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Discussions**

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 dor-
5   mant 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 important 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 CO_2 Exchange (NEE) were
10   examined for an alpine wetland meadow at the Haibei Research Station of the Chinese Academy of Sciences. The measurements covered three years and were made using the eddy covariance method. Seasonal trends of both GPP and R_{eco} followed closely changes in Leaf Area Index (LAI). R_{eco} exhibited the same exponential variation as soil temperature with seasonally-dependent R_{10} (the ecosystem respiration
15   rate (μmol CO_2 m^{-2} s^{-1}) at the soil temperature reach 283.16 K (10°C)). Yearly average GPP, R_{eco}, and NEE (which were 575.7, 676.8 and 101.1 gCm^{-2}, respectively, for 2004 year, and 682.9, 726.4 and 44.0 gCm^{-2} for 2005 year, and 630.97, 808.2 and 173.2 gCm^{-2} for 2006 year) values indicated that the alpine wetland meadow was a moderately important source of CO_2. The observed carbon dioxide fluxes in this alpine
20   wetland meadow plateau are high in comparison with other alpine meadow environments such as *Kobresia humilis* meadow and shrubland meadow located in similar areas. And the cumulative NEE data indicated that the alpine wetland meadow is a source of atmospheric CO_2 during the study years. CO_2 emissions are large on elevated microclimatology areas on the meadow floor regardless of temperature. Fur-
25   thermore, relatively low R_{eco} levels occurred during the non-growing season after a late rain event. This result is contradicted observations in alpine shrubland meadow. The timing of rain events had more impact on ecosystem GPP and NEE.

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1 Introduction

Estimates of global wetland area vary between 5.3 and 6.4 Mkm^2 (Matthews and Fung, 1987; Lappalainen, 1996). Northern wetlands play an important role in the global carbon cycle. Development of such wetlands has reduced atmospheric CO_2 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). Wetlands characterized by deep organic soils have been accumulating carbon for 4000–5000 years. Temperature increase due to climate change and drainage of wetlands may provide conditions that will 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 km^2; 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, 2007; Kato et al., 2006). 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, an 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. The rate of decomposition of organic carbon, i.e., the CO_2 flux from the plateau, is high because of the rich organic carbon load in 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 been conducted in alpine *K. humilis* meadow or *P. fruticosa* shrubland ecosystems (Kato et al., 2006; Zhao et al., 2005a, 2005b, 2006). Much less attention has been given to CO_2 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 the world's other high-altitude grassland ecosystems.

Eddy covariance technology provides a reliable way of measuring the net CO_2 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 measured the CO_2 exchange between the atmosphere and the ecosystem from January 2004 to December 2006 in an alpine wetland meadow on the Qinghai-Tibetan Plateau, using the eddy covariance method. The aims of this study were to (1) understand more fully the complex interrelationship between climate and phenology and their influence on CO_2 flux; (2) explore the causes of interannual variability of CO_2 flux; (3) examine how CO_2 cycle will change under different climatic conditions.

2 Materials and methodology

2.1 Site description

Measurements were conducted in an alpine wetland meadow at the Haibei Research Station, Chinese Academy of Sciences, in Qinghai, China (37°35′ N, 101°20′ E, 3250 m a.s.l.) from October 2003 to December 2006. The eddy covariance method was used to examine carbon dynamics and variability. This wetland is characterized by non-patterned, hummock-hollow terrain, with hummocks representing 40%, hollows 55%, and other features 5% of the landscape. The catchment was flooded at an average water depth of 30 cm during the growing season. Wetland vegetation was 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 recoded 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 starts to green at the end of April or the beginning of May, depending on the year. The aboveground biomass increases from May to August and reaches a maximum in late July or August, becoming senescent in early October. 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 1 October 2003 to 31 December 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, USA) and an open-path infrared gas analyzer (CS7500, Campbell Scientific Inc.). Wind speed, sonic virtual temperature, and CO_2 and H_2O concentrations were sampled at a 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, USA). The collected data were then 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 fluctuation 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 CO_2 flux calculations. The regression line slopes 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 CO_2/H_2O analyzer system was calibrated on 10 May 2004, 15 May 2005 and 11 May 2006, respectively. Zero points were established using 99.999% N_2 gas, the CO_2 span was calibrated using a standard gas bottle of CO_2, 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 CO_2 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 as insignificant.

Mean air temperature (T_a), humidity, wind speed, Photosynthetic Photon Flux Density (PPFD), net radiation (R_n), soil heat flux (G), and soil temperature (T_s) 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. There is a good agreement between half-hourly values of turbulent ($H+LE$) and radiative (R_n+G) fluxes. The slope of regression line is 0.74 with an intercept of 22.45 W m^{-2} and a correlation coefficient, r^2, of 0.94. This slope was falls 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 become accepted as an important new test of eddy covariance (Mahrt, 1998).We were not trying to specify a particular cause for the imbalance because several possibilities may be involved in the lack of energy closure (for details see Wilson et al., 2002).

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 using exponential regression Eq. 2) between measured nighttime R_{eco} with strong turbulence ($u^*>0.1$ ms^{-1}, Aubinet et al., 2000; Lloyd, 2006), and soil temperature at 5-cm 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 using a 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):

$$F_c = \frac{F_{\max} \cdot \alpha \cdot Q_p}{F_{\max} + \alpha \cdot Q_p} + R_{\text{eco}} \, , \tag{1}$$

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

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

where R_{eco} is the nighttime ecosystem respiration rate ($\mu\text{mol CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$), $R_{e,\text{Tref}}$ 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 J K^{-1} mol^{-1}), and T_{soil} is the soil temperature at a depth of 5 cm. $R_{e,\text{Tref}}$ 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_{soil} as a constant value throughout each year (for 2004, 2005, and 2006, the values were 50 093.43, 61 084.73, and 44 743.55 J mol^{-1}, respectively).

GPP was calculated as the sum of NEE (net ecosystem production as CO_2 uptake, i.e., NEE) and R_{eco}, as follows:

$$\text{GPP} = -\text{NEE} + R_{\text{eco}}. \tag{3}$$

3 Results

3.1 Information on weather conditions, biomass, and leaf area

Figure 1 shows daily PPFD, average air temperatures at a height of 2.2 m, average soil temperatures at depths of 3 cm, 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 3 cm depth), and 0 to 8.5°C (soil temperature at 40 cm depth), with maximum temperatures recorded from the end of July to the beginning 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 (year-to-year 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 that in 2005, but slightly less than in 2006 (Table 1). Above-ground biomass increased from mid-April (DOY 100) each year and reached a maximum of 305.3~335.6 g m^{-2} during late August. Maximum Leaf Area Index (LAI) tracked green biomass and ranged about 3.9 m^2 m^{-2} in 2005.

3.2 Response of R_{eco} to temperature

A specific response curve for every month of the growing period was developed (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). During the growing season, 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 was highly active (July and August, Fig. 2). Figure 3 shows the relationship between R_{eco} and soil temperature (at 5 cm) in the non-growing season. R_{10} values were estimated

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to be 2.7, 2.7, and 2.6 in 2004, 2005, and 2006, respectively. Those values were 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 R_{10} was 3.05, 2.98, and 3.24 μmol Cm^{-2} s^{-1} for 2004, 2005, and 2006, whereas the values for annual active energy (E_a) were 50 093.43, 61 084.73, and 44 743.5 J mol^{-1}, respectively. Thus, the temperature dependence was higher in 2004 and 2006 than in 2005.

3.3 GPP in relation to PPFD

Figure 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 daytime hours, the GPP slightly decreased as PPFD increased. The values of GPP increased from June to August when compared for constant PPFD. In September, however, the dependence of GPP on PPFD did not change greatly, despite the increase in LAI.

Based on statistical analysis using Eq. (1), GPP$_{\mathrm{SAT}}$ values for July and August were 14.30 and 16.21 μmol m^{-2} 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 much higher than the values from other eddy covariance studies in temperate C_3 grassland (Flanagan et al., 2002). Quantum yield values measured in the alpine wetland were higher than the values reported in Zhao et al. (2006) (0.0056 and 0.0082 for July and August, respectively) for near site in the alpine shrubland meadow on the Qinghai-Tibetan Plateau. However, photosynthetic capacity is smaller than that in the alpine shrubland meadow (17.93 and 20.54 μmol m^{-2} s^{-1} for July and August, respectively), probably due to larger canopy size, more vascular plants, and the presence of enough moisture.

Before 01:00 p.m. (Beijing Standard Time, BST) at the study site, light response in-

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creased with increasing PPFD values, up to 830 μmol m^{-2} s^{-1} (Fig. 4), and then started to decline. These results indicate a decrease in light-use efficiency when PPFD increases. This result is probably due to enhanced ecosystem respiration with increasing temperature: at afternoon the soil respiration increased as the temperature increased.

In the afternoon, the values of GPP responded linearly to PPFD (GPP=b+a×PPFD) during all months, with small a (Fig. 5).

3.4 GPP in relation to LAI, R_{eco} and depth of water table (D_{WT})

The highest rate of GPP occurred during the period of greatest LAI in all years, and GPP decreased with decreasing LAI. Figure 6 illustrates the role of LAI in controlling GPP. In general, GPP increased by about 2.23 gCm^{-2} per day for each unit increase in LAI. A few studies have presented information on GPP and R_{eco} (Law et al., 2002; Xu and Baldocchi, 2004). When R_{eco} was plotted against GPP, a strong linear relation was observed (r^2=0.82, Fig. 7). This result indicates that there was a high R_{eco} along with large GPP.

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 poor (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 5 October 2004 to 1 February 2005, are presented in Fig. 8. The I rain event occurred on 9 October 2004, with total precipitation of only 1.7 mm/day (Fig. 8). On 11 October, R_{eco} suddenly decreased to 4.74 gCm^{-2} per day from the background level of 8.70 gCm^{-2} per day observed on the previous day. Then in just two days, R_{eco} increased to 7.25 gCm^{-2}

per day, as observed on 13 October. After the II rain event (6.5 mm rainfall), R_{eco} again greatly decreased from 8.98 gCm^{-2} per day on 30 October to 4.40 gCm^{-2} per day on 1 November. After the X rain event (1.1 mm) on 8 January 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. 8).

3.6 Diurnal variations in NEE

Seasonal variations in the diurnal patterns of NEE change can provide insights into how PPFD and LAI interact to control photosynthesis and respiration. Diurnal sequences of mean NEE and PPFD values from different growth periods are presented in Figs. 9 and 10 to illustrate this point; 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 in any case is very small (Fig. 9). During the two periods, CO_2 release typically occurs. Comparing the release rates in both periods, it was clear that the differences in amplitude of the diurnal variations in NEE between periods were very small. It can also be noted from Fig. 9 that NEE from 01:00 p.m. to 05:00 p.m. 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 moves from a positive value (release) to a negative value (uptake). The uptake rate is highest around noon and begins to decrease afterwards. At dusk, NEE moves 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 be-

tween 11:00 a.m.–12:00 noon and 04:00–05:00 p.m., respectively. The maximum net CO_2 uptake for the two growing periods, -2.5 and $-11.5\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$, respectively, indicated that the diurnal variations in NEE depended mainly on LAI. Figure 10 shows that nighttime R_{eco} was much higher in the peak growth stage (DOY 206–215) than in the early season (DOY 151–160), reflecting the importance of photosynthetic activity for ecosystem respiration (Xu et al., 2004). We compared the observed maximum values of CO_2 uptake with those at other sites located in similar latitudes. The maximum CO_2 uptake observed in this research was slightly larger than that for alpine *K. humilis* meadow ($-10.8\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$; Kato et al., 2004a) and for alpine shrubland meadow ($-10.87\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$; Zhao et al., 2005) in the same latitudes. The values fall 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 $-8\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ in serpentine grassland in California. By contrast, much higher maximum rates of CO_2 uptake (between -30 and $-40\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$) 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

Figure 11 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 late May. Then as the temperature warmed up and LAI and day length increased, GPP and R_{eco} increased at a faster rate in June, July, and August, making the ecosystem a strong carbon sink. The daily maximum net CO_2 uptake ($-3.9\,\text{gCm}^{-2}$ per day), is within the observed range for other alpine meadow ecosystems at similar latitudes (-1.7 to $-5\,\text{gCm}^{-2}$ per day; Kato et al., 2004a; Zhao et al., 2006). The maximum net CO_2 uptake observed in this

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research was 20–55% less than values observed for tallgrass prairies in Kansas, California, and Oklahoma, United States (-4.8 to $-8.4\,\text{gCm}^{-2}$ 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 ($-1.0\,\text{gCm}^{-2}$ per day) at similar altitude (3050 m). GPP and R_{eco} plummeted to near-zero values about 26 October. After grass senescence, the grassland continuously lost carbon via soil respiration, but at a very low rate (0.3–$0.9\,\text{gCm}^{-2}$ per day) due to the low soil temperature.

The authors observed slightly different 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 $0.72\,\text{Cgm}^{-2}$ per day and $0.76\,\text{Cgm}^{-2}$ per day, respectively, compared to $0.58\,\text{Cgm}^{-2}$ per day in 2005 (Fig. 11). 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} of $1.00\,\text{gm}^{-2}$ per day in 2004 and of $0.95\,\text{gm}^{-2}$ per day in 2006 were higher than the value of $0.83\,\text{gm}^{-2}$ per day in 2005, a difference probably caused by the difference in soil temperature.

GPP reached a maximum value of 7.15–$10.15\,\text{gCm}^{-2}$ per day during mid-August. Information on cumulative carbon exchange (GPP, R_{eco}, and NEE) for the alpine wetland meadow from 1 January 2004 to 31 December 2006, is shown in Fig. 12. Since the growing season for the grass does not extend across two calendar years, cumulative GPP and NEE values were computed over the calendar year. As shown in Fig. 12, GPP, R_{eco}, and NEE were 575.7, 676.8, and $101.1\,\text{gCm}^{-2}$ for 2004, 682.9, 726.4 and $44.0\,\text{gCm}^{-2}$ for 2005, and 631.0, 808.2, and $173.2\,\text{gCm}^{-2}$ 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.

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4   Discussion

A seasonal variation occurred in NEE, which is the difference between two large CO_2 fluxes of CO_2 release by R_{eco} and CO_2 uptake 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. 11). Opposite patterns of R_{eco} and GPP caused this seasonal variation in NEE.

4.1   Gross primary production (GPP)

The daily maximum GPP showed a pattern of seasonal variation similar to the daily mean GPP. The relationship between GPP and PPFD as shown in Fig. 4 resulted from the fact that LAI was so small that the rate of canopy photosynthesis was smaller 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 increase in LAI from 0.09 (7 May) to 3.95 (16 July) and the corresponding increase of leaf-level photosynthetic capacity. However, in September, the dependence of GPP on PPFD did not changed greatly, despite the LAI increased. That 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 when compared 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 diurnal fluctuation of GPP, the differences between before noon and afternoon ($GPP_{rate,\ before\ noon} > GPP_{rate,\ afternoon}$) indicated that there apparently was no PPFD saturation in the afternoon (Figs. 3 and 4). This observation is consistent with GPP status in the morning, and probably due to enhanced ecosystem respiration with increasing temperature in the morning, whereas in the afternoon, ecosystem respi-

ration is more nearly constant because the temperature of the soil surface does not change very much.

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. The linear relation between GPP and R_{eco} are in agreement with a number of recent studies that have demonstrated a close linkage between photosynthetic activity and respiration (Xu et al., 2004). 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 was girdled. Thus, the exponential function for ecosystem respiration holds for a limited time period when LAI and soil moisture are similar. 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 CO_2 uptake, the GPP/LAI values calculated for this meadow ecosystem were 2.8–3.6 Cm^{-2} per day, higher than 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 C_3 grassland near Alberta, Canada, but the maximum GPP values obtained here were lower than values reported for a tallgrass prairie and mid-latitude deciduous forest (19 and 16 gCm^{-2} per day respectively; Turner et al., 2003). The 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), was larger than that for 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 contributed 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 alpine wetland had a daily CO_2 assimilation equal to that of a 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 that their seasonal variations were associated more closely with the seasonal pattern of soil temperature than with that of PPFD (Fig. 1). R_{eco}, however, increased even though soil temperature decreased

during the same period, as seen by changes in R_{10} (Figs. 2, 3). In general, seasonal changes in respiratory processes are controlled by climatic factors more strongly than by 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 within the range (1.8–6.1) of the numerous observations for R_{10} in wetlands reported in literatures (Svensson, 1980; Chapman and Thurlow, 1996; Silvola et al., 1996). These values for R_{10} are based on seasonal changes in soil temperature; the temperature dependence 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 is caused by different vegetation and soil organic matter. This values outside the range (1.3–3.3) 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 reflects different temperature sensitivities for 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 for the three months of April, May, and 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 those obtained for alpine meadow (1.60–1.89 μmol C m^{-2} s^{-1}) by Kato, et al. (2006) and showed that the effects of temperature change on ecosystem respiration in the wetland meadow were larger than that in 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 loca-

tion. However, recently Lloyd (2006), using 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} to depths of 0.3–0.4 m. In this case, as D_{WT} increased, the air-filled porosity also increased, supporting greater aerobic degradation of peat. In the current research, while D_{WT} varied little at the field site, the site was generally waterlogged. Therefore, oxygen availability in peat would have been fairly constant, and D_{WT} therefore 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 the findings of others (Zhao et al., 2006). These different conclusions regarding the coupling between R_{eco} and rain events may explain the differences of opinion regarding the coupling between R_{eco} and rain events may explain the differences of opinion regarding 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. From this, 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 (>2 mm per day), small pulses of increased R_{eco} were observed immediately. After the CR rain event, the increases in R_{eco} were in the range of 0.7–1 gCm^{-2} per day. 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 CO_2 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), that of our study site (44.0–173.2 gCm^{-2}), was a source of atmospheric CO_2 for the alpine wetland meadow, yet, *Kobresia humilis* meadow and alpine shrubland meadow of which climate is 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. We suppose that not only high soil organic matter (wetland: 28.06%; shrubland: 7.54%; *Kobresia humilis* meadow: 5.19%, Zhao et al., 2005b) but also relatively low grazing intensity (wetland: 38.8–62.6%; *Kobresia humilis* meadow: 82.7–87.1%) promote ecosystem respiration, as a result, this ecosystem may release a substantial amount of C. 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 is similar to that observed in other northern ecosystems. The calculated whole-year NEE is similar to those obtained from other wetland sites and falls within the range of data reported elsewhere in the literature (Table 2). For example, in a high-Arctic location in northern Alaska, Coyne and Kelly (1975) observed a net seasonal uptake of 40 $gCm^{-2}y^{-1}$, while Suyker et al. (1997) measured a net uptake of 88 gCm^{-2} for a period from mid-May to early October in boreal fen. The most significant carbon loss for wet Arctic ecosystems through CO_2 exchange has been reported by Oechel et al. (1997) for both tussock (122 $gCm^{-2}y^{-1}$) and wet sedge tundras (25.5 $gCm^{-2}y^{-1}$), and by Oechel et al. (1993), 156 $gCm^{-2}y^{-1}$ for a tussock tundra and 34 $gCm^{-2}y^{-1}$ 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 $gCm^{-2}y^{-1}$ respectively by Oechel and Billings (1992), and a sedge-dominated fen at Zackenberg has been observed to be a

sink with uptake of $64.4\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$ (Soegaard and Nordstroem, 1999).

5   Conclusions

The conclusions that can be drawn from the current research can be summarized as follows: (i) seasonal trends in both GPP and R_{eco} followed closely the changes in LAI. R_{eco} followed the exponential variation of soil temperature with seasonally-dependent R_{10} values, (ii) carbon dioxide fluxes in an alpine wetland meadow are large in comparison with those in alpine meadow environments such as *K. humilis* meadow and *P. fruticosa* shrubland meadow located in cooler seasonal climate areas, (iii) CO_2 emissions are large on elevated microclimatology areas on the meadow floor regardless of temperature, but emission rates decrease notably after rain events, especially in the non-growing season, and (iv) the alpine wetland meadow was a moderate source of CO_2.

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Table 1. Average daily values of photosynthetically active radiation (PPFD), air temperature (T_a), vapor pressure deficit (VPD), soil temperature (T_s: 3 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 (1 January to 20 April), Growing season (21 April to 26 October), Senescence (27 October to 31 December), and Annual. Data were from 1 January 2004 to 31 December 2006.

Period	Year	PPFD mol m^{-2} d^{-1}	T_a °C	T_s °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 study site characteristics, environmental variables and carbon fluxes.

| Site	Latitude	Longitude	Elevation (m)	LAI m^2 m^{-2}	Period	Ta °C	GPP gCm^{-2}y^{-1}	NEE gCm^{-2}y^{-1}	R_{eco} gCm^{-2}y^{-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 *Kobresia humilis* 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	16.2	867	−131	735	Xu and Baldocchi (2004)
					2001–2002		729	29	758	
Sedge-dominated fen	74°28′ N	20°34′ W	1500	1.2	1996	−19.5	−	−64.4	−	Soegaard and Nordstroem (1999)
Boreal minerotrophic patterned fen	53°57′ N	105°57′ W		1.3	Mid-day to early October 1994	9.2–28.2	−	−88		Suyker et al. (1997)
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)
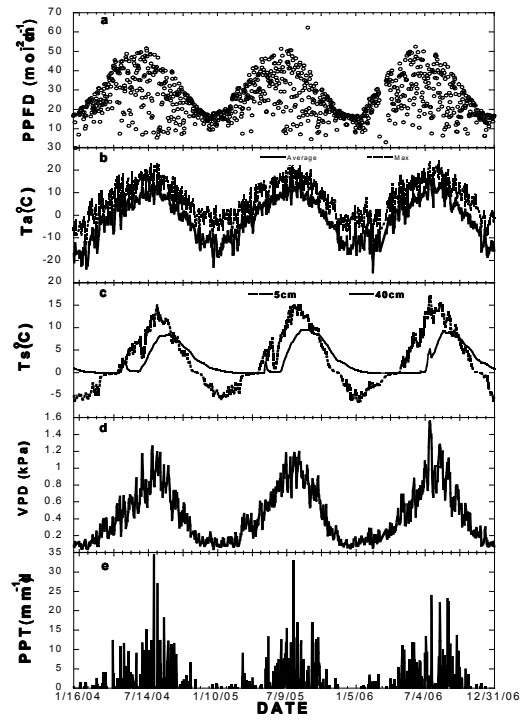
Fig. 1. Seasonal variability of **(a)** photosynthetically active radiation (PPFD), **(b)** average daily air temperature (Ta), **(c)** soil temperature at a depth 5 and 40 cm (T_s), **(d)** vapor pressure deficit (VPD), and **(e)** daily total precipitation (PPT). The lines are 1-day running means plotted from 1 January.
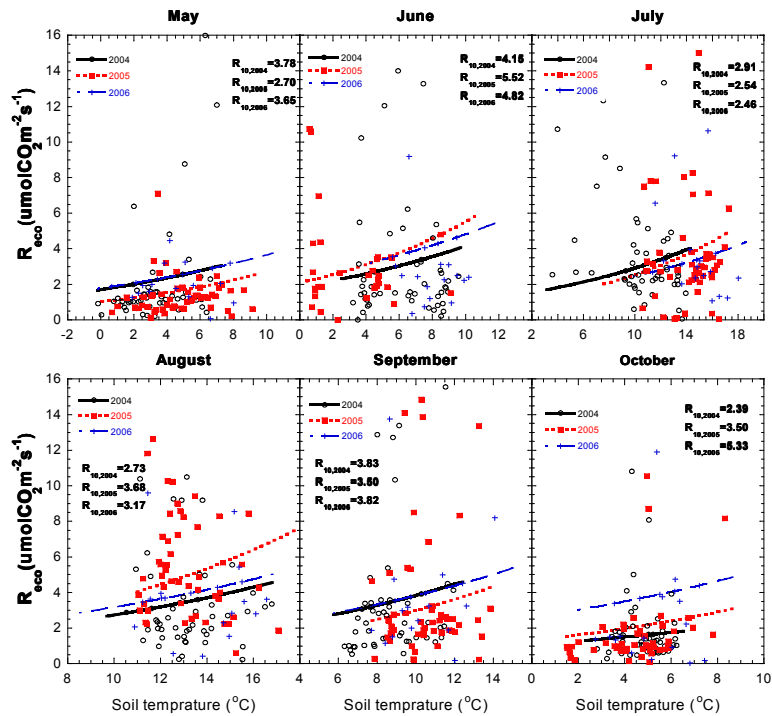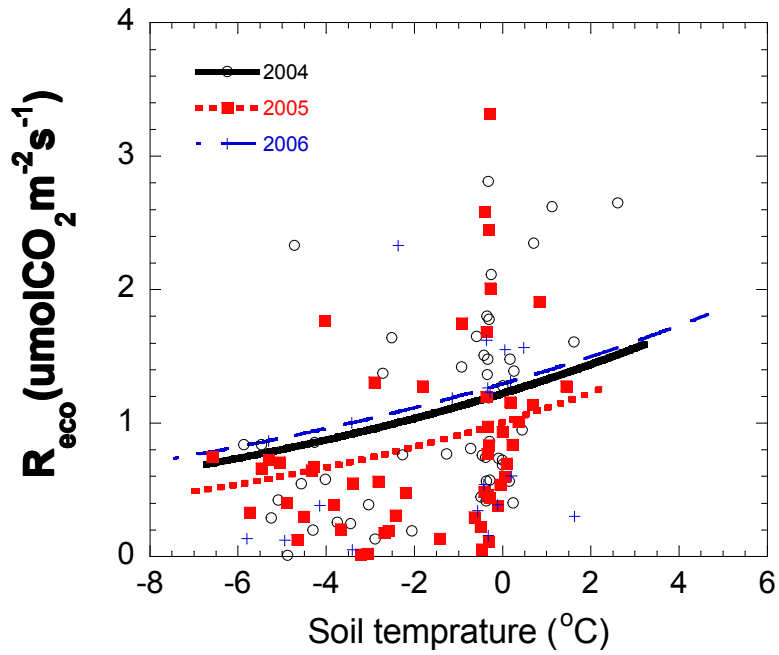
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Fig. 2. Response of ecosystem respiration (R_{eco}) to change in soil temperature at the depth of 5 cm during growing season. Data were from 2004 to 2006 season, and half-hourly during high turbulence conditions ($u^* > 0.1\,\mathrm{m\,s}^{-1}$).

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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 from 2004 to 2006 season, and half-hourly during high turbulence conditions ($u^* > 0.1 \, \text{m s}^{-1}$).

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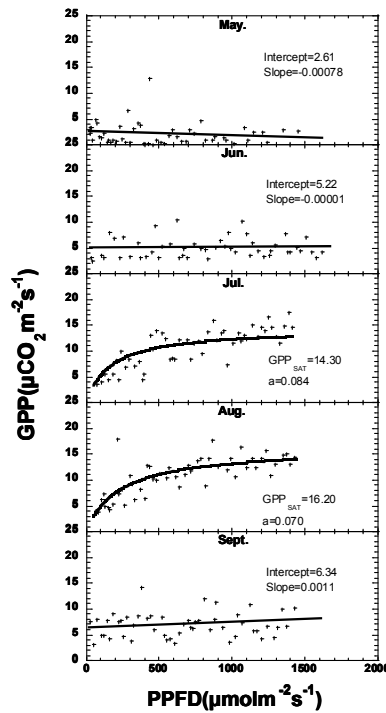
Fig. 4. Relationship between photosynthetic photon flux density (PPFD) and the gross primary production (GPP) measured in each month over a growing season. Fitted curves are rectangular hyperbolic as described in Eq. (1) for July and August, linear described in GPP=b+a×PPFD for May, June and September. Positive values denote CO_2 assimilation by the canopy. Data were from 06:00–13:00.

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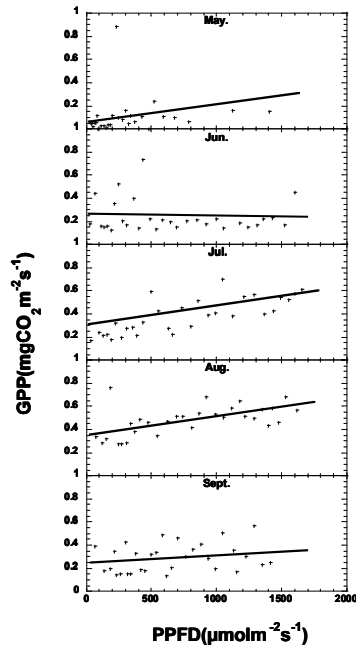
Fig. 5. Linear regression of daytime gross primary production (GPP) on incident photosynthetic photon flux density (PPFD). Data were from 13:00–20:00.The regression follows a linear relationship: GPP=b+a×PPFD. Monthly values are presented as follows: month (a, r^2) – May (0.00015, 0.10**), June (−0.00002, 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.

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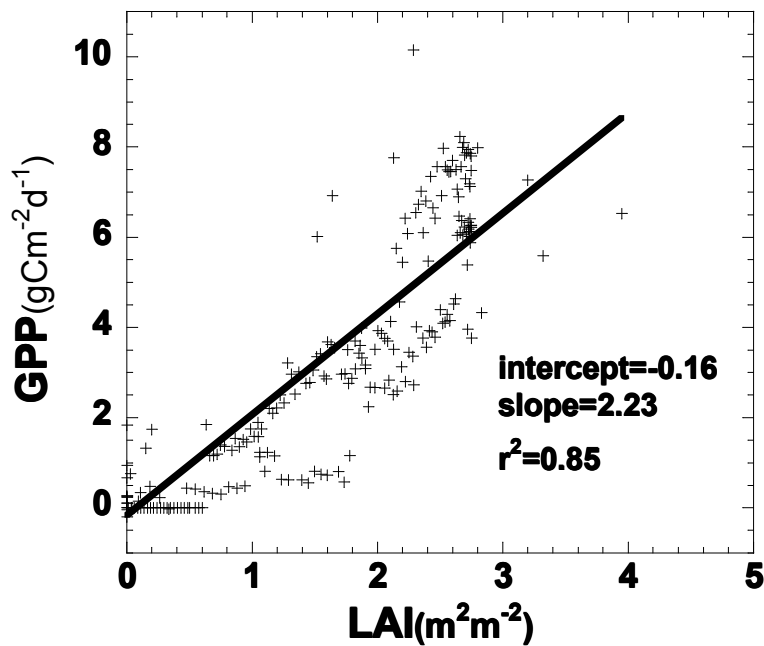
Fig. 6. The relationship of daily total gross primary production (GPP) and leaf area index (LAI). Data were obtained from the growing period in 2003.
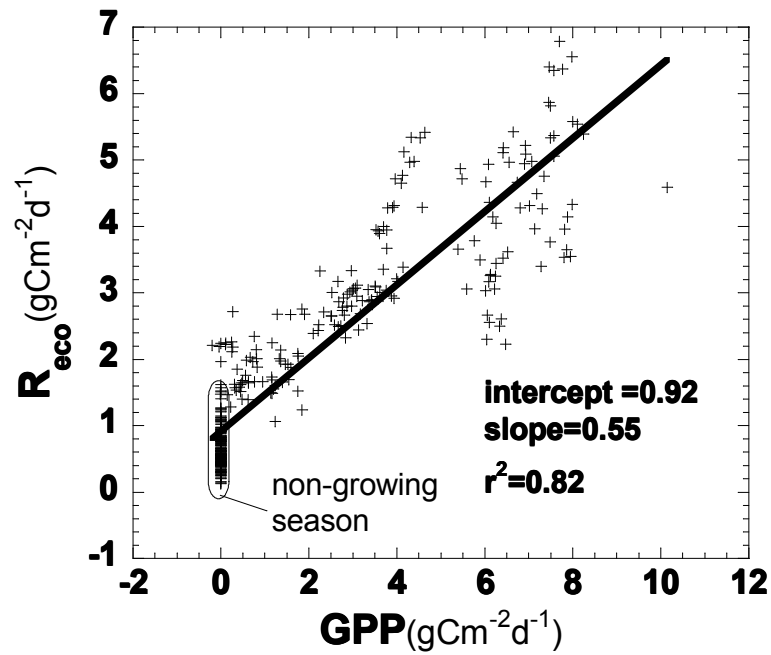
Fig. 7. The linear relation between daily gross primary production (GPP) and ecosystem respiration (R_{eco}). Data were compiled from 2003 to 2004. Data points from rain events and non-growing seasons were excluded in the linear regression analysis.
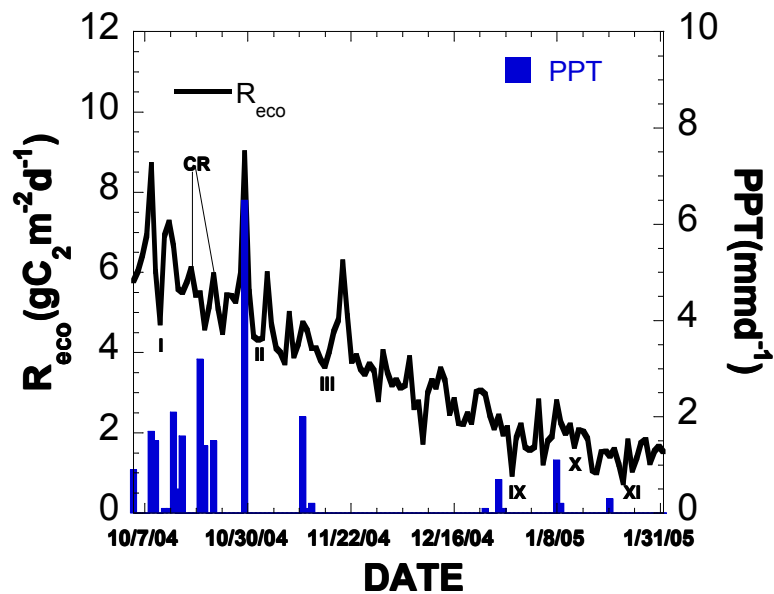
Fig. 8. Examples of influence of rain events on the ecosystem respiration (R_{eco}) from 1 October 2004 to 10 February 2005. Data in are the daily total R_{eco} and precipitation (PPT).
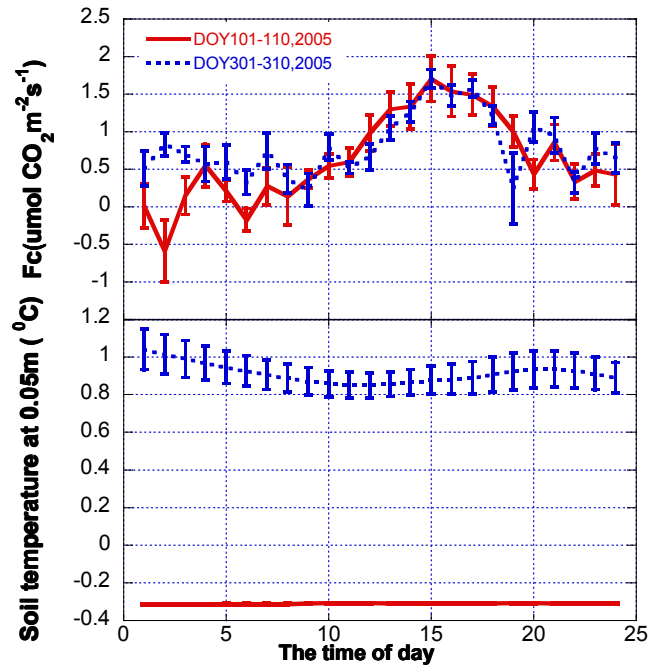
Fig. 9. Examples of 10-day binned diurnal variations in CO_2 flux (F_c) and soil temperature non-growing periods. DOY 101–110, and DOY 301–310, 2005. Error bars represent the standard deviation.
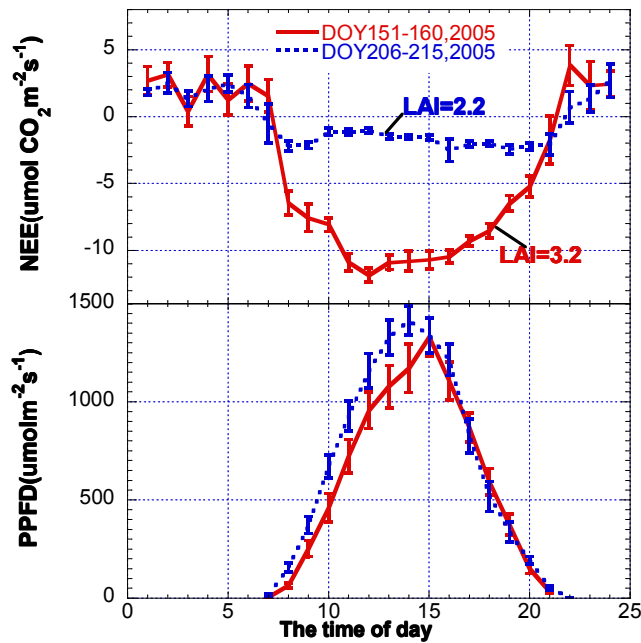
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Fig. 10. Examples of 10-day binned diurnal variations in CO_2 flux (NEE) and photosynthetic photon flux density (PPFD) during growing periods. DOY 151–160, and DOY 206–215, 2005. LAI was around 2.2 and 3.2, respectively. Error bars represent the standard deviation.
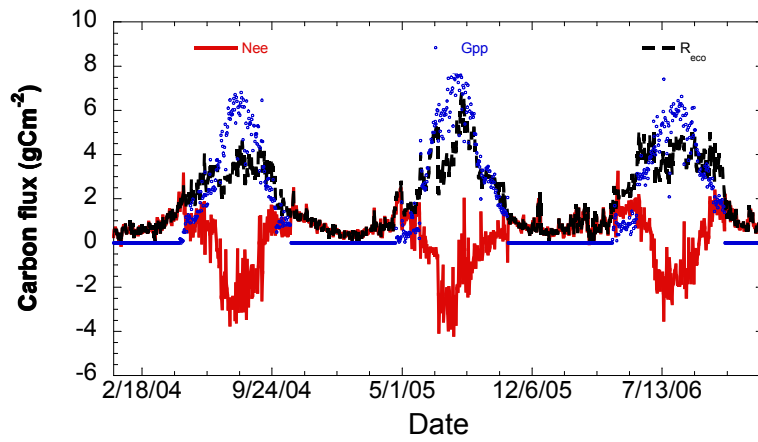
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Fig. 11. Seasonal pattern of daily total gross primary production (GPP) , net ecosystem exchange (NEE) , and ecosystem respiration (R_{eco}) over the course of the alpine wetland meadow from 1 January 2004 to the end of 2006.
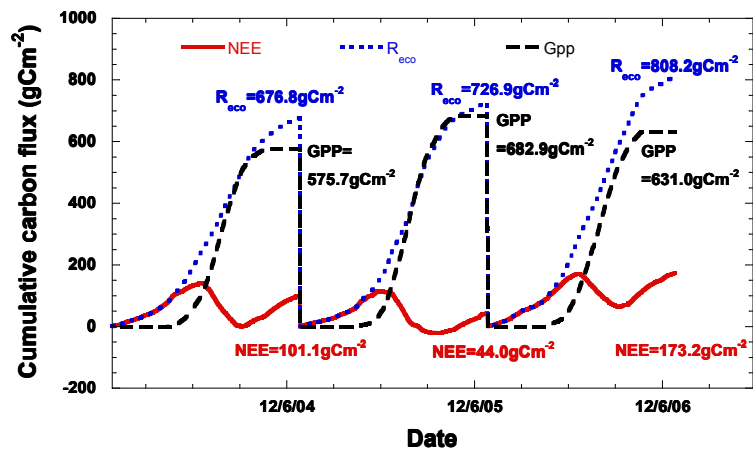
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Fig. 12. Cumulative gross primary production (GPP), net ecosystem exchange (NEE), and ecosystem respiration (R_{eco}) over the three seasons.