radiation (*PPFD*), (b) average daily air temperature (T_a), (c) soil temperature at the depth of 5 and 40 cm (T_s), (d) vapor pressure deficit (*VPD*), and (e) daily total precipitation (*PPT*).The lines are plotted from January 1.

Fig.2 Response of ecosystem respiration (R_{eco}) to change in soil temperature at the depth of 5 cm during growing season. Data were half-hourly under high turbulence conditions ($u^* > 0.1 \text{ms}^{-1}$) from 2004 to 2006.

Fig. 3 Response of ecosystem respiration (R_{eco}) to variety of soil temperature at the depth of 5 cm during non-growing season. Data were half-hourly under high turbulence conditions ($u^* > 0.1 \text{ ms}^{-1}$) from 2004 to 2006.

Fig. 4 Relationship between photosynthetic photon flux density ($PPFD$) and the gross primary production (GPP) from May to September. Fitted curves are exponentially for July and August, linear described in $GPP = b + a \times PPFD$ for May, June and September. Positive values denote CO_2 assimilation by the canopy. Data were from 6:00-13:00(BST).

Fig.5 Linear regression of daytime gross primary production (GPP) on incident photosynthetic photon flux density ($PPFD$). Data were from 13:00-20:00. The regression follows a linear relationship: $GPP = b + a \times PPFD$. Monthly values are presented as follows: month (a, r^2) — May (0.00015, 0.10**), June (-0.00002, 0.01 n.s.), July (0.00017, 0.25**), August (0.00016, 0.26**) and September (0.00006, 0.04**). The linear relationships were significant at** $P < 0.01$ level of correlation coefficients. The term n.s. shows insignificant linear relationships.

Fig. 6. The relationship of daily total gross primary production (GPP) and leaf area index (LAI). Data were obtained from the growing period in 2003.

Fig. 7. Examples of influence of rain events on the ecosystem respiration (R_{eco}) during 1 October 2004 to 10 February 2005. Data are the daily total R_{eco} and precipitation (PPT).

Fig. 8. Examples of 10-day binned diurnal variations in CO_2 flux (F_c) and soil temperature during non- growth periods. (DOY101–110, and DOY301–310, 2005.) Error bars represent the standard deviation.

Fig. 9. Examples of 10-day binned diurnal variations in CO₂ flux (*NEE*) and photosynthetic photon flux density (*PPFD*) during growing periods. (DOY151–160, and DOY206–215, 2005.) *LAI* was around 2.2 and 3.2, respectively. Error bars represent the standard deviation.

Fig. 10. Seasonal pattern of daily total gross primary production (*GPP*), net ecosystem exchange (*NEE*), and ecosystem respiration (*R_{eco}*) over the course of the alpine wetland meadow from 1 January 2004 to the end of the year 2006.

Fig. 11. Cumulative gross primary production (*GPP*), net ecosystem exchange (*NEE*), and ecosystem respiration (*R_{eco}*) over the three seasons.

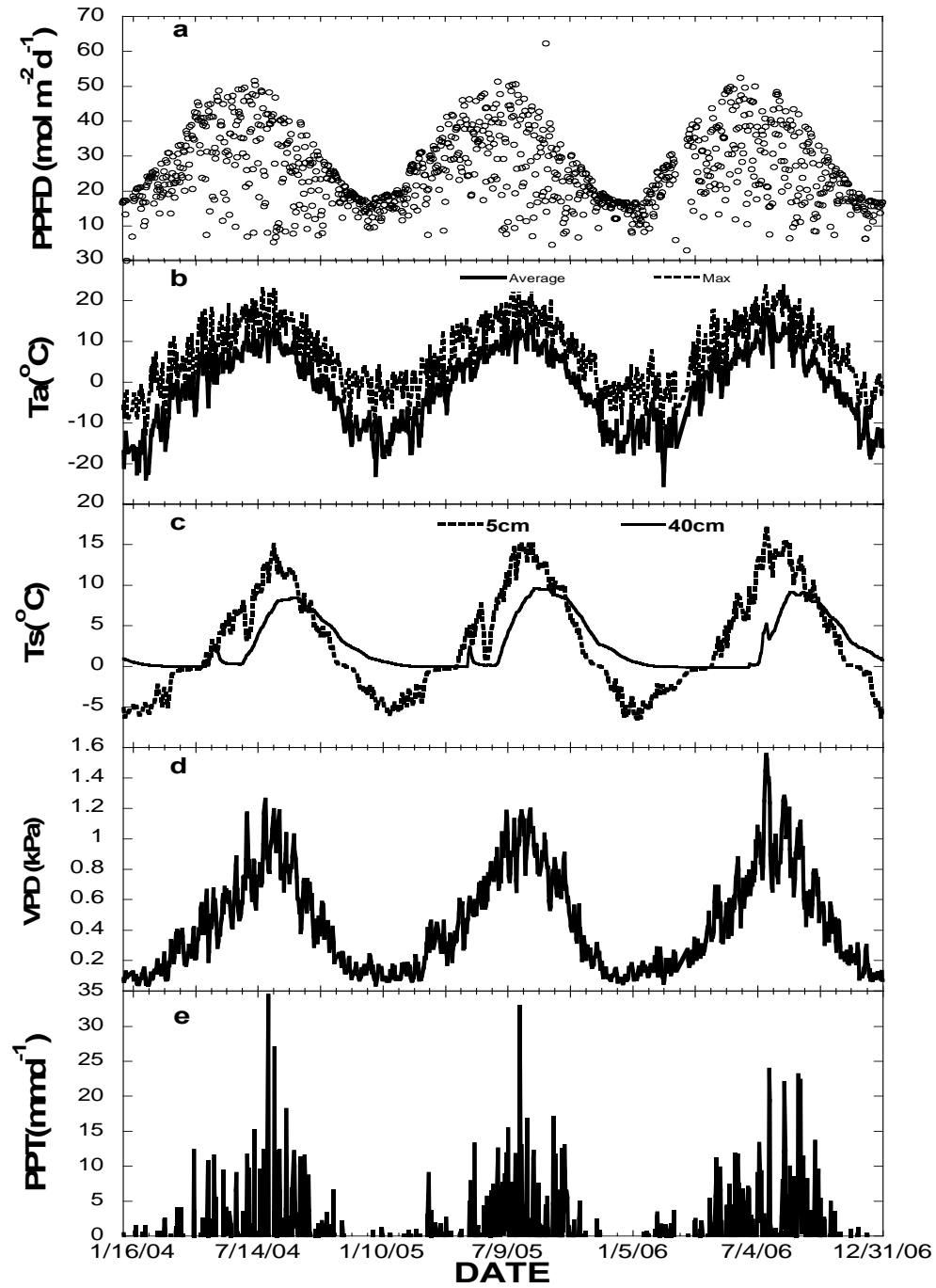


Fig. 1 Seasonal variability of (a) photosynthetically active radiation (*PPFD*), (b) average daily air temperature (*Ta*), (c) soil temperature at the depth of 5 and 40 cm (*Ts*), (d) vapor pressure deficit (*VPD*), and (e) daily total precipitation (*PPT*). The lines are plotted from January 1 to December 31.

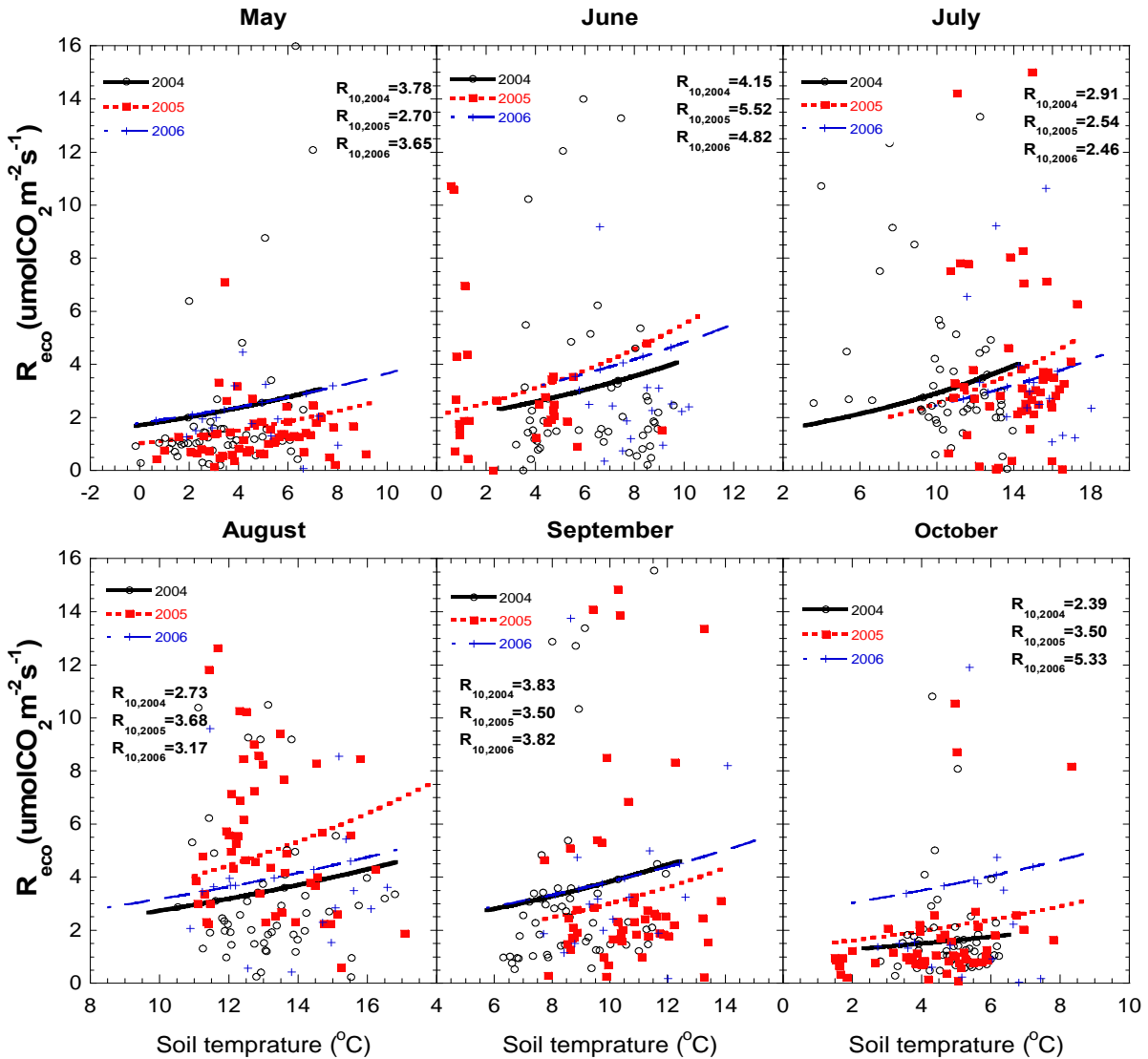


Fig.2 Response of ecosystem respiration (R_{eco}) to change in soil temperature at the depth of 5 cm during growing season. Data were half-hourly under high turbulence conditions ($u^* > 0.1\text{ms}^{-1}$) from 2004 to 2006.

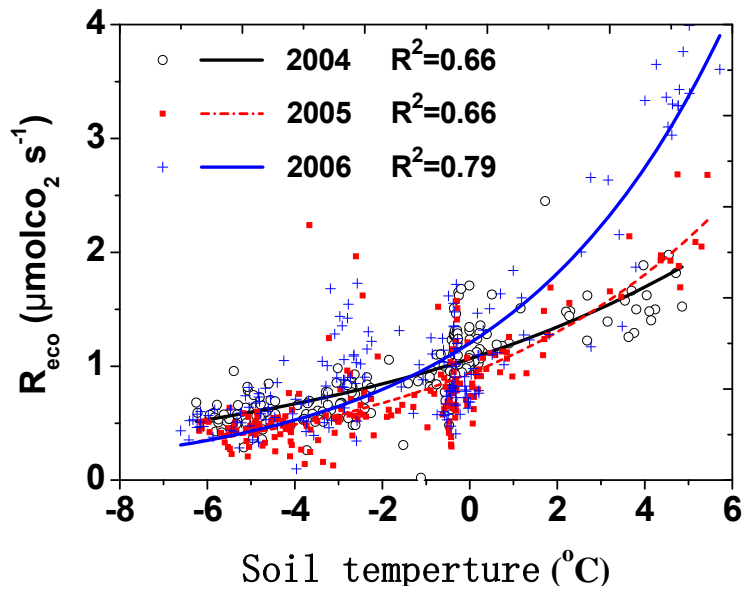


Fig. 3 Response of ecosystem respiration (R_{eco}) to change in soil temperature at the depth of 5 cm during non-growing season. Data were half-hourly under high turbulence conditions ($u^* > 0.1 \text{ms}^{-1}$) from 2004 to 2006.

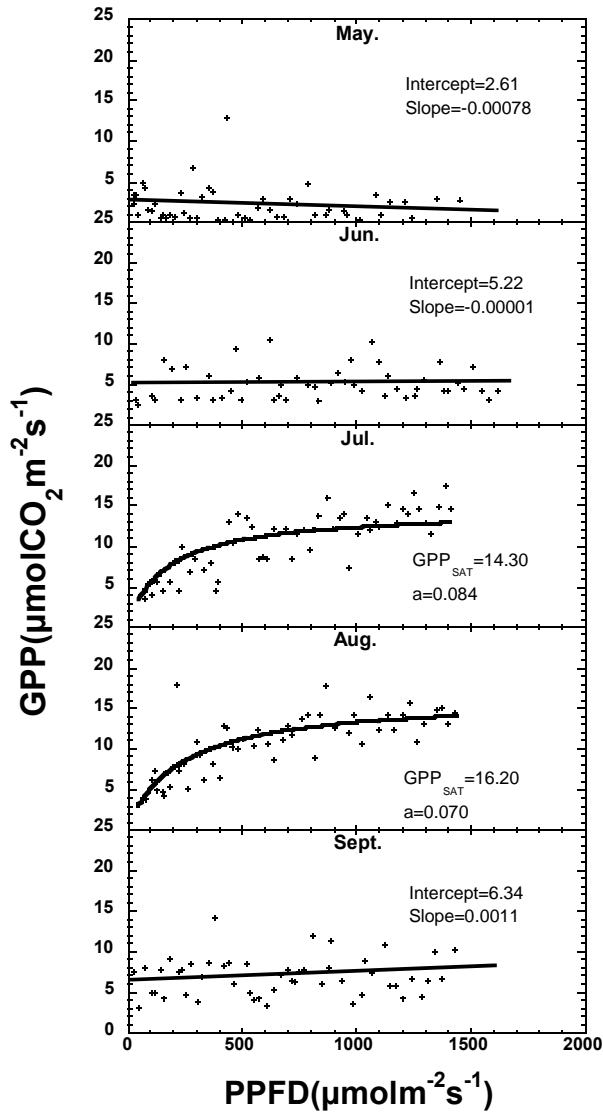


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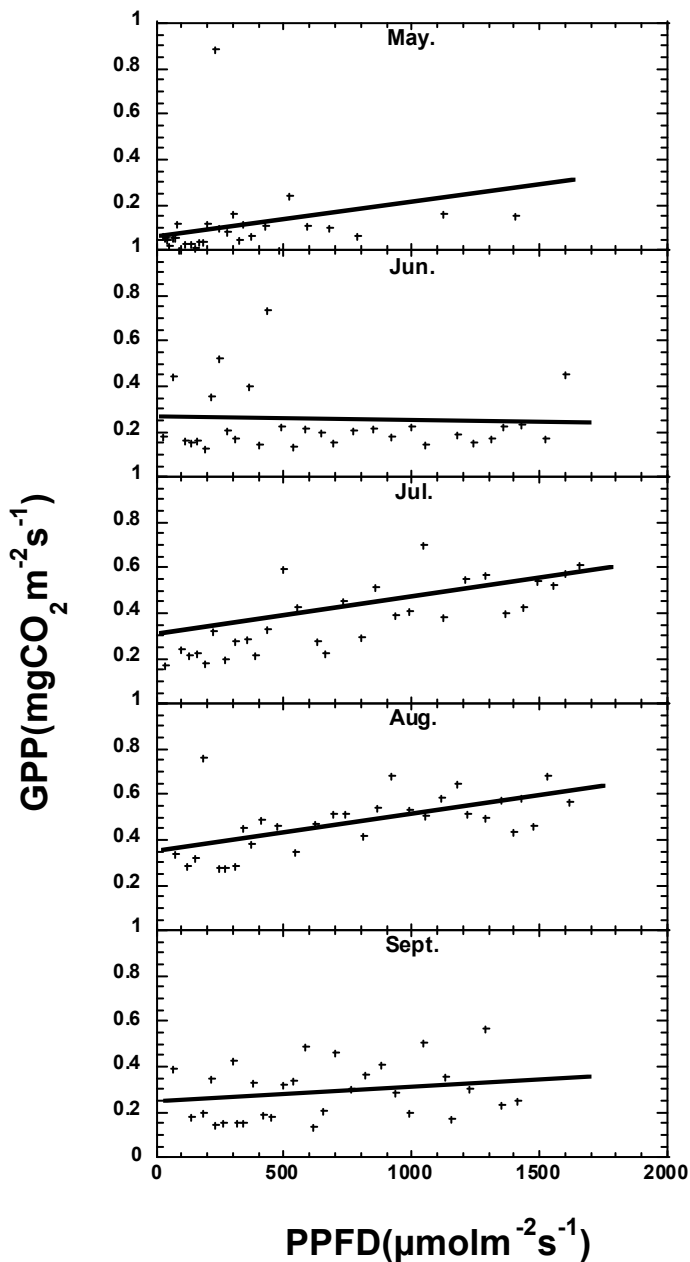


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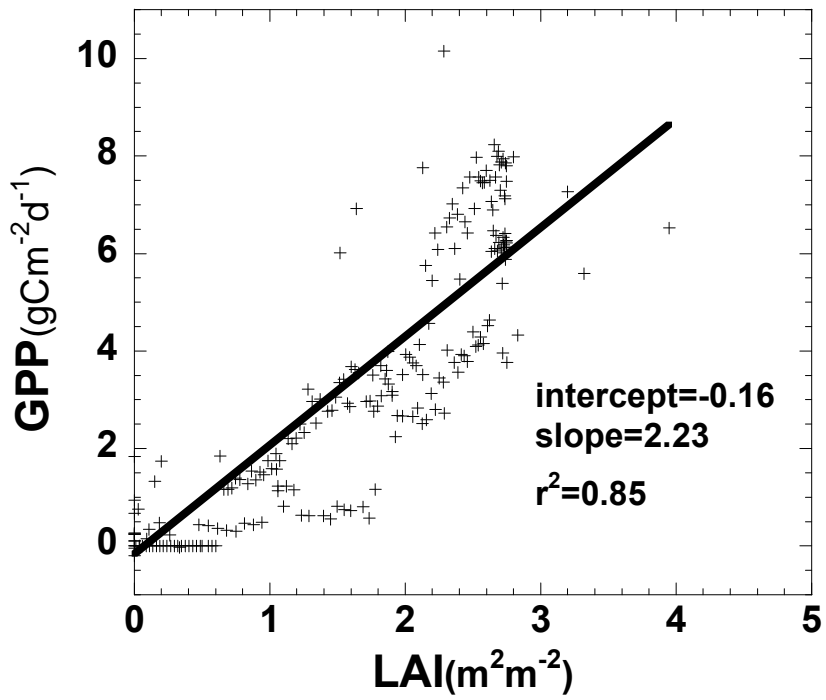


Fig. 6 The relationship of daily total gross primary production (*GPP*) and leaf area index (*LAI*).
Data were obtained from the growing period in 2003.

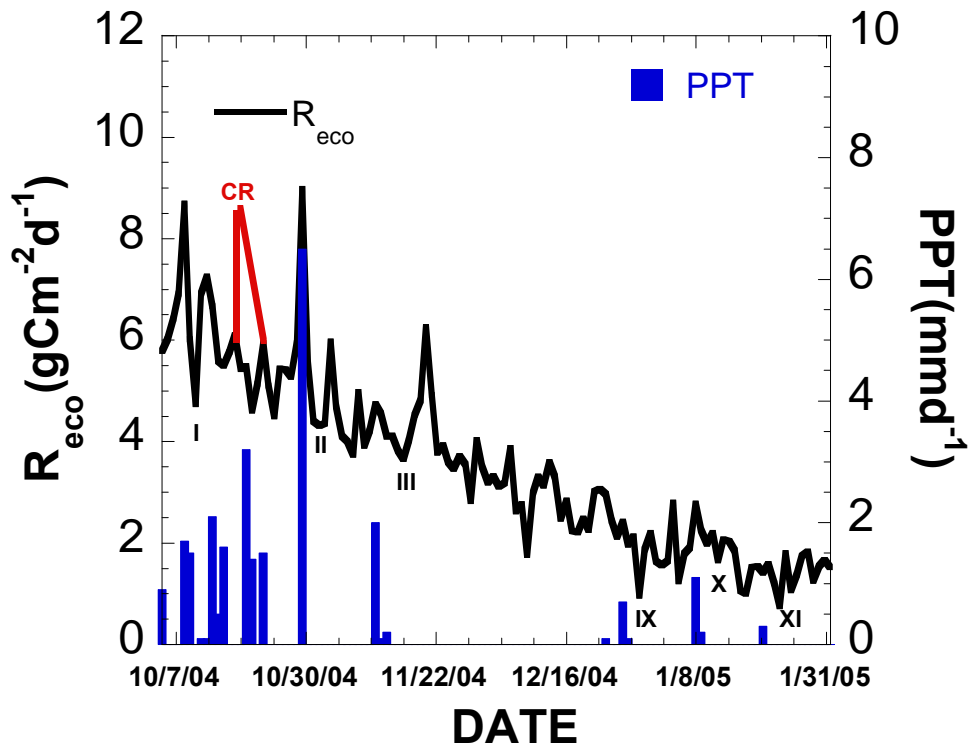


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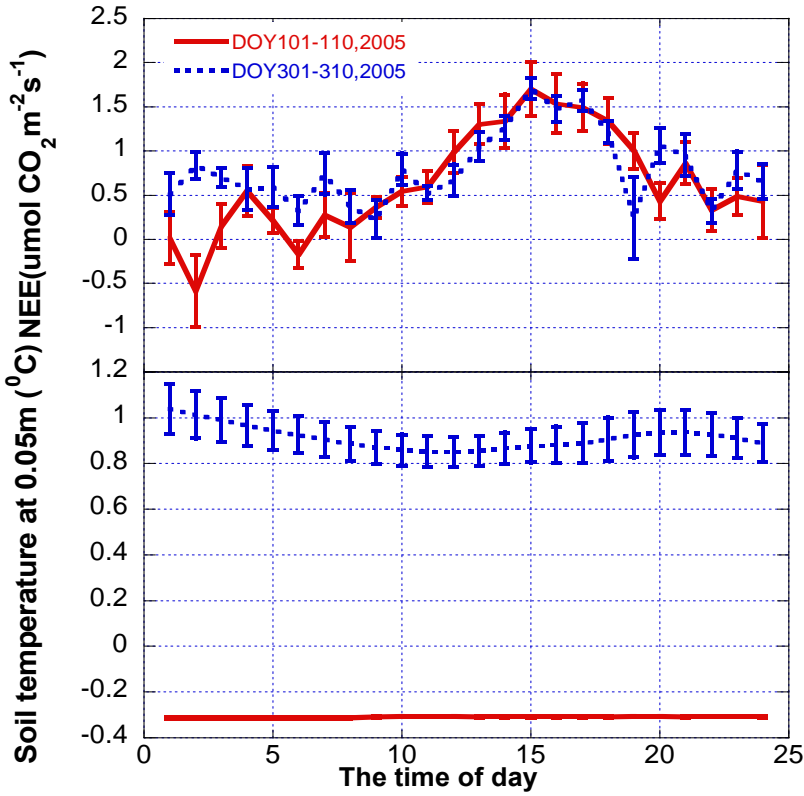


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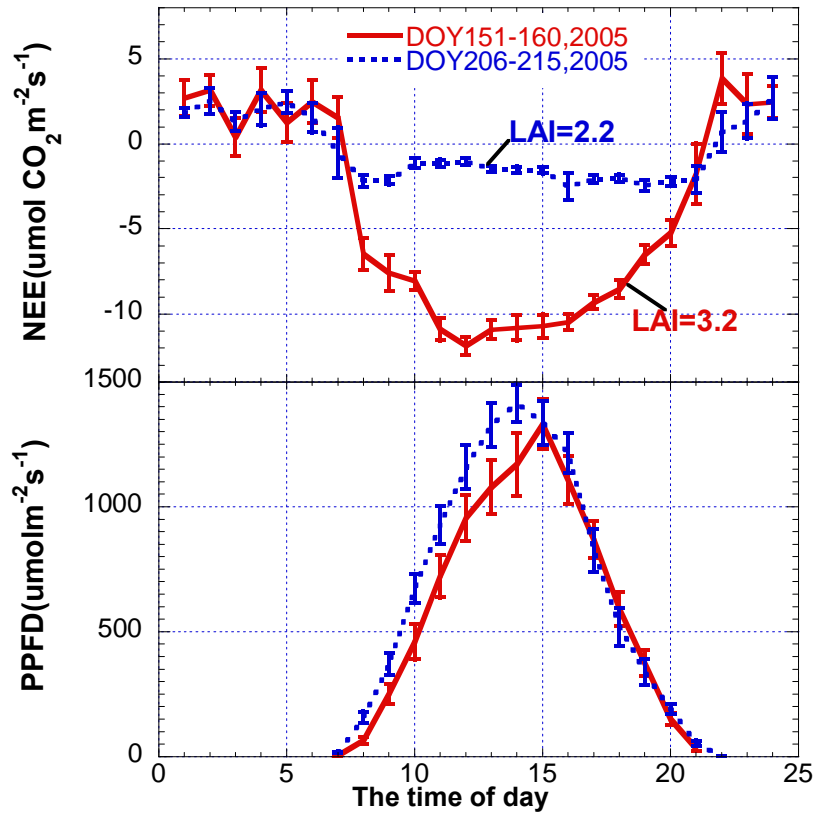


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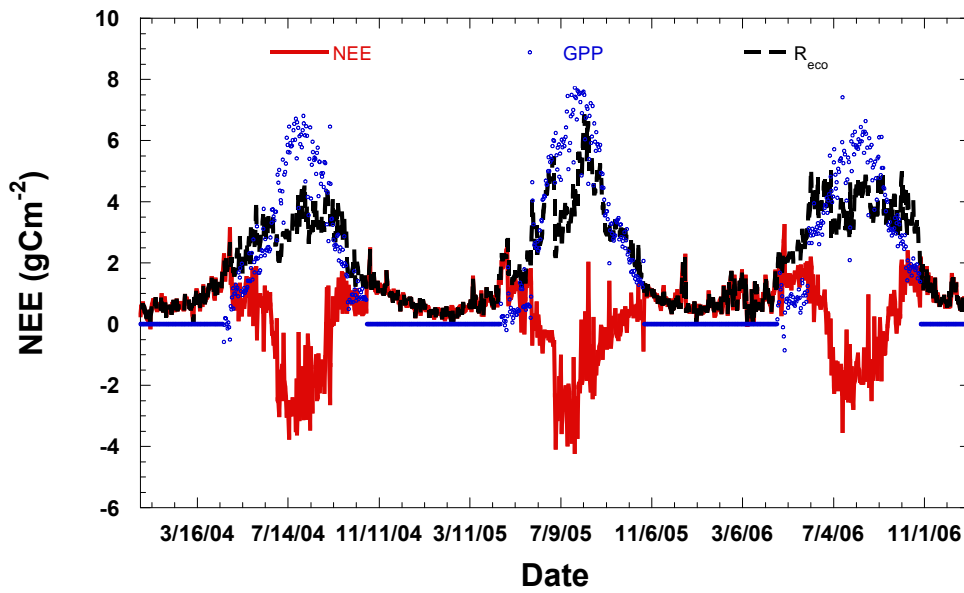


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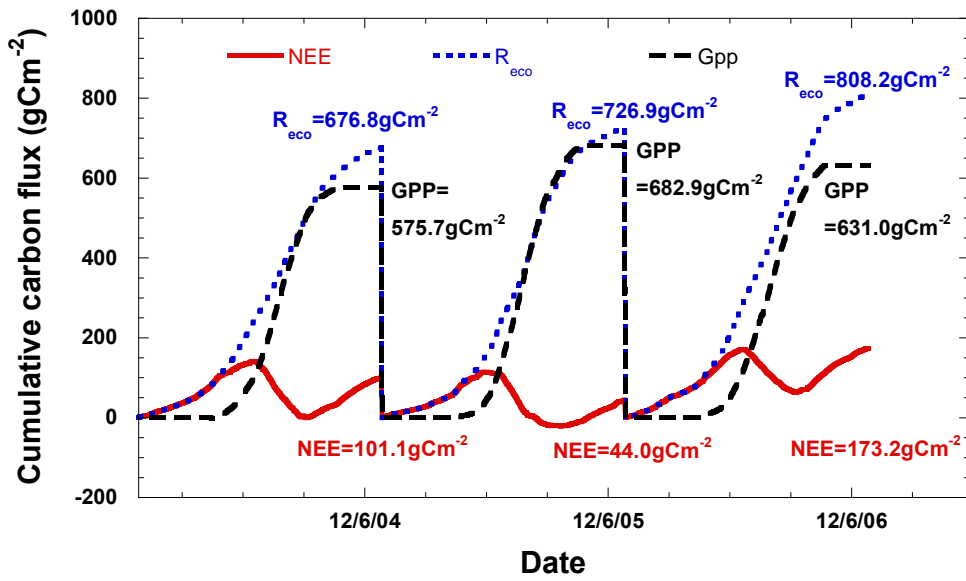


Fig. 11. Cumulative gross primary production (GPP), net ecosystem exchange (NEE), and ecosystem respiration (R_{eco}) over the three seasons.