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**Carbon fluxes over
grasslands in China**

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Environmental controls on carbon fluxes over three grassland ecosystems in China

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Abstract

This study compared the CO₂ fluxes over three grassland ecosystems in China, including a temperate steppe (TS) in Inner Mongolia, an alpine shrub-meadow (ASM) in Qinghai and an alpine meadow-steppe (AMS) in Tibet. The measurements were made in 2004 and 2005 using the eddy covariance technique. Objectives were to document the different seasonality of net ecosystem exchange of CO₂ (NEE) and its components, gross ecosystem photosynthesis (GEP) and ecosystem respiration (R_{eco}), and to examine how environmental factors affect carbon exchange in the three grassland ecosystems. It was warmer in 2005 than in 2004, especially during the growing season (from May to September), across the three sites. The annual precipitation at TS in 2004 (364.4 mm) was close the annual average (350 mm), whereas the precipitation at TS in 2005 (153.3 mm) was significantly below the average. Both GEP and R_{eco} of the temperate steppe in 2005 were significantly reduced by the extreme drought stress, resulting in net carbon release during almost the whole growing season. The magnitude of CO₂ fluxes (daily and annual sums) was largest for the alpine shrub-meadow and smallest for the alpine meadow-steppe. The seasonal trends of GEP, R_{eco} and NEE of the alpine shrub-meadow tracked closely with the variation in air temperature, while the seasonality of GEP, R_{eco} and NEE of the temperate steppe and the alpine meadow-steppe was more related to the variation in soil moisture. The alpine shrub-meadow was a local carbon sink over the two years. The temperate steppe and alpine meadow-steppe were acting as net carbon source, with more carbon loss to the atmosphere in warmer and drier year of 2005. Annual precipitation was the primary climate driver for the difference in annual GEP and NEE among the three sites and between the two years. We also found the annual GEP and NEE depended significantly on the growing season length, which was mainly a result of the timing and amount of precipitation for the temperate steppe and the alpine meadow-steppe, but was more linked to the variation in air temperature for the alpine shrub-meadow.

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1 Introduction

Carbon cycle in terrestrial ecosystems has not only attracted considerable attention by scientists in recent years, but also that of policy makers in its potential for sequestering atmospheric CO₂. Many studies have focused on carbon exchange in forests ecosystems because of their potential to sequester large amounts of carbon (Pacala et al., 2001). Less attention had been given to CO₂ exchange in grasslands, even though they occupy approximately 32% of the earth's natural vegetation (Syuker et al., 2003). There is evidence that some grasslands can be significant sources or sinks of atmospheric CO₂ (Harazono et al., 2003; Novick et al., 2004; Gilmanov et al., 2007) and some show a carbon neutral (Suyker et al., 2003). However, most grassland ecosystems show large interannual variability in the annual net ecosystem exchange of CO₂ (NEE), or negative annual uptake (Flanagan et al., 2002; Ma et al., 2007).

There is clearly a great deal of uncertainty regarding the role of grasslands in the global carbon budget, and the drivers of carbon dynamics differ among a range of grasslands under various climatic conditions and management practices (Knapp et al., 2002; Verburg et al., 2004; Derner et al., 2006). Studies have shown that the annual amount and the timing of precipitation dominated the carbon exchange in temperate semiarid grassland and Mediterranean grassland (Suyker et al., 2003; Hunt et al., 2004; Xu and Baldocchi, 2004). In addition, the temperate grasslands show obviously asymmetric responses to inter-annual variations in precipitation, i.e, productivity increases in wet years are much more pronounced than the reductions in productivity in dry years (Wever et al., 2002; Flanagan et al., 2002). Studies also suggested that alpine meadows are very sensitive to temperature change (Harazono et al., 2003; Kato et al., 2006) and may have great potential in releasing carbon under global warming because of the sensitivity of frigid soil to increase of temperature (Wang et al., 2002).

There are large areas of temperate and alpine grasslands on Inner Mongolia Plateau and Qinghai-Tibet Plateau, respectively, in China. The temperate steppe represents one of the typical vegetation types in Eurasian continent and is ecologically fragile and

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sensitive to climate change (Li et al., 2005). Precipitation is usually the limiting factor for plant growth in such semiarid grassland ecosystems (Fu et al., 2006a; Wang et al., 2008). A gradually warmer and drier climate in this area has been documented (McCarthy et al., 2001; Chen et al., 2003). It is expected that such climate change might considerably affect the carbon exchange in the temperate semiarid steppe (Li et al., 2005; Niu et al., 2008). The alpine meadows on Qinghai-Tibet Plateau, which are characterized by low temperatures and strong solar radiation owing to their high elevation, may play an important role in terrestrial carbon sink due to their low decomposition rate of organic matter and relatively high photosynthesis and thus high soil carbon storage over a large area of about 128 million ha (Wang and Zhou, 1999; Xie et al., 2003).

Several studies have been conducted on addressing carbon fluxes over the grasslands in China (e.g. Kato et al., 2004; Zhao et al., 2005; Shi et al., 2006; Hao et al., 2007; Wang et al., 2008), but none synthetically studied the carbon exchange and their relationships with environmental factors across different grassland ecosystems or biomes. In this study we presented the measurements of CO_2 flux over three grassland ecosystems in China in 2004 and 2005. The objectives of this study were to (1) compare the seasonal and interannual variation in NEE and its major components, gross ecosystem production (GEP) and ecosystem respiration (R_{eco}) among the three grasslands, (2) quantify the role of carbon sink or source of the three ecosystems during the two study years, and (3) examine how environmental factors affect carbon fluxes (i.e. NEE, GEP and R_{eco}) across the three ecosystems.

2 Methods

2.1 Site description

The study sites include one temperate *Leymus chinensis* steppe in Inner Mongolia, an alpine *Potentilla fruticosa* shrub-meadow in Qinghai, and an alpine *Kobresia* meadow-steppe in Tibet, China, respectively.

2.1.1 Temperate *Leymus chinensis* steppe

The temperate *Leymus chinensis* steppe (TS in abbreviation) is located in the Xilin River Basin in Inner Mongolia (43°32' N, 116°32' E, 1189 m a.s.l.). There are low hills in the study area with relative height difference of 20~30 m and terrain slope is less than 3%. This region has a distinct temperate semiarid continental climate and mean annual air temperature (MAT) is -1.1~0.2°. Mean annual precipitation (MAP) is 350 mm, with large seasonal variation and year-to-year fluctuation. The vegetation at this site is dominated by warm season grasses as *Leymus chinensis*, *Stipa grandis*, *Koeleria cristata* and *Agropyron cristatum* etc. The grasses coverage averages 30~40%. There is a substantial amount of litterfall on the ground surface due to enclosure from grazing for more than 20 years. The soil is dark chestnut (Mollisol) with 21% clay, 60% sand and 19% silt on average (Hao et al., 2007).

2.1.2 Alpine *Potentilla fruticosa* shrub-meadow

The alpine *Potentilla fruticosa* shrub-meadow (ASM in abbreviation) is located in the northeast of the Qinghai-Tibet Plateau (37°39.92' N, 101°19.87' E, 3293 m a.s.l.). The study area one kilometer around the flux tower is fairly flat with terrain slopes less than 1%. The climate at this region is described as plateau continental climate. The MAT and MAP are -1.7°C and 570 mm, respectively. More than 80% of the precipitation occurred during the period from May to September. The constructive species of this alpine shrub-meadow is *Potentilla fruticosa* L. shrub with a height of 55~70 cm. The understory grass layer is dominated by *Stipa aliena*, *Elymus nutans*, *Festuca rubra*, *Kobresia capillifolia*, *Aster flaccidus*, *Poa orinosa*, *Oxytropis ochrocephala* etc. The soil is a silty clay loam classified as Mollic Gric Cambisols, with heavy clay between 0.1 m and 1.0 m layer (Zhao et al., 2006). This alpine shrub-meadow is grazed by yaks and Tibetan sheep every summer from June to September with a low grazing intensity about 1 bod ha⁻¹.

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2.1.3 Alpine *Kobresia* meadow-steppe

The alpine *Kobresia* meadow-steppe (AMS in abbreviation) is located at the Damxung County in the south of the Qinghai-Tibet Plateau (30°51′N, 91°05′E, 4333 m a.s.l.). The study field is fairly open and flat with terrain slopes less than 2% (Shi et al., 2006). This site belongs to semiarid and semihumid region with a plateau monsoon climate. The MAT and MAP are 1.3°C and 480 mm, respectively, with 80% falling in June, July and August. The dominant species of this alpine meadow-steppe are *Stipa capillacea*, *Carex montis-everestii* and *Kobresia pygmaea*. The grass height is usually less than 15 cm and the coverage is 50%~80%. The soil is classified as meadow soil with sandy loam. The depth of soil is 0.3~0.5 m, with 30% of gravel content and 0.9%~2.97% of organic matter content. More details on site descriptions have been reported in companion papers (Fu et al., 2006b; Zhao et al, 2006; Shi et al., 2006).

2.2 Field measurements

Eddy covariance fluxes of CO₂, sensible heat, latent heat were measured at a height of 2.5 m at the three sites with same instruments. The instrumentation of eddy covariance system included a three-dimensional sonic anemometer (Model CSAT-3, Campbell Scientific, Logan, Utah, USA) and an open path infrared CO₂/H₂O analyzer (Model LI-7500, Li-cor Inc., Nebraska, USA). The fluxes data were recorded by a datalogger (CR5000, Campbell Scientific) at 30 min intervals. Prior to the scalar flux computation, the mean vertical velocity was forced to zero by using traditional triple coordinate rotation to correct the effect of sensors tilt and sloping field. The fluxes were adjusted for the variation in air density due to the transfer of water vapor following the algorithm (Webb et al., 1980).

Additionally, mean air temperature (T_a), relative humidity, photosynthetically active radiation (PAR), soil temperature (T_s), soil moisture and precipitation were also measured at same heights or depths with same instruments at the three sites. Soil moisture was monitored using time domain reflectometry (TDR, Model CS615-L, Campbell Sci-

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entific) at 3 depths (5, 20 and 40 cm) at TS and AMS and 2 depths (20 and 40 cm) at ASM. The above measurements were all recorded at half-hour intervals.

2.3 Data processing

The eddy covariance data were screened for anomalous or spurious values outside the range normally encountered. Possible causes for such values can be sensor malfunction and interference from rain, dew, hoarfrost and birds, etc. The eddy covariance technique has been found to underestimate night-time CO₂ fluxes (ecosystem respiration, R_{eco}) under low-atmospheric turbulence conditions (Wohlfahrt et al., 2005; Massman and Lee, 2002). Here, we followed the current practice of screening the nighttime data by using site-specific thresholds of fraction velocity (u_*) (Aubinet et al., 2000). The threshold of u_* was identified as 0.2 m s⁻¹ for TS and 0.15 m s⁻¹ for ASM and AMS, respectively. Thus, data gaps were produced. The average data coverage during the two years was 46%, 48% and 50% for TS, ASM and AMS, respectively.

In order to obtain the information on annual sums of the carbon flux, the data gaps were filled by using several strategies suggested by Falge et al. (2001) and Reichstein et al. (2005). Linear interpolation was used to fill the gaps less than 2 h. For larger gaps (2 h to several consecutive days), the daytime CO₂ flux (net ecosystem exchange of CO₂, NEE) was estimated as a function of PAR with the Michaelis-Menten equation (Falge et al., 2001, their Eq. A8). The missing nighttime CO₂ flux was estimated by using the empirical relationships between R_{eco} and soil temperature and soil moisture. The Lloyd and Taylor equation (Lloyd and Taylor, 1994, their Eq. 11) was applied to fill the nighttime data gaps at ASM and AMS. Whereas, a Q_{10} model was used to fill the nighttime data gaps at TS, considering the effects of soil moisture on R_{eco} and its temperature sensitivity (Fu et al., 2006a).

These estimates of ecosystem respiration were also used to calculate daytime respiration ($R_{\text{eco,day}}$) at each site. Using the daytime respiration values, gross ecosystem production (GEP) could then be derived by subtracting the estimated daytime respiration ($R_{\text{eco,day}}$) from the corresponding daytime NEE. Positive values represent carbon

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release from ecosystem to the atmosphere, whereas negative values signify ecosystem carbon uptake from the atmosphere. The above computations were done with MATLAB software (Math Works Inc., Natick, MA).

2.4 Vegetation measurements

5 Leaf area index (LAI) was measured by clipping vegetation of 0.25 m² quadrates within a radius of 250 m around the observation tower during growing season in 2004 and 2005 at TS (every one month) and AMS (every two weeks). However, LAI was measured only in 2005 at ASM with LI3100A (LI-Cor, USA). The MODIS NDVI products (8 days averaged with 1 km resolution, <http://remotesensing.unh.edu>) were used to estimate the integrated LAI datasets during the growing seasons of 2004~2005 by fitting the relationship between NDVI and measured LAI at corresponding site ($R^2 > 0.94$) (Hu et al., 2008).

3 Results

3.1 Comparison of environmental conditions

15 Variation in environmental conditions at the three grassland sites during 2004~2005 are plotted in Fig. 1, including monthly values of air temperature (T_a), photosynthetically active radiation (PAR) and vapor pressure deficit (VPD). Annual trends in volumetric soil moisture and daily precipitation at the three sites are also presented in Fig. 2. Influenced by continental climate at different extent, the three grassland ecosystems showed distinct seasonal and interannual variations in the environmental variables. The PAR during growing season at TS was generally higher than that at ASM and AMS due to more cloudy conditions in the summer rainy seasons at ASM and AMS (Fig. 1a). Although the mean annual T_a among the three sites was comparable (Table 1), T_a during the growth season at TS was generally higher than that at ASM and AMS in the

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two years (Fig. 1b). A common point among the three sites is that it was warmer in 2005 than in 2004. The T_a in January through February and May through September in 2005 was generally higher than that in 2004 at ASM. Both the mean annual T_a and the mean T_a from May to September in 2005 was higher than that during the same period in 2004 at AMS.

Another major environmental difference among the three sites was the amount and timing of precipitation (Fig. 2). The precipitation at ASM during the two years was close to the 30-year average value. The abundant precipitation at ASM resulted in relative high soil moisture throughout the growing seasons and no water stress was detected at this site, although the relatively less rain in the spring of 2004 caused decrease in soil moisture (Fig. 2b). Although there was considerable precipitation at AMS from June to August, the soil moisture at AMS was generally lower than that at ASM, with higher seasonal fluctuation due to the low water holding capability of sandy soil and high surface evaporation (Fig. 2c). The precipitation at TS in 2004 was near to the average, with a dry spring due to little rainfall during April through mid June. However, it was extremely dry in 2005 at TS, with precipitation significantly below the average that led to soil drying out from May throughout the whole growth season (Fig. 2a). The VPD from May to September at TS was much higher than that at ASM and AMS (Fig. 1c).

3.2 Leaf area index and growing season length

Leaf area index (LAI) reached the peak around early August at TS and ASM, but in late August at AMS in both years. The maximum LAI of the three ecosystems occurred in 2004, with a peak value of 2.8, 1.58 and $0.95 \text{ m}^2 \text{ m}^{-2}$ for ASM, TS and AMS, respectively (Fig. 3). There was no major difference for LAI between the two years at ASM because of the similar meteorological conditions. As compared to 2004, the LAI at TS in 2005 was significantly reduced by drought stress (Fig. 3). A slight decrease of LAI at DX in 2005 was also the result of the water stress in spring.

Due to lack of observation on grass phenology in the study years, we defined the growing season length (GSL) as starting when the grassland became net carbon up-

take on five consecutive days in spring, and ending with net carbon release on five consecutive days in autumn. We found that the ASM had the longest growing season among the three sites (Table 1), although the air temperature at ASM from April to October was general lower than the other two sites. The TS experienced a growing season of 74 days in average rainfall year of 2004, but almost without an obviously consecutive growing season in 2005 due to the drought stress. The GSL of AMS was comparable between 2004 and 2005, although the timing was different.

3.3 Seasonality of carbon fluxes and relevant controls

The seasonal dynamics of GEP, R_{eco} and NEE over the three grassland ecosystems during the two years is shown in Fig. 4. The GEP, R_{eco} and NEE of ASM showed similar seasonal trends with that of air temperature (Fig. 4b), with frequent precipitation during the growing seasons (Fig. 2b). Both the GEP and R_{eco} began to increase rapidly since early May and reached their peak values by mid/late July through early August in both years, resulting in maximum net carbon uptake in mid or late July at AMS (Fig. 4b). The ASM shifted to net carbon sink from the beginning of June through mid September in both years, with net carbon release on a few extremely rainy or cloudy days.

As compared to ASM, the ecosystem carbon fluxes of TS tracked closely with rain events and soil moisture in warm season. The TS continued to release carbon until late June in 2004, (Fig. 4a) due to rare precipitation during April through mid June (Fig. 2a), which substantially delayed the grass green-up until late June after several critical rain events (18.3, 24 and 10.5 mm on June 20, 22 and 24, respectively). But these rain pulses enhanced R_{eco} quicker than GEP, leading to an increase in net carbon release first and then a change from carbon source to carbon sink in early July. During the second drought stress period in mid July of 2004, the reduction in both GEP and R_{eco} was apparent. Although several major rain events occurred in early and late July (totaling 60.5 mm), the maximum net carbon uptake occurred in late August one week after the largest rainfall (44 mm on 14 August 2004), which sustained the steppe as a carbon sink until mid September before the onset of grass senescence due to

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decreasing temperature. Both GEP and R_{eco} of TS in 2005 were significantly reduced by the drought stress, resulting in net carbon release during almost the whole growing season (Fig. 4a). The different seasonal trends and daily values of GEP, R_{eco} and NEE at TS between the two years were mainly resulted from the difference in the amount and timing of precipitation received.

The seasonality of GEP, R_{eco} and NEE of AMS indicated their responses to the variation in both temperature and moisture. The magnitude of GEP, R_{eco} and NEE of AMS in 2005 was generally smaller than those in 2004, as a result of less precipitation during June and July in 2005. The R_{eco} of AMS in 2004 reached relatively large values in early July and maintained this level until early September before grass senescence. However, its R_{eco} peaked in mid July in 2005 and then declined steadily, which might be ascribed to the decreased autotrophic respiration due to drought-induced lower GEP in 2005. This spring drought also caused a 20 days delay for the ecosystem shift from carbon source to carbon sink in 2005. The peak daily values of GEP and NEE at AMS were observed in early July in 2004, whereas in mid August in 2005.

It has been well documented that at short time scales (e.g. hourly and diurnal) ecosystem photosynthesis and respiration responded functionally to changes in PAR and temperature, respectively (Lloyd and Taylor, 1994; Falge et al., 2001). However, the dominant factor of ecosystem carbon fluxes would transfer with time scales. We examined the relationships of ecosystem carbon fluxes (e.g. NEE, GEP, R_{eco}) with radiation, temperature, and moisture conditions (precipitation or soil moisture) at monthly scale with the data during the growth period (from May to September). Results showed that monthly NEE, GEP, and R_{eco} of TS were significantly related to monthly total precipitation ($P < 0.05$, Fig. 5, Table 2), but were not correlated with monthly mean air temperature (Table 2), indicating the dominant effect of precipitation on carbon fluxes at TS. Contrast to TS, the monthly NEE, GEP, and R_{eco} of ASM were significantly correlated with monthly mean air temperature ($P < 0.001$) and less correlated with precipitation (Table 2). Temperature explained 82%, 95%, and 93% of the seasonal variation in NEE, GEP, and R_{eco} , respectively, which indicated the overwhelming controls of tem-

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perature on the carbon budget of ASM. Our results showed that the GEP and NEE of AMS were more related to soil moisture ($P < 0.001$) than to monthly precipitation, while R_{eco} has a linear but insignificant relationship with both air temperature and soil moisture (Table 2). This result indicated the importance of soil water retention for carbon sequestration despite of the considerable precipitation the AMS received during the growth season.

3.4 Annual carbon budgets

The annually integrated GEP, R_{eco} and NEE for the three grassland ecosystems were presented in Table 2. Annual NEE of the three grassland ecosystems ranged from -85.3 to $139.9 \text{ gC m}^{-2} \text{ yr}^{-1}$. The ASM is a local carbon sink, with a total accumulation of -137 gC m^{-2} over the two study years. Although the higher precipitation and temperature enhanced GEP in 2005, the enhancement of R_{eco} was larger, resulting in less carbon sequestration in 2005 than in 2004 (Fig. 4a and Table 1). The AMS and TS were both acting as net carbon source during the two years, with more carbon loss in drought-stressed year of 2005. Both GEP and R_{eco} of TS were significantly suppressed by the extreme drought stress in 2005. However the substantial ground litterfall due to non-grazing at TS effectively contributed to R_{eco} , resulting in more carbon release in 2005 than in 2004. The magnitude of annual carbon budget (GEP, R_{eco} , and NEE) of the AMS was much lower than TS and ASM in this study. This could be ascribed to the poor vegetation development and shallow soil with low nutrient content and low soil water retention.

Annual GEP and NEE showed a linear relationship with growing season length across the study sites and years, although the level of significance of this relationship were different (Fig. 6a and b). And the best-fit line was significant for the relationship between NEE and GSL ($P = 0.024$, $R^2 = 0.76$, Fig. 6b). To understand the mechanisms behind the relationship of annual GEP and NEE with GSL, we examined how GEP, R_{eco} and NEE responded to changes in temperature, precipitation and radiation at annual scale. Results showed that annual GEP and NEE had a linear relationship with annual

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total precipitation (Fig. 6c and d), other than mean annual air temperature or radiation. It indicated that the ecosystem increased carbon assimilation with greater annual precipitation. This is a little different from that the annual GEP and R_{eco} of an oak/grass savanna and open grassland were significantly related to precipitation during the active growing season, but were not related to annual precipitation (Ma et al., 2007). It might be partly attributed to the difference in the in-phase or out of phase of temperature and water availability between east-Asian monsoon climate and Mediterranean climate. It is interesting to notice that PAR, which was an important factor at hourly and diurnal time scale, did not show a stronger relationship with monthly and annual NEE or GEP. Although air temperature played an essential role in seasonal dynamics of carbon fluxes in ASM, it's hard to relate the annual sums of carbon fluxes to mean annual temperature across the three sites, partly due to the small difference in mean annual temperature among the three sites and between the two years.

4 Discussion

4.1 Comparison of ecosystem carbon sink-source activity

We compared our results with other grasslands located in same latitudes or with similar vegetation type. The peak daily NEE of the TS ($-2.2 \text{ gC m}^{-2} \text{ d}^{-1}$ on 21 August 2004) in this study was much lower than other northern temperate grasslands, such as a mixed-grass prairie in North Dakota ($-4.9 \text{ gC m}^{-2} \text{ d}^{-1}$, Frank and Dugas, 2001) and a Canadian prairie ($-2.4 \sim -5 \text{ gC m}^{-2} \text{ d}^{-1}$, Flanagan et al., 2002), which have comparable mean annual precipitation with the temperate steppe in this study. The peak daily NEE (largest carbon uptake) of the ASM ($-4.3 \text{ gC m}^{-2} \text{ d}^{-1}$ on 12 July 2004) was coincident with earlier study at this site (Zhao et al., 2006), and was similar to a close-by alpine *K. humilis* meadow ($-3.68 \text{ gC m}^{-2} \text{ d}^{-1}$ on 10-days average, Kato et al., 2006) and a Mediterranean warm grassland in California ($-4.8 \text{ gC m}^{-2} \text{ d}^{-1}$, Xu and Baldocchi, 2004). It was somewhat less than the warm tallgrass prairies in Kansas and Oklahoma

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(5~8.4 gC m⁻² d⁻¹; Kim et al., 1992; Dugas et al., 1999), which likewise released more carbon (average in 0.7 gC m⁻² d⁻¹ from mid November to mid-March) than the ASM (average in 0.3 gC m⁻² d⁻¹) during dormant season. The peak daily values of the AMS (-1.9 gC⁻² d⁻¹ on 6 July 2004) fell in the lower half of the range (-1.75~-9.3) reported in other literature (Li et al., 2005).

The annual carbon sink of the ASM was close to a sub-alpine grassland in Italy (Gilmanov et al., 2007) and a C₄-dominant prairies in Texas (Dugas et al., 1999), but considerably lower than some C₄-tallgrass prairies in north America (Suyker et al., 2003) and those intensively managed grasslands in central and northern Europe (Gilmanov et al., 2007). The annual NEE of the TS is similar to a temperate *Stipa krylovii* steppe in neighboring area, with similar climate conditions (Wang et al., 2008); but much higher than a Canadian prairie (Flanagan et al., 2002) and a Mongolia temperate steppe (Li et al., 2005), which were located in similar latitude with comparable or even less annual precipitation. The annual NEE of the AMS is close to a sparse, seasonally dry tussock in New Zealand (Hunt et al., 2004). Large variability and uncertainty regarding the role of grasslands in the global carbon budget have been reported. A literature summary by Novick et al. (2004) and Gilmanov et al. (2007) found annual sums of net ecosystem carbon exchange (NEE) in grasslands ranging from a net uptake of 800 gC m⁻² yr⁻¹ to a net loss of 521 gC m⁻² yr⁻¹. Alternations between carbon sink and carbon source are very common for grassland, such as a Canadian cool temperate grassland (Flanagan et al., 2002) and a Mediterranean grassland (Ma et al., 2007). Although the alpine shrub-meadow in this study showed as a carbon sink under current climatic conditions, it would possibly alternate into a carbon source under a warmer climate change scenario in future (IPCC, 2001).

4.2 Environmental controls on carbon fluxes

Our study showed that the determinant factors on the season variations in carbon fluxes were different for TS, ASM and AMS (Fig. 5), although annual precipitation

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played an important role in regulating annual NEE across the three sites. In order to understand the mechanisms behind the difference in determinant factor for GEP, R_{eco} and NEE among the three sites, we further examined the relationships between the critical parameters of ecosystem photosynthesis (i.e. P_{max} , the gross primary productivity at infinite light, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) with environmental factors. P_{max} values were derived from rectangular model with a window of 10 days data during the growing seasons (from May to October) for the three sites, respectively. The results showed that air temperature explained 81% of the seasonal variation in P_{max} of ASM (Fig. 7), which indicated that air temperature during the growing season was the primary factor that drives the variation in ecosystem photosynthesis of the ASM. Compared to ASM, about 50% of the variance in P_{max} of TS and AMS was ascribed to changes in soil moisture (Fig. 7), and the remaining variation was likely to be explained by the variation in temperature, VPD and LAI (Figure and data omitted).

Actually, with sufficient precipitation almost evenly falling during the growing season, soil moisture availability was no longer a limiting factor for the grass growth at ASM. In this case, great contribution of temperature to carbon flux dynamics often characterizes ecosystems that experience low temperatures, for example, relatively cold, humid ecosystems such as tundra (Harazono et al., 2003) and alpine meadows (Kato et al., 2006). The higher temperature during early spring (April) in 2004 at ASM induced an early onset and rapid increase of GEP; and furthermore, the lower temperature from May throughout September in 2004 resulted in a smaller R_{eco} . Therefore, the difference in GEP, R_{eco} and NEE of ASM between the two years was mainly a results of the combined effect of temperature difference. Compared with ASM, the air temperature during the growth season for TS and AMS was generally higher. With appropriate thermal condition, the processes of ecosystem photosynthesis and respiration were easily apt to be affected by soil moisture, especially for an ecosystem often encounters drought stress as the temperate steppe in Inner Mongolia (Wang et al., 2008). The strong limitation of soil moisture on ecosystem GEP and NEE of AMS was possibly due to the poor soil water retention and high surface evaporation (Hu et al., 2008),

although the ecosystem received considerable precipitation during the growth season.

In our analysis, annual R_{eco} did not show significant relationship with mean annual air temperature or annual precipitation. Indeed, annual R_{eco} was significantly correlated with annual GEP across the sites (Fig. 8). Although there might be some artificial mechanism in the dependence of R_{eco} on GEP due to separation of GEP and R_{eco} from eddy covariance derived NEE, we cannot deny the strong influence of canopy photosynthesis on R_{eco} by controlling the substrate availability for autotrophic respiration and heterotrophic respiration (Davidson et al., 2006). Evidences exist in literatures about the similar relationship between R_{eco} and GEP for many ecosystem types (Valentini et al., 2000; Law et al., 2002; Li et al., 2005; Aires et al., 2008), suggesting the shadowing effect of canopy photosynthesis activity on ecosystem respiration. Besides, annual NEE also showed a positive relationship with annual GEP across the sites, indicating the ecosystem with greater GEP possibly produce greater net carbon uptake (Fig. 8).

Therefore, we can draw a conclusion that, at the ecosystem level, air temperature was the most important factor controlling the ecosystem carbon budget at ASM by regulating its P_{max} and the development of leaf area. This is coincident with a similar study in an alpine meadow nearby (Kato et al., 2006). However, precipitation and soil moisture was the primary factor affecting the carbon flux in TS and AMS. Annual precipitation controls the year-to-year and site-to-site variations in net ecosystem carbon budget, by regulating the growing season length for development of leaf area and thus gross ecosystem production.

4.3 Effects of growing season length on ecosystem carbon exchange

Earlier studies have reported the effects of growing season length on inter-annual variability in NEE for a savanna and Mediterranean grassland (Ma et al., 2007), a temperate deciduous forests (Baldocchi and Wilson, 2001) and a boreal aspen forest (Barr et al., 2004). Our data at the three sites also show that the longer the growing seasons were, the more carbon could be sequestered and the less carbon would be released (Fig. 6). Averagely, net carbon uptake of the three grasslands in our study increased

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by 2.0 g C m^{-2} with one day increase of the growing season.

A variety of biophysical factors drive length of growing season, and these factors differ from year to year (Menzel et al., 2006). Studies have suggested the timing of rainfall in previous fall and later spring is the predominant factor determining the length of growing season in a savanna and Mediterranean grassland (Xu and Baldocchi, 2004; Ma et al., 2007). In this study, we found that the growing season length was significantly correlated with annual total precipitation across the sites and years (Fig. 9). But we noticed that the driving factors for growing season length differed from site to site. For the temperate semiarid steppe, after soil thawing with rising temperature in spring, water availability becomes the critical factor driving the grasses green-up in spring and continuous growth before grass senescence in autumn. It requires frequent precipitation to maintain the soil wetting period and thus prolong the growing season length for carbon assimilation by grass. Otherwise, frequent spring or summer drought often cause alternations between carbon sink and carbon source in grassland and thus shorten the growing season length (Fu et al., 2006a). Therefore, the growing season length for temperate semiarid steppe correlates with not only the timing but also the amount of precipitation.

For the alpine shrub-meadow in this study, variation of ecosystem carbon exchange coincided more with air temperature, with sufficient moisture availability from spring throughout autumn. The longer growing season length for the alpine shrub-meadow in 2004 than in 2005 could be partly ascribed to the higher temperature in early spring (April), which resulted in relatively earlier start of vegetation growth and greater GEP and NEE. Our results corroborated previously findings in a nearby alpine meadow that the period of net carbon absorption (equivalent to GSL in our study) agrees well with the days of the mean air temperature $>5.0^\circ\text{C}$ (Kato et al., 2006). Thus, we concluded that the growing season length for the alpine shrub-meadow was primarily linked to air temperature, other than precipitation.

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This study showed the difference in the seasonality of GEP, R_{eco} , and NEE and relevant environmental controls over a temperate steppe, an alpine shrub-meadow and an alpine meadow-steppe in China. With frequent precipitation during the growing season, the seasonality of NEE, GEP and R_{eco} of the alpine shrub-meadow were in phase with that of air temperature. However, the seasonality of NEE, GEP and R_{eco} of the temperate steppe and the alpine meadow-steppe was more strongly related to the variations in soil moisture resulted from precipitation.

The alpine shrub-meadow was a local carbon sink, and the temperate steppe and the alpine meadow-steppe were acting as net carbon source in the two study years. We found that precipitation and soil moisture were the primary factors that control the seasonal variations in GEP and NEE of the temperate steppe and alpine meadow-steppe, whereas air temperature dominated the variations in GEP and NEE of the alpine shrub-meadow. Annual precipitation was the primary climate driver for the difference in annual GEP and NEE across the sites. The ecosystem carbon uptake depended significantly on the growing season length, which was mainly determined by the timing and amount of precipitation in temperate steppe and the alpine meadow-steppe, and by air temperature in the alpine shrub-meadow. The different climate driving mechanism for carbon exchange among grassland ecosystems inspires us further thinking and study on their complex response to future climate changes.

Acknowledgements. This study was supported in part by Knowledge Innovation Program of the Chinese Academy of Sciences (Grant No. KZCX2-YW-432) and National Natural Science Foundation of China (Grant No. 30700110, 30721140307, and 30590381). Other sources of support included the front subject of Institute of Geographic Sciences and Natural Resources Research (Grant No. O66U0604SZ) and the “HundredTalents” Program of Chinese Academy of Sciences (CXTD-Z2005-1). The authors thank all staffs of ChinaFLUX for their contribution to field work and data processing.

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Table 1. Annual statistics of environmental factors and carbon fluxes for the 3 grassland ecosystems during 2004~2005, including mean annual air temperature (MAT), annual precipitation (AP), growing season length (GSL), annual sums of net ecosystem exchange of CO₂ (NEE), total ecosystem respiration (R_{eco}), and gross ecosystem production (GEP).

Site	Year	MAT (°C)	AP (mm)	GSL (days)	GEP/ gC m ⁻² yr ⁻¹	$R_{\text{eco}}/$ gC m ⁻² yr ⁻¹	NEE/ gC m ⁻² yr ⁻¹
Temperate steppe (TS)	2004	1.65	364.4	74	-313.4	420.2	106.8
	2005	1.08	153.3	8	-40.8	179.8	139.9
Alpine shrub- meadow (ASM)	2004	-1.90	493.5	120	-501.5	416.2	-85.3
	2005	-1.31	541.5	109	-553.9	502.2	-51.7
Alpine meadow- steppe (AMS)	2004	1.66	550.4	96	-238.8	280.1	37.3
	2005	2.41	489.9	95	-173.7	232.3	54.8

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Table 2. Results of a linear regression analysis on the relationship between ecosystem carbon flux (GEP, R_{eco} , and NEE) and air temperature or precipitation at a monthly time scale for the temperate steppe (TS), alpine shrub-meadow (ASM), and alpine meadow-steppe (AMS). The data during May~September in both years were used.

Site	Carbon Flux	T_a		Precipitation	
		R^2	P	R^2	P
TS	GEP	0.09	0.400	0.65	0.005**
	R_{eco}	0.12	0.339	0.78	0.001**
	NEE	0.003	0.883	0.46	0.030*
ASM	GEP	0.95	0.000***	0.45	0.034*
	R_{eco}	0.93	0.000***	0.45	0.035*
	NEE	0.82	0.000***	0.38	0.058
AMS	GEP	0.55	0.014*	0.77 ^a	0.001**
	R_{eco}	0.37	0.063	0.23 ^a	0.157
	NEE	0.48	0.027*	0.81 ^a	0.000***

^a the relationship between carbon flux and soil moisture content at AMS. * the significance of the correlation.

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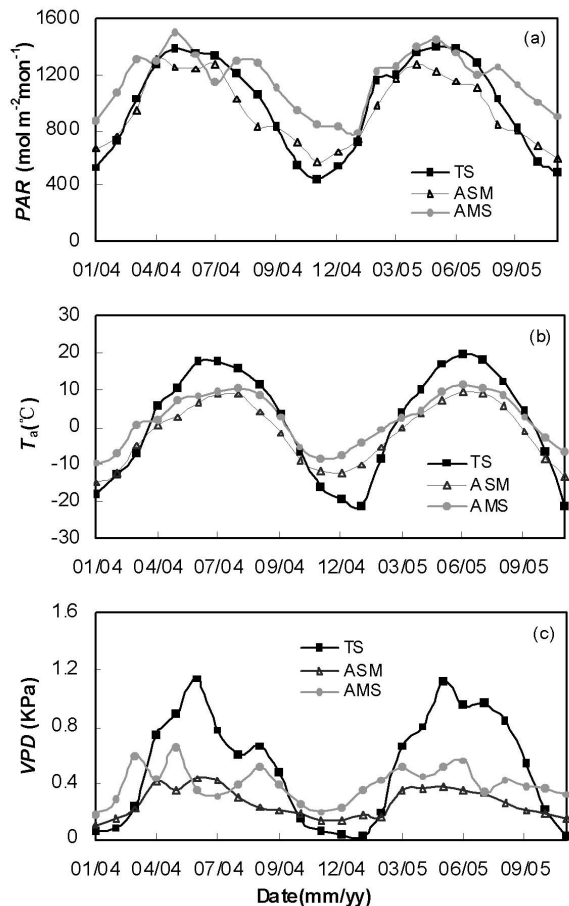


Fig. 1. Seasonal variation of monthly photosynthetically active radiation (PAR), monthly average air temperature (T_a) and vapor pressure deficit (VPD) during 2004 and 2005 at the temperate steppe (TS), alpine shrub-meadow (ASM) and alpine meadow-steppe (AMS).

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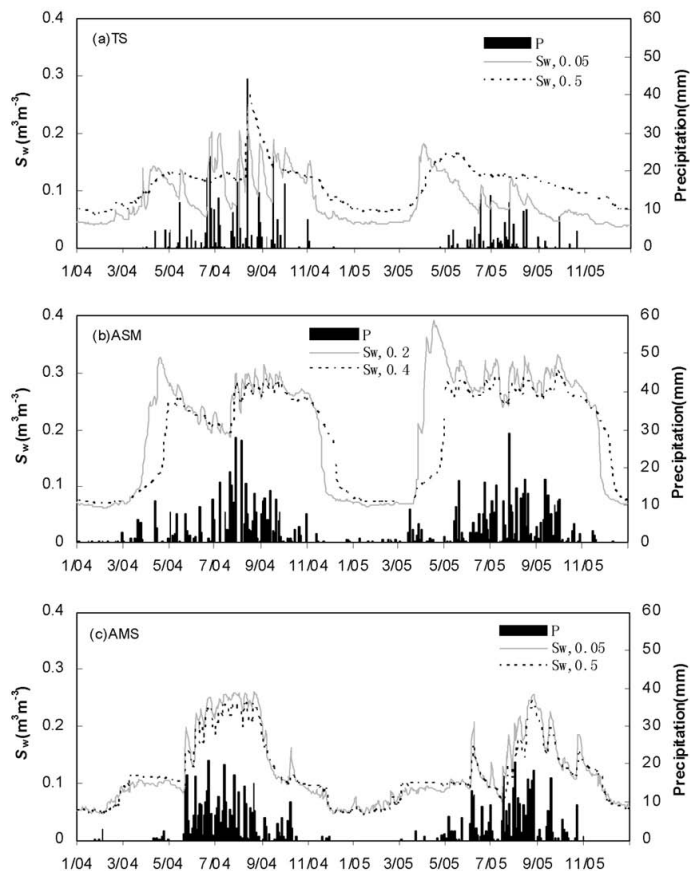


Fig. 2. Seasonal trends of daily average soil moisture content (S_w) and daily total precipitation during the two continuous observation years at (a) the temperate steppe (TS), (b) alpine shrub-meadow (ASM) and (c) alpine meadow-steppe (AMS).

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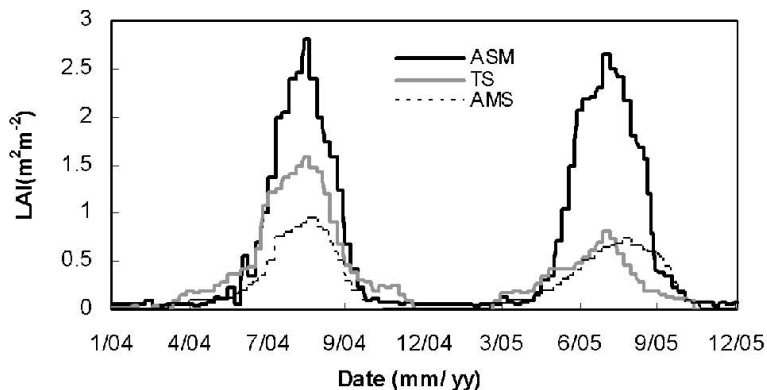


Fig. 3. Seasonal variation of leaf area index (LAI) at the temperate steppe (TS), alpine shrub-meadow (ASM) and alpine meadow-steppe (AMS) during 2004 and 2005.

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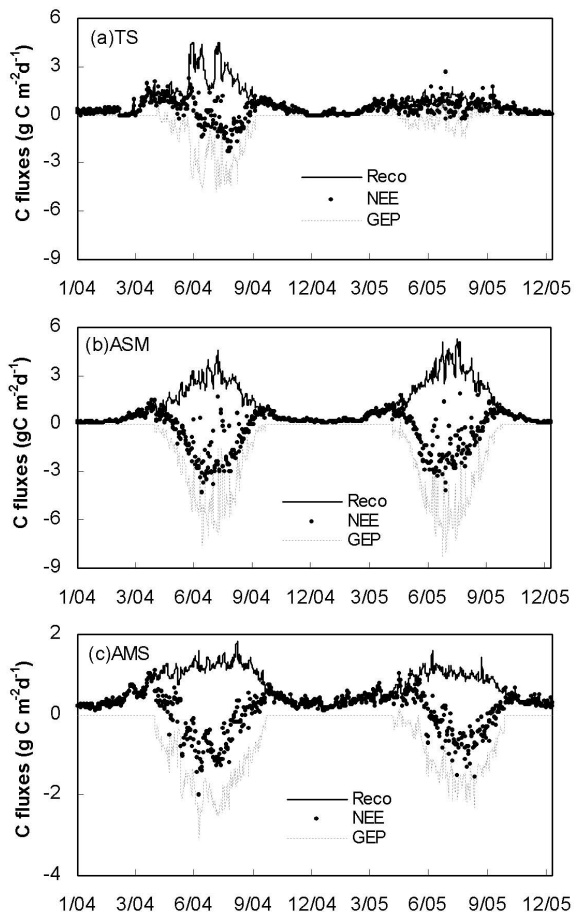


Fig. 4. Seasonal variation of daily integrated net ecosystem exchange of CO_2 (NEE), total ecosystem respiration (R_{eco}), and gross ecosystem production (GEP) at the temperate steppe (TS), (b) alpine shrub-meadow (ASM) and (c) alpine meadow-steppe (AMS) during 2004 and 2005.

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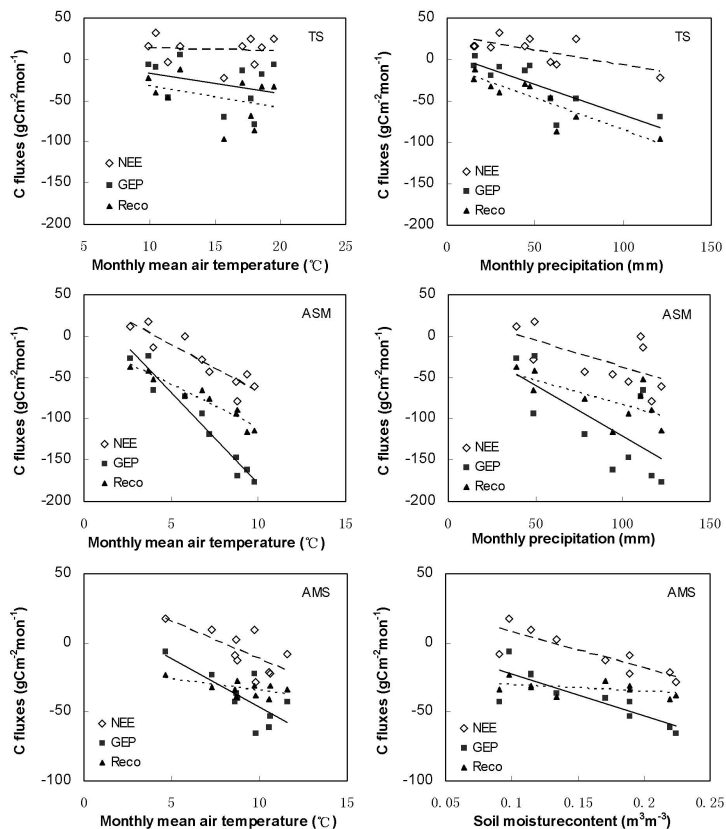


Fig. 5. Relationships of monthly net ecosystem exchange of CO_2 (NEE), ecosystem respiration (R_{eco}), and gross ecosystem production (GEP), to monthly mean air temperature, monthly precipitation (for the temperate steppe, TS, and alpine shrub-meadow, ASM) and monthly mean soil moisture content (for alpine meadow-steppe, AMS). The data during May~September in 2004 and 2005 were used for analysis here.

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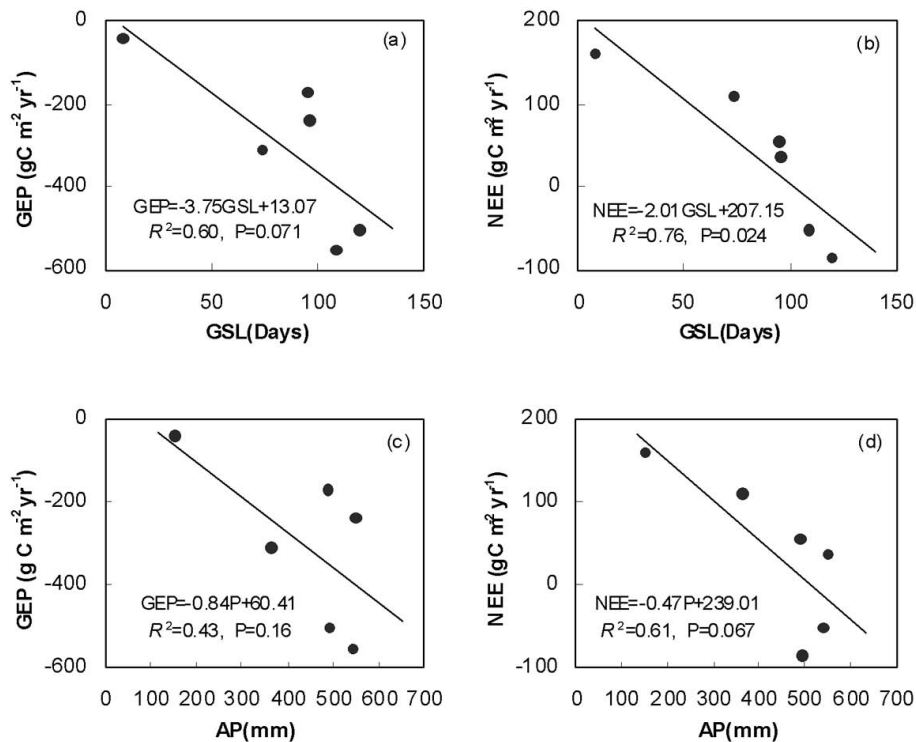


Fig. 6. Relationships of annual gross ecosystem production (GEP) and net ecosystem exchange of CO_2 (NEE) to growing season length (GSL) and annual precipitation (AP) across the three sites in 2004 and 2005.

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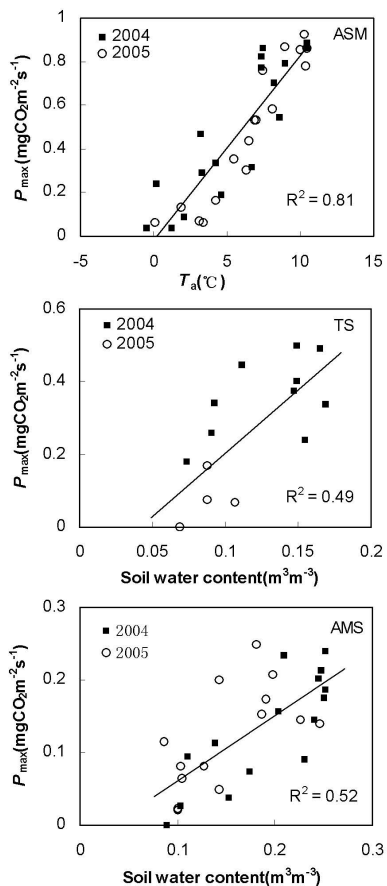


Fig. 7. The relationships between ecosystem photosynthesis parameter (P_{max}) and air temperature (for the alpine shrub-meadow (ASM)) and soil moisture (for the temperate steppe (TS) and alpine meadow-steppe (AMS)) during the growing season in 2004 and 2005. P_{max} values were derived from the rectangular hyperbolic model with a window of 10 days data. For most periods in 2005 at TS, P_{max} could not be derived from rectangular hyperbolic model due to the severe drought stress.

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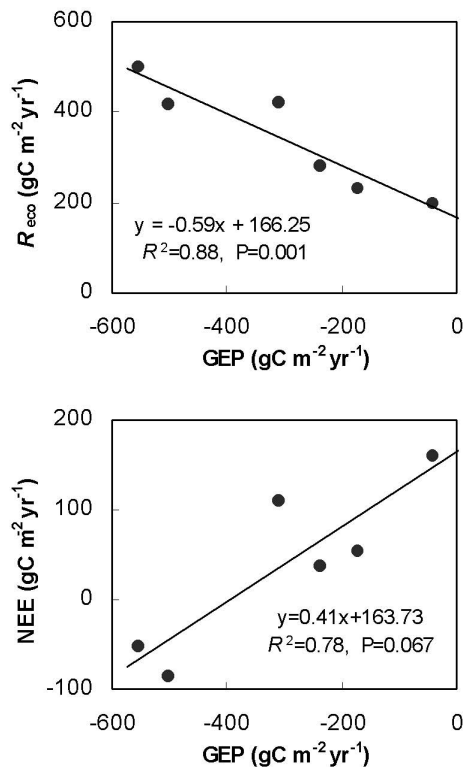


Fig. 8. Ecosystem respiration (R_{eco}) and net ecosystem exchange of CO_2 (NEE) versus gross ecosystem production (GEP) across the three sites in 2004 and 2005.

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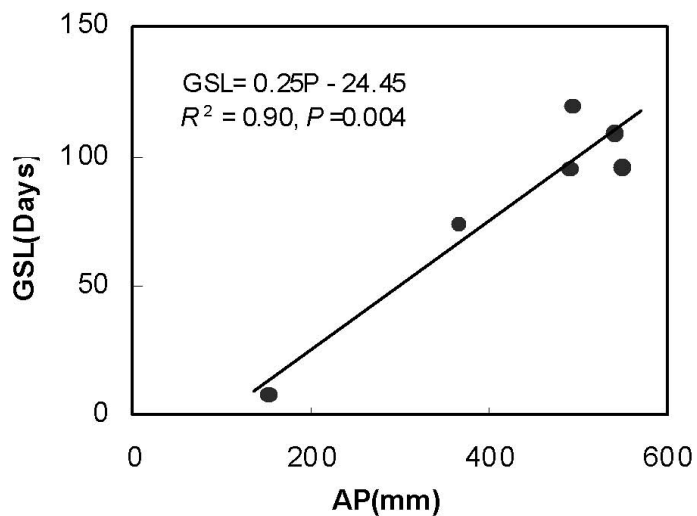


Fig. 9. Relationships between growing season length (GSL) and annual precipitation (AP) across the three grasslands sites in 2004 and 2005.

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