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Ecosystem carbon exchange under different land use on the Qinghai-Tibetan plateau

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Abstract

There is a great uncertainty about the effect of land use change on grassland ecosystem in the Tibetan Plateau. Net ecosystem carbon exchange (NEE) was measured for native alpine meadow with winter grazing (NAM), abandoned cropland/pasture (APL), perennial *Elymus nutans* (PEN), and annual oat pasture (AO) on the Tibetan plateau, during the growing seasons in 2009 and 2010 using a transparent chamber technique (*Licor-6400*). AO significantly decreased annual average NEE by 21.6, 23.7, and 15.7% compared to PEN, NAM, and APL during the growing season in 2010. Compared to PEN, NAM, and APL, AO significantly decreased average ecosystem respiration (R_e) by 21.1, 52.3, and 39.3%, respectively, during the growing season in 2009. Soil moisture and total aboveground and belowground biomass together explained 39.6% of NEE variation and 71% in gross primary productivity variation. Soil moisture and belowground biomass explained about 83.1% of the R_e variation. Our results indicated that it is possible to convert APL to PEN in the region because it could result in a higher NEE together with higher forage production compared to AO.

Additional key words: ecosystem carbon exchange; land use; Tibetan plateau.

Introduction

Land use change is one of the most important contributors to globally increasing atmospheric CO_2 concentrations, particularly in developing countries (IPCC 2007), because it affects the ecosystem carbon (C) cycling (Guo and Gifford 2002). Net exchange of CO_2 in ecosystems (NEE) is mainly controled by water availability, air temperature, and vegetation type (Flanagan *et al*. 2002, Monson *et al*. 2002, Wohlfahrt *et al*. 2003, Schmitt *et al*. 2010, Liu *et al*. 2011, Wolf *et al*. 2011a,b). NEE depends on the balance between net photosynthesis (P_N) and carbon loss during respiration (R_e) (Cai *et al*. 2010, 2011). GPP is mainly controled by the level of photosynthetically active radiation, temperature, and water availability, whereas R_e is primarily driven by soil microbial activity and plant growth (Bond-Lamberty *et al*. 2004a, 2004b, Bahn *et al*. 2008, Gilmanov *et al*. 2010). Relationships between NEE and its abiotic and biotic drivers have been analyzed in mountain grasslands (Gu *et al*. 2003, Kato *et al*. 2004a,b; Wohlfahrt *et al*. 2008, Fu *et al*. 2009, Hirota *et al*. 2009, Yashiro *et al*. 2010).

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Abbreviations: AB – aboveground biomass; AB/BB – the ratio of aboveground to belowground biomass; AO – annual oat pasture; APL – abandoned cropland/pasture; BB – belowground biomass for 0–20 cm; GPP – gross primary production; P_N – net photosynthesis; NAM – native alpine meadow; NEE – net ecosystem exchange; PEN – perennial *Elymus nutans* pasture; R_e – ecosystem respiration; SM – seasonal average soil moisture at 5 cm; ST – seasonal average soil temperature at 5 cm; TB – total biomass.
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The importance of grasslands for the global carbon balance is increasingly recognized (Hunt *et al*. 2004, Novick *et al*. 2004, Xu and Baldocchi 2004). In the traditional farming system of the alpine region on the Tibetan Plateau, China, degraded grasslands and insufficient fodder in the winter season limit grazing livestock productivity (Dong *et al*. 2003, Harris 2010). Annual oats (*Avena sativa* L.) and perennial grass species have been widely used as winter feed supplements for grazing livestock in the region (Dong *et al*. 2002). However, there is little information about NEE in alpine meadows under different land uses (Zhang *et al*. 2012).

The central government of China has invested significant financial resources to restore degraded grasslands in the region since 2000. Nevertheless, some croplands were abandoned after a few years of cultivation. There are two main options for management of abandoned cropland: natural restoration to alpine meadow, and conversion to pasture to meet the forage requirement for livestock in the region. Thus, the aims of this study were to assess (*1*) the effects of land use on NEE, R_e, and GPP, and (*2*) variations of NEE, R_e, and GPP on the Qinghai-Tibetan plateau.

Materials and methods

Site description: The experimental site is located at the Haibei Alpine Meadow Ecosystem Research Station at 37°37′N, longitude 101°12′E. The station is located in the northeastern portion of the Qinghai-Tibet plateau in a large valley surrounded by the Qilian Mountains (3,200 m a.s.l., Zhao and Zhou 1999). The station experiences a typical plateau continental climate, which is dominated by the southeast monsoons from May to September during the summer and high pressure systems from Siberia in the winter. The summer is short and cool, and the winter is long and severely cold. Mean annual temperature is –1.14°C; mean annual precipitation is 529.9 mm from 1981 to 2010, 80% of which falling during the summer monsoon season. The mean temperature and mean rainfall from 1 May to 30 September in 2009 and 2010 were 8.3 and 8.9°C, and 317 and 413 mm, respectively.

Plant community of a natural alpine meadow at the experimental site is dominated by *Kobresia humilis, Festuca ovina, Elymus nutans, Poa pratensis, Carex scabrirostris, Scripus distigmaticus, Gentiana straminea, Gentiana farreri, Leontop odiumnanum, Blvsmus sino-compressus, Potentilla nivea*, and *Dasiphora fruticosa*. Average aboveground and belowground (0–20 cm) biomass was about 350 and 3,000 g m^{-2}, respectively. The soil is Mat-Gryic Cambisol (Chinese Soil Taxonomy Research Group 1995), corresponding to Gelic Cambisol (WRB 1998).

Land-use experiments: There were two kinds of land utilization before the experiment: the natural alpine meadow with grazing during the winter and abandoned croplands/pastures. Some farmers changed the abandoned croplands/pastures into annual oat and perennial *Elymus nutans.* A part of the abandoned croplands/pastures (*i.e.*, 100 × 100 m) was fenced in 2007. Totally 12 plots of three different land utilizations were randomly located within the area, with four replicate plots for each treatment: (*1*) the abandoned cropland/pasture that had been restored for eight years after cultivation in the 1960s (APL); (*2*) the sown perennial *Elymus nutans* pasture in May 2008 (PEN), and (*3*) the sown annual oat [600 kg(seed) ha^{-1}] pastures cultivated on former APL by the end of May with tillage from 2009 to 2010 (AO). Similar to local farmers, the abandoned pasture was plowed into about 15 cm soil depth by a small tractor in the middle of May before the experiment. There was no control of the tillage activities. Four plots were distributed randomly in the natural alpine meadow with winter grazing (NAM) outside the land never cultivated before the experiment. All aboveground biomass was clipped with 5 cm height stubble by the end of October for the abandoned cropland and pastures. Natural alpine meadow was used for grazing during the winter. Each plot (4.0 × 4.5 m) was separated by a 2 m buffer zone (Zhang *et al*. 2012). Transparent chamber-based measurements of NEE and its components (GPP and R_e) were used for NAM, APL, PEN, and AO during the growing seasons of 2009 and 2010 to determine whether certain strategies can be developed to balance forage production and environmental conservation.

Soil: Soil temperature was measured by digital thermometers at 5 cm depth in all plots during both 2009 and 2010 using time domain reflectometry (*CS615, Campbell Scientific, Inc*., USA), at the same time as R_e and NEE measurements.

Biomass: Peak aboveground biomass was estimated by clipping a 1 m × 1 m quadrat in each plot during late August each year. At the center of each quadrat, two soil cores of 0–20 cm depth were collected using an 8 cm diameter soil auger. Samples of soil cores were washed to remove the soil in order to estimate belowground biomass. All samples were oven-dried at 65°C to constant mass (Zhang *et al*. 2012).

Gas-exchange: Ecosystem C fluxes were measured with a transparent chamber (0.4 × 0.4 × 0.6 m^3) with a wall material of acrylic sheet, allowing over 90% light transmittance, attached to an infrared gas analyzer (*LI-6400*; *LiCor*, Lincoln, NE, USA) (Huxman *et al*. 2004, Bubier *et al*. 2007). The square box was inserted directly into the meadow soil about 10 cm below the soil surface at a location about 0.5 m away from the edges of the plots. The frames provided a flat base between the soil surface and the CO_2 sampling chamber (Lin *et al*. 2009, 2011). Ecosystem gas exchange was measured at 1-week intervals (9:00–11:00 h) which may stand for the daily average value (Lin *et al*. 2011) from May to October each year. When measuring NEE, the transparent chamber was put on the metal base rim with the sink filled with water to seal air. Two small electric fans ran continuously to promote air mixing within the chamber during measurement. Six consecutive recordings of CO_2 and water vapor concentrations were taken on each frame at 10-s intervals during a 60-s period. CO_2 concentrations were allowed to build up or draw down over time, from which flux rates were determined from the time-course of the concentration to NEE. Respiration at ecosystem level (R_e) was measured using a lightproof cloth mantle to cover the transparent chamber. Details of the static-chamber flux calculations can be found in the soil-flux calculation procedure of the *LI-6400* manual (*LiCor Inc.* 2004):

$$NEE = slope \times H \times P \times 293/[22.4 \times 0.001 \times 101.325 \times (273 + T)/10]$$

where slope was calculated using data for each group of CO_2 flux; H is sampling chamber height; P is atmospheric pressure; and T is the temperature in the chamber. Positive and negative NEE values represent net C release by, and uptake from, the ecosystem, respectively.

The relationship between NEE [$\mu mol(CO_2)\ m^{-2}\ s^{-1}$] and GPP [$\mu mol(CO_2)\ m^{-2}\ s^{-1}$] was assessed according to Kowalski *et al*. (2003): GPP = R_e – NEE.

Statistical analysis: A general linear model-repeated measures define factors (*SPSS 13.0*, *SPSS Inc*., Chicago, IL, USA) was used to assess the significance of the impacts of the treatment, year, sampling day, and their interactions on soil temperature and soil moisture, aboveground and belowground biomass, NEE, R_e, and GPP with the year and sampling day as within subject variables and treatment as a between-subject variable. For each sampling day per year, significant differences in NEE, R_e, and GPP between treatments were assessed by one-way analysis of variance (*ANOVA*) and least significance difference (LSD). To test the correlations between soil temperature and soil moisture and NEE, *Pearson*'s correlation and partial correlation analysis were performed. Stepwise multiple linear regression analysis was performed to test the possible dependency of NEE on soil moisture, soil temperature, aboveground biomass, belowground biomass (0–20 cm), total aboveground and belowground biomass, and the ratio of aboveground biomass to belowground biomass. All significances mentioned in the text were at the 0.05 level.

Results

Soil temperature and soil moisture: The average soil temperature at 5-cm depth for PEN, NAM, APL, and AO was 10.8,12.2,10.6, and 10.4°C; the average soil moisture at 5-cm depth was 30.9, 38.0, 34.0, and 27.8% across the experiment years for PEN, NAM, APL, and AO, respectively (Fig. 1). Land use, year, sampling date, and interactions between year and sampling date significantly affected soil temperature and soil moisture. Comparing NAM with PEN, APL and AO, the mean seasonal soil temperature increased by 1.04, 1.07, and 1.58°C in 2009 and 1.90, 2.21, and 2.05°C in 2010, respectively (Fig. 1*E*). No significant difference was observed between PEN, APL, and AO treatments in 2010, while AO significantly decreased seasonal average soil temperature compared to PEN and APL in 2009 (Fig. 1*A*,*B*). Compared to PEN, APL, and AO, NAM increased seasonal mean soil moisture at 5-cm depth by approximately 8.2, 4.4, and 9.1% in 2009 and by 6.0, 3.6, and 11.3% in 2010 (Fig. 1*F*). Seasonal average soil moisture was the lowest for AO treatments in both 2009 and 2010 (Fig. 1*F*).

Biomass: Land use, year, and their interactions significantly affected aboveground and belowground biomass. In 2009, aboveground biomass was the highest for AO compared to the other land uses. The aboveground biomass was 2–3 times higher for PEN and AO than that for NAM and APL in both 2009 and 2010. NAM had the highest belowground biomass compared to PEN and AO in 2009 and 2010 (Fig. 2*B*). Differences in total biomass among treatments followed the same pattern as the differences in belowground biomass in 2009 and 2010 (Fig. 2*C*). Compared with NAM and APL, ratios of aboveground and belowground biomass were higher for PEN and AO in 2009 and 2010; PEN had the lower ratio of aboveground to belowground biomass in AO in 2009 and the higher ratio in 2010 (Fig. 2*D*).

NEE, R_e, and GPP: Land use and year significantly affected R_e. There were significant interactive effects between land use, sampling date, and/or year on NEE and/or R_e and GPP (Table 1). There were significant differences in daily NEE from 13 of 23 samples in 2009 (Fig. 3A) and 7 out of 23 samples in 2010 (Fig. 3C), respectively, in daily R_e from 10 out of 23 samples in 2009 (Fig. 4A) and 5 out of 23 samples in 2010 (Fig. 4C), and in daily GPP from 10 out of 23 samples in 2009 (Fig. 5A) and 8 out of 23 samples in 2010 (Fig. 5C), respectively.

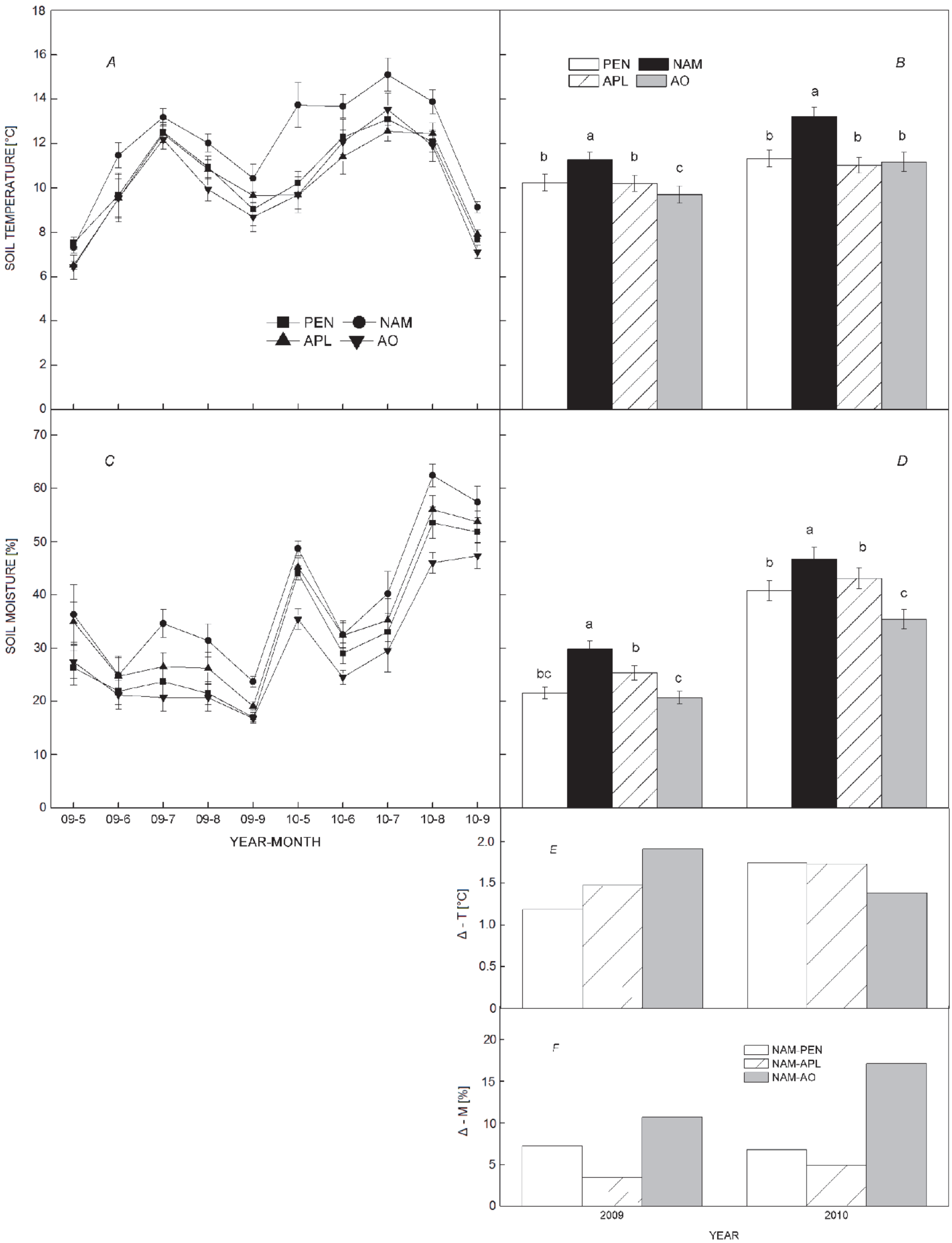

Fig. 1. Daily (*A*) and yearly (*B*) average soil temperature, and daily (*C*) and yearly (*D*) average soil moisture at depth of 5 cm for different land uses, soil temperature (*E*), and soil moisture (*F*) differences between NAM and PEN, APL, AO at 5-cm soil depths in 2009 and 2010. PEN – perennial *Elymus nutans* pasture; NAM – native alpine meadow; APL – abandoned cropland/pasture; AO – annual oat pasture. Bars indicate mean ± 1 SE. *Different letters* indicate significant differences at $p = 0.05$.

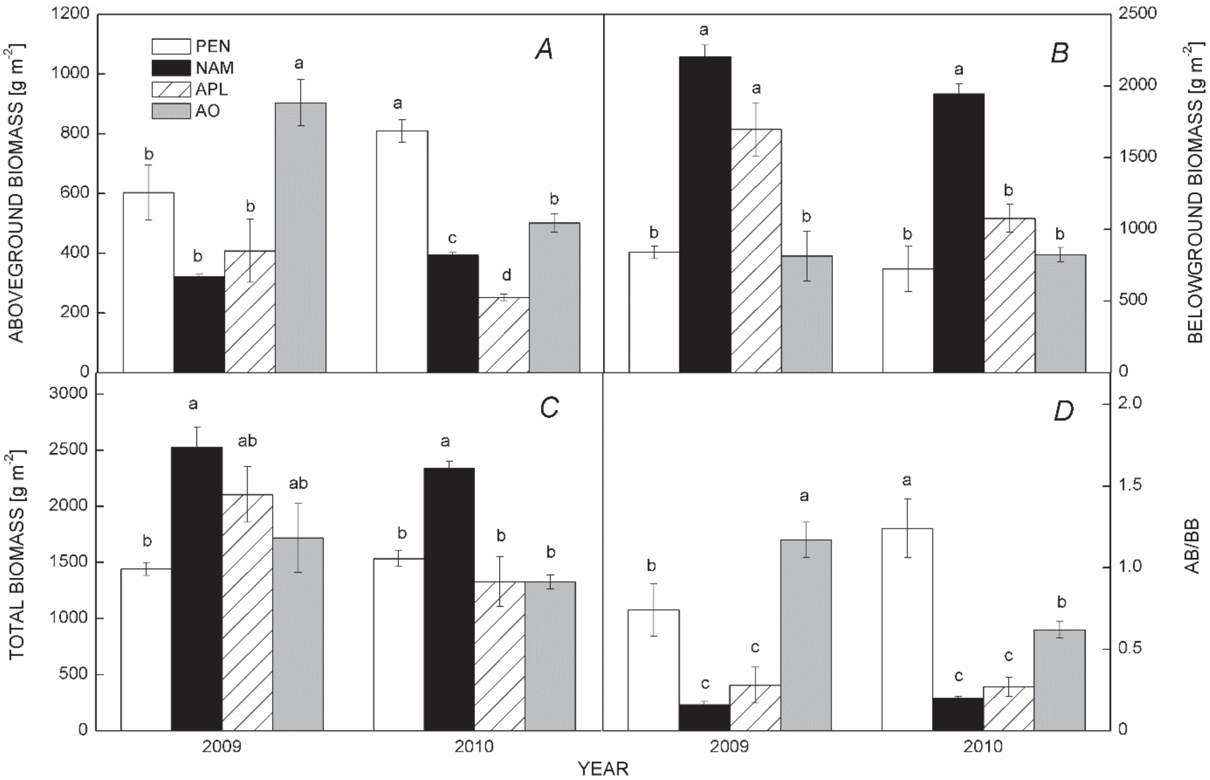

Fig. 2. Aboveground (*AB*), belowground (*BB*) and total biomass, *AB/BB* (the ratio of aboveground to belowground biomass) for NAM, APL, PEN, and AO in 2009 and 2010. PEN – perennial *Elymus nutans* pasture; NAM – native alpine meadow; APL – abandoned cropland/pasture; AO – annual oat pasture. Bars indicate mean ± 1 SE. *Different letters* indicate significant differences at $p = 0.05$.

Table 1. Net ecosystem exchange of CO_2 (NEE), ecosystem respiration (R_e), and gross primary productivity (GPP) from repeated-measure *ANOVA* using PEN, NAM, APL, and AO as main factors from 2009 to 2010.

Model	NEE		R_e		GPP	
	F	*p*	*F*	*p*	*F*	*p*
Land use	1.670	0.250	10.263	0.004	3.644	0.064
Year	4.767	0.061	39.351	<0.001	0.405	0.543
Year × land use	0.241	0.866	2.777	0.110	0.269	0.846
Day	20.339	0.002	96.710	<0.001	39.255	<0.001
Day × land use	7.252	0.011	9.008	0.006	7.864	0.009
Year × day	49.853	<0.001	49.651	<0.001	74.703	<0.001
Year × day × land use	13.875	0.002	0.769	0.543	11.018	0.003

The NEE peaked in July and August (Figs. 3*A*,*C*) in 2009 and 2010, respectively. Land use did not significantly affect seasonal NEE in 2009 (Fig. 3*B*), however, AO significantly decreased seasonal average NEE by 21.6, 23.7 and 15.7% during the growing season compared with PEN, NAM, and APL in 2010, respectively (Fig. 3D).The daily NEE of AO decreased after harvest in September in 2009 and 2010 (Fig. 3*A*,*C*).

The seasonal average R_e of NAM was significantly greater (by 60.9 and 53.0%) than that of PEN and AO during the growing season in 2009. The seasonal average R_e of AO significantly decreased by 21.1, 52.3 and 39.3% compared with PEN, NAM, and APL treatments, respectively (Fig. 4). However, R_e for PEN, NAM, and APL peaked in July, while AO in August 2010 (Fig. 4*A*,*C*).

There were no significant differences between land uses in seasonal average GPP during the growing season in 2009 (Fig. 5*B*). However, AO significantly decreased the seasonal average GPP by 20.1, 28.2, and 20.9% during the growing season in 2010 compared with PEN, NAM and APL, respectively. The seasonal dynamics of GPP followed a one-peak pattern with higher values in the middle of the growing seasons (Fig. 5*A*,*C*).

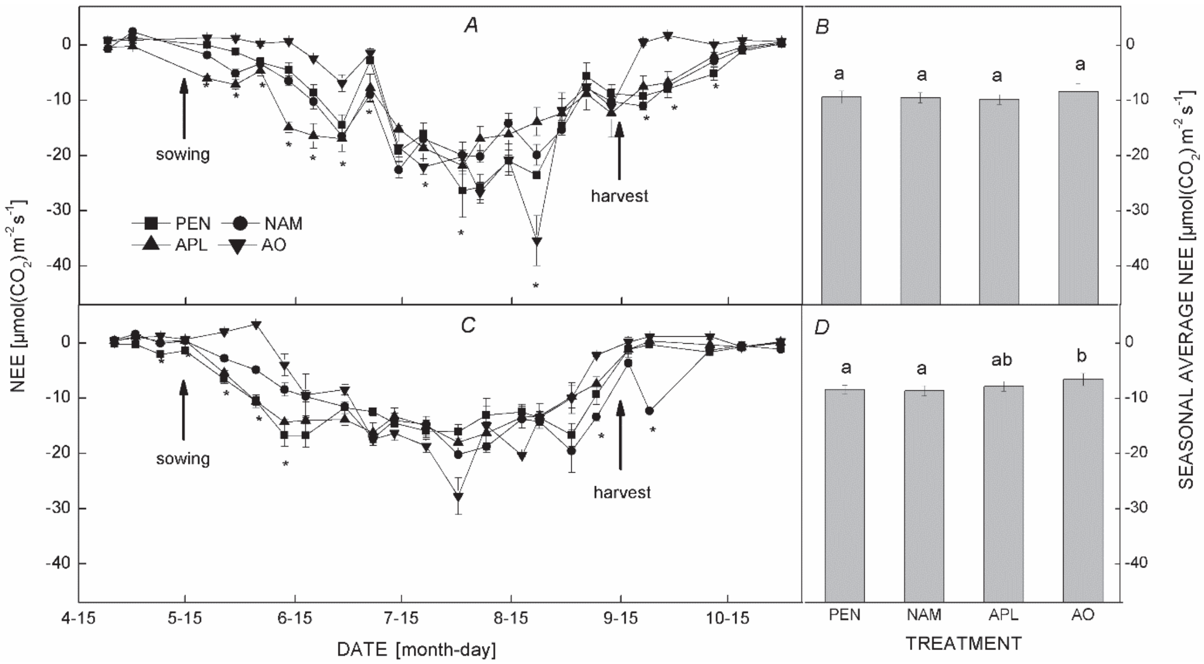

Fig. 3. Daily and seasonal average values in net ecosystem exchange (NEE) under different land uses in 2009 (*A*,*B*) and 2010 (*C*,*D*). PEN – perennial *Elymus nutans* pasture; NAM – native alpine meadow; APL – abandoned cropland/pasture; AO – annual oat pasture. Bars indicate SE. * – significant difference between treatments. *Different letters* indicate significant differences at $p<0.05$.

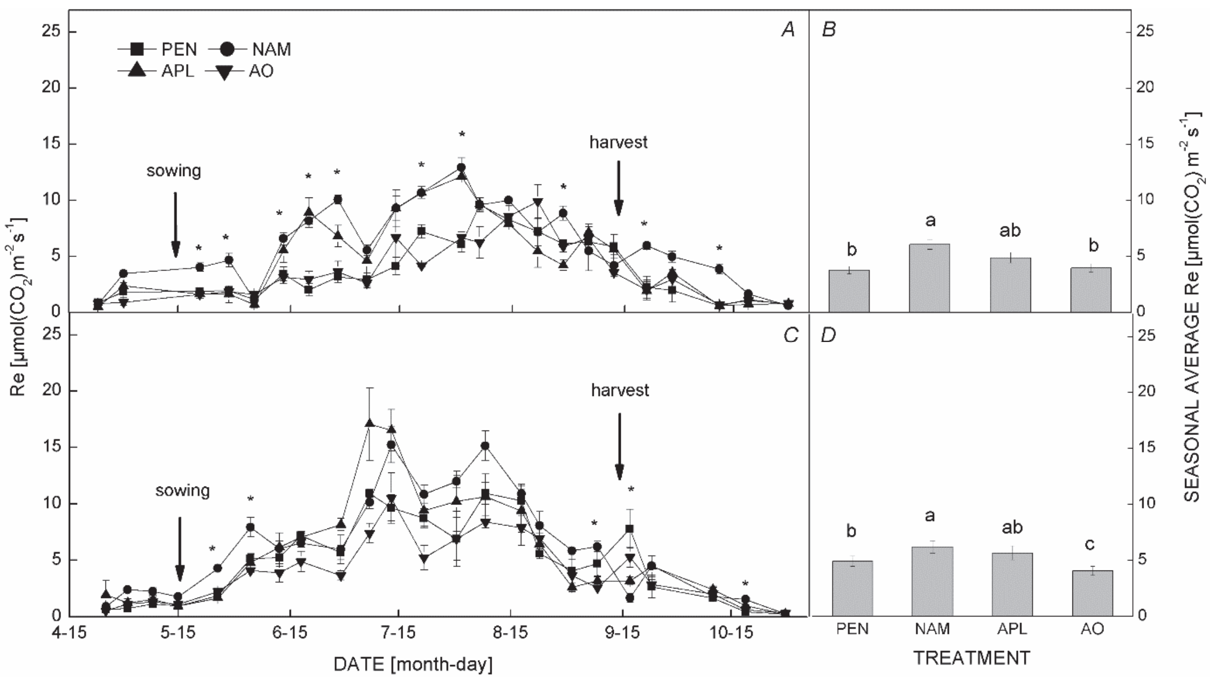

Fig. 4. Daily and seasonal average values in ecosystem respiration (R_e) under different land uses in 2009 (*A*,*B*) and 2010 (*C*,*D*). PEN – perennial *Elymus nutans* pasture; NAM – native alpine meadow; APL – abandoned cropland/pasture; AO – annual oat pasture. Bars indicate SE. * – significant difference between treatments. *Different letters* indicate significant differences at $p<0.05$.

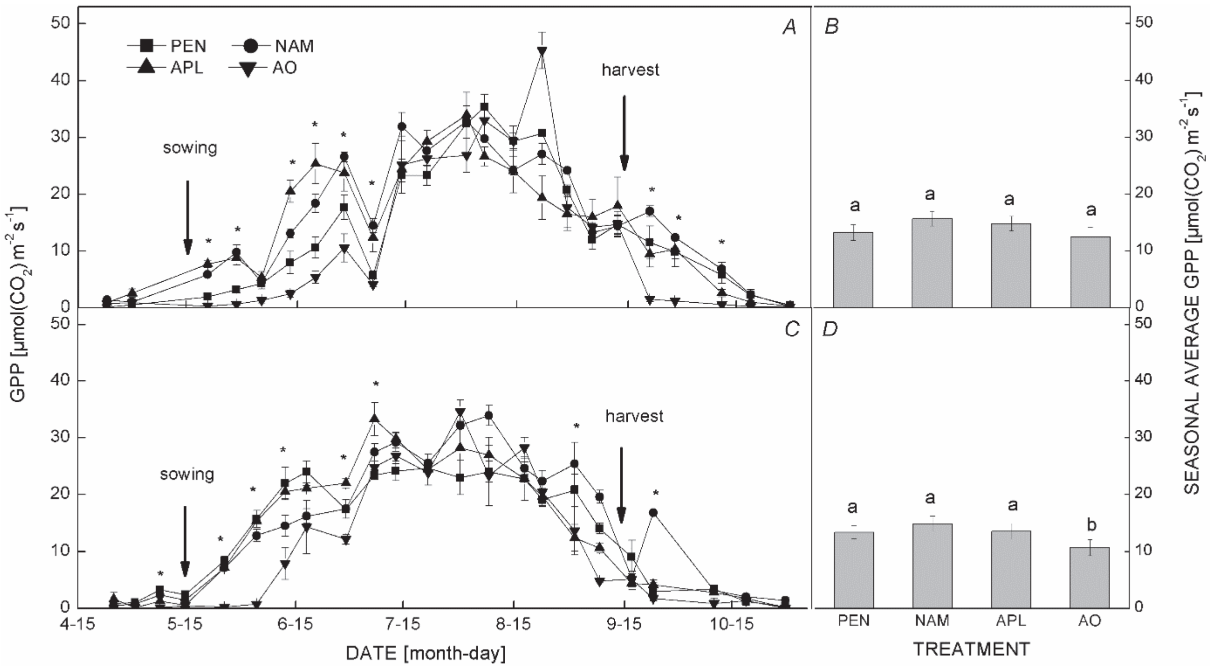

Fig. 5. Daily and seasonal average values in gross primary productivity (GPP) under different land uses during 2009 (*A*,*B*) and 2010 (*C*,*D*). PEN – perennial *Elymus nutans* pasture; NAM – native alpine meadow; APL – abandoned cropland/pasture; AO – annual oat pasture. Bars indicate SE. * – significant difference between treatments. *Different letters* indicate significant differences at p<0.05.

Table 2. Models of daily NEE, R_e, and GPP, soil temperature, and soil moisture through stepwise regression under different land uses. Y_1 – net ecosystem exchange (NEE); Y_2 – ecosystem respiration (R_e); Y_3 – gross primary production (GPP). SMb – soil moisture at 5 cm; ST – soil temperature at 5 cm. PEN – perennial *Elymus nutans* pasture; NAM – native alpine meadow; APL – abandoned cropland/pasture; AO – annual oat pasture.

Activity	Treatment	Linear model	r^2	p
Land use	Pooled data	Y_1 = 2.246 – 1.082 ST – 0.053 SM	0.18	<0.001
		Y_2 = –2.856 + 0.650 ST + 0.059 SM	0.29	<0.001
		Y_3 = –5.102 + 1.732 ST + 0.112 SM	0.26	<0.001
Land use	NAM	Y1 = 0.650 – 0.697 ST – 0.115 SM	0.20	<0.001
		Y_2 = –1.710 + 0.596 ST + 0.058 SM	0.28	<0.001
		Y_3 = –2.360 + 1.293 ST + 0.173 SM	0.27	<0.001
	APL	Y_1 = –0.927 – 1.041 ST	0.22	<0.001
		Y_2 = –6.132 + 1.037 ST + 0.056 SM	0.37	<0.001
		Y_3 = –2.981 + 2.045 ST	0.34	<0.001
	PEN	Y_1 = –0.953 – 0.986 ST	0.15	<0.001
		Y_2 = –2.090 + 0.544 ST + 0.055 SM	0.27	<0.001
		Y_3 = 0.795 + 1.505 ST	0.21	<0.001
	AO	Y_1 = 7.532 – 1.645 ST	0.22	<0.001
		Y_2 = 1.097 + 0.369 ST	0.13	<0.001
		Y_3 = –6.135 + 1.991 ST	0.22	<0.001

Relationships between NEE, R_e, GPP, and abiotic and biotic variables measured: The soil temperature was the main factor (Table 2) explaining 16.4, 23.6, and 23.4% of variations in daily NEE, R_e, and GPP, respectively (Table 2). The relationships between GPP and R_e and soil temperature and moisture were positive, while it was negative with NEE; the dependency of daily NEE, R_e, and GPP on soil temperature varied with land use (Table 2). For the NAM, APL, PEN, and AO treatments, soil temperature explained about 10.1, 22.2, 14.8, and 21.6% of variation in NEE, 21.1, 33.8, 20.8, and 12.9% of variation in R_e, and 17.1, 34.4, 21.0, and 21.9% of variation in GPP, respectively. Soil moisture explained 9.5, 6.6, and 13.3% of–daily variations in NEE, R_e, and GPP for NAM, while it did not significantly affect daily NEE, R_e, or GPP for APL, PEN, or AO (Table 2). Soil moisture explained 23.2, 74.9, and 56.7% of seasonal variations in NEE, R_e and GPP, while total biomass explained 14.3, 8.1, and 16.4% of their seasonal variations, respectively. However, seasonal GPP of NAM and APL was controled by the ratio of AB and BB, whereas it was mainly controled by soil moisture for PEN. AB explained 84.4 and 91.4% of variations NEE and GPP for NAM, and 91.6 and 8.5% of for PEN. However, seasonal GPP and NEE were mainly affected by the ratio of AB and BB for APL, which explained 82.9 and 84.2% of variations of GPP and NEE, respectively. There were no variables retained in the stepwise multiple regression model for NEE and GPP of AO.

Discussion

Variations in daily NEE, R_e and GPP: The daily variation of NEE, R_e, and GPP were significantly correlated with soil temperature and soil moisture (Table 2) according to the results of Cai *et al*. (2011) and Liu *et al*. (2011). This suggests that temperature and water availability affect GPP and respiration shapes the carbon balance over a range of spatio-temporal scales, similarly to previous reports (Anderson-Teixeira *et al*. 2011). Generally, daily R_e was significantly affected by the land use, whereas daily NEE and GPP by interactive effects between the land use and sampling date. This could have different reasons. R_e was mainly derived from soil respiration in grasslands (Wohlfahrt *et al*. 2005, Zhang *et al*. 2012). Higher soil temperature and soil moisture with higher belowground biomass caused greater R_e for NAM and APL before July compared to PEN and AO. However, the greater aboveground biomass of PEN and AO in July and August partially compensated for the difference in belowground biomass between the land uses, which eliminated the R_e differences. PEN and AO were clipped after September; it did not decrease R_e because it increased soil temperature by increasing soil and root respiration (Bahn *et al*. 2006). Moreover, GPP was mainly controled by photosynthetically active radiation, temperature, and water availability (Niu *et al*. 2008, Saito *et al*. 2009). Compared with NAM and APL, PEN in 2009 and AO in 2009 and 2010 had smaller aboveground biomass with lower soil temperature and soil moisture before July, which caused smaller daily GPP. However, daily GPP was greater for PEN and AO in August due to higher aboveground biomass, decreasing after harvesting in the middle of September. Meanwhile, in grasslands, some studies indicated that NEE is affected by interactions of microclimate, canopy structure, photosynthesis, and respiration (Gu *et al*. 2003, Wohlfahrt *et al*. 2003, Flanagan and Johnson 2005). Differences in daily NEE between NAM, APL, and PEN and AO mainly occurred before July. In particular, AO was sown by the end of May and harvested after the middle of September. Hussain *et al*. (2011) reported that it was a carbon source before June and after harvesting. Therefore, these results indicate that although AO pasture reduced daily R_e and GPP simultaneously due to lower soil temperature and soil moisture with lower aboveground biomass before July, the magnitude of the decline in daily GPP could be greater than that in daily R_e, which causes lower daily NEE in the alpine region.

Variations in seasonal average NEE, R_e and GPP: In general, when all data for all land uses were pooled, seasonal average NEE, R_e, and GPP were mainly affected by soil moisture and/or total aboveground and belowground biomass (Table 3). Compared with NAM and APL, PEN in 2009 and AO in 2009 and 2010 had smaller aboveground biomass with lower soil temperature and soil moisture before July, which caused smaller daily GPP.

Moreover, seasonal average NEE for NAM and PEN were positively correlated with the aboveground biomass, suggesting that aboveground biomass might have played a more important role in variations of seasonal NEE for NAM and PEN variations. However, positive correlation between seasonal average NEE and the ratio of aboveground to belowground biomass for APL suggested that higher aboveground biomass and lower belowground biomass might result in a lower carbon sink capacity in APL; it implies that belowground biomass could determine the seasonal average NEE for APL. Seasonal average R_e for AO was mainly influenced by abiotic factors (*i.e.*, soil moisture), whereas seasonal average NEE and GPP was significantly related to all variables measured for AO. This suggested that the controling factors on carbon sink capacity could be complex for annual forage production. Monson *et al*. (2002) highlighted that control of NEE could involve phenological variability, temporal variation in moisture availability, seasonal and interannual temperature variation, canopy structure, and variation in light intensity.

Seasonal average R_e was higher for NAM compared to PEN and AO in 2009 and 2010 (Fig. 4). First, PEN and AO significantly decreased soil temperature and soil moisture (Fig. 1) and belowground biomass (Fig. 2*B*) compared with NAM, which could decrease R_e (Lin *et al*. 2009, 2011, Li and Sun 2011, Ma *et al*. 2006).

Second, grazing during the winter might increase R_e in NAM due to urine and dung patches reported by Lin *et al*. (2009). Third, similar to other findings (Liu *et al*. 2002, Rey *et al*. 2002), shallower roots of PEN and AO, compared with NAM, could be more sensitive to water limitation and seasonal drought which decreased R_e. Fourth, belowground biomass of NAM was 2–3 times higher than that of PEN and AO (Fig. 3*B*,*D*) and thus causing greater CO_2 respiration (Almagro *et al*. 2009) by the greater root biomass, where lack of disturbance provides rich carbon supply for microbial activity (Frank *et al*. 2002, 2006).

Table 3. Relationships between seasonal average NEE, R_e, and GPP seasonal average soil temperature and moisture at 5-cm soil depth, aboveground biomass, belowground biomass, the ratio of aboveground to belowground biomass and total biomass (aboveground and belowground biomass). Y_1 – net ecosystem exchange (NEE); Y_2 – ecosystem respiration (R_e); Y_3 – gross primary production (GPP). SM – seasonal average soil moisture at 5 cm; ST – seasonal average soil temperature at 5 cm; AB – aboveground biomass; BB – belowground biomass for 0–20 cm; TB – total biomass; AB/BB – the ratio of aboveground to belowground biomass. PEN – perennial *Elymus nutans* pasture; NAM – native alpine meadow; APL – abandoned cropland/pasture; AO – annual oat pasture.

Activity	Treatment	Linear model	r^2	p
Land use	Pooled data	$Y_1 = -5.889 - 0.084$ SM $- 0.001$ TB	0.40	0.005
		$Y_2 = 1.616 + 0.124$ SM $+ 0.001$ BB	0.83	<0.001
		$Y_3 = 6.866 + 0.227$ SM $+ 0.002$ TB	0.71	<0.001
Land use	NAM	$Y_1 = -3.438 - 0.024$ AB	0.84	0.010
		$Y_2 = -1.915 + 0.034$ AB $- 14.429$ AB/BB	0.98	0.003
		$Y_3 = 3.169 + 0.047$ AB	0.91	0.003
	APL	$Y_1 = -15.530 + 12.923$ AB/BB	0.84	0.010
		$Y_2 = 2.333 + 0.131$ SM	0.71	0.034
		$Y_3 = 23.878 - 18.649$ AB/BB	0.83	0.012
	PEN	$Y_1 = -6.950 - 0.007$ AB	0.92	0.003
		$Y_2 = 1.891 + 0.116$ SM	0.92	0.002
		$Y_3 = 10.125 + 0.135$ SM $+ 0.006$ AB $- 0.001$ BB	1.00	<0.001
	AO	$Y_2 = 1.699 + 0.154$ SM	0.72	0.033

Conclusion: Our results showed that aboveground biomass were 2–3 times higher for PEN and AO than that of NAM and APL, but belowground biomass was significantly lower for PEN and AO compared with NAM and APL in both 2009 and 2010. AO reached lower NEE compared with NAM, APL, and PEN in 2010, when precipitation was rich. These results imply that the conversion of historical cropland to pasture, and especially to perennial pasture, is preferable to natural restoration to alpine meadow, because of the strong demand for forage production by local farmers and herders.

References

Almagro M., López J., Querejeta J.I. *et al.*: Temperature dependence of soil CO_2 efflux is strongly modulated by seasonal patterns of moisture availability in a Mediterranean ecosystem. – Soil Biol. Biochem. **41**: 594-605, 2009.

Anderson-Teixeira K.J., Delong J.P., Fox A.M. *et al.*: Differential responses of production and respiration to temperature and moisture drive the carbon balance across a climatic gradient in New Mexico. – Glob. Change Biol. **17**: 410-424, 2011.

Bahn M., Knapp M., Garajova Z. *et al.*: Root respiration in temperate mountain grasslands differing in land use. – Glob. Change Biol. **12**: 995-1006, 2006.

Bahn M., Rodeghiero R, Anderson-Dunn M. *et al.*: Soil respiration in European grasslands in relation to climate and assimilate supply. – Ecosystems **11**: 1352-1367, 2008.

Bond-Lamberty B., Wang C.K., Gower S.T.: Contribution of root respiration to soil surface CO_2 flux in a boreal black spruce chronosequence. – Tree Physiol. **24**: 1387-1395, 2004a.

Bond-Lamberty B., Wang C.K., Gower S.T.: A global relationship between the heterotrophic and autotrophic components of soil respiration? – Glob. Change Biol. **10**: 1756-1766, 2004b.

Bubier J.L., Moore T.R., Bledzki L.A.: Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. – Glob. Change Biol. **13**: 1168-1186, 2007.

Cai T.B., Flanagan L.B., Syed K.H.: Warmer and drier conditions stimulate respiration more than photosynthesis in a boreal peatland ecosystem: Analysis of automatic chambers and eddy covariance measurements. – Plant Cell Environ. **33**: 394-407, 2010.

Cai T.B., Price D.T., Orchansky A.L. *et al.*: Carbon, water, and energy exchanges of a hybrid poplar plantation during the first five years following planting. – Ecosystems **14**: 658-671, 2011.

Chinese Soil Taxonomy Research Group: Chinese Soil Taxonomy. Pp. 58-147. Science Press, Beijing 1995.

Dong S.K., Hu Z.Z., Long R.J. *et al.*: Effect of mixtures of perennial grasses on the vegetation and soil of grassland and the economic values of mixture grassland in an alpine region. – J. Soil Water Conserv. **16**: 98-101, 2002.

Dong S.K., Long R.J., Hu Z.Z. *et al.*: Productivity and nutritive value of some cultivated perennial grasses and mixtures in the alpine region of the Tibetan Plateau. – Grass Forage Sci. **58**: 302-308, 2003.

Flanagan L.B., Johnson B.G.: Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. – Agr. Forest Meteorol. **130**: 237-253, 2005.

Flanagan L.B., Wever L.A., Carlson P.J.: Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. – Glob. Change Biol. **8**: 599-615, 2002.

Frank A.B., Liebig M.A., Hanson J.D.: Soil carbon dioxide fluxes in northern semiarid grasslands. – Soil Biol. Biochem. **34**: 1235-1241, 2002.

Frank A.B., Liebig M.A., Tanaka D.L.: Management effects on soil CO_2 efflux in northern semiarid grassland and cropland. –

Soil Till. Res. **89**: 78-85, 2006.
Fu Y., Zheng Z., Yu G. *et al.*: Environmental influences on carbon dioxide fluxes over three grassland ecosystems in China. – Biogeosciences **6**: 2879-2893, 2009.
Gilmanov T.G., Aires L., Barcza Z. *et al.*: Productivity, respiration, and light-response parameters of world grassland and agro-ecosystems derived from flux-tower measurements. – Rangeland Ecol. Manag. **63**: 16-39, 2010.
Gu S., Tang Y.H., Du M.Y. *et al.*: Short-term variation of CO_2 flux in relation to environmental controls in an alpine meadow on the Qinghai-Tibetan Plateau. – J. Geophys. Res. **108**: 4670-4678, 2003.
Guo L.B., Gifford R.M.: Soil carbon stocks and land use change: A meta-analysis. – Glob. Change Biol. **8**: 345-360, 2002.
Harris R.B.: Rangeland degradation on the Qinghai-Tibetan plateau: A review of the evidence of its magnitude and causes. – J. Arid Environ. **74**: 1-12, 2010.
Hirota M., Zhang P., Gu S. *et al.*: Altitudinal variation of ecosystem CO_2 fluxes in an alpine grassland from 3600 to 4200 m. – J. Plant Ecol. **2**: 197-205, 2009.
Hunt J.E., Kelliher F.M., McSeveny T.M. *et al.*: Long-term carbon exchange in sparse, seasonally dry tussock grassland. – Glob. Change Biol. **10**: 1785-1800, 2004.
Hussain M.Z., Gruenwald T., Tenhunen J.D.: Summer drought influence on CO_2 and water fluxes of extensively managed grassland in Germany. – Agr. Ecosyst. Environ. **141**: 67-76, 2011.
Huxman T.E., Snyder K.A., Tissue D. *et al.*: Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. – Oecologia **141**: 254-268, 2004.
IPCC. Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment. – In: Solomon S., Qin D., Manning M. (ed.): Report of the Intergovernmental Panel on Climate Change. Pp. 996. Cambridge University Press, Cambridge 2007
Kato T., Tang Y.H., Gu S. *et al.*: Carbon dioxide exchange between the atmosphere and an alpine meadow ecosystem on the Qinghai-Tibetan Plateau, China. – Agr. Forest Meteorol. **124**: 121-134, 2004a.
Kato T., Tang Y.H., Gu S. *et al.*: Seasonal patterns of gross primary production and ecosystem respiration in an alpine meadow ecosystem on the Qinghai-Tibetan Plateau. – J. Geophys. Res. **109**: D12109, 2004b.
Kowalski S., Sartore M., Burlett R. *et al.*: The annual carbon budget of a French pine forest (*Pinus pinaster*) following harvest. – Glob. Change Biol. **9**: 1051-1065, 2003.
Li G.Y., Sun S.C.: Plant clipping may cause overestimation of soil respiration in a Tibetan alpine meadow, southwest China. – Ecol. Res. **26**: 497-504, 2011.
Lin X.W., Wang S.P., Ma X.Z. *et al.*: Fluxes of CO_2, CH_4, and N_2O in an alpine meadow affected by yak excreta during summer grazing periods on the Qinghai-Tibetan plateau. – Soil Biol. Biochem. **41**: 718-725, 2009.
Lin X.W., Zhang Z.H., Wang S.P. *et al.*: Response of ecosystem respiration to warming and grazing during the growing seasons in the alpine meadow on the Tibetan plateau. – Agr. Forest Meteorol. **151**: 792-802, 2011.
Liu J., Jiang P.K., Wang H.L. *et al.*: Seasonal soil CO_2 efflux dynamics after land use change from a natural forest to Moso bamboo plantations in subtropical China. – Forest Ecol. Manag. **262**: 1131-1137, 2011.
Liu X.Z., Wan S.Q., Su B. *et al.*: Response of soil CO_2 efflux to water manipulation in a tallgrass prairie. – Plant Soil **240**: 213-223, 2002.
Ma X.Z., Wang S.P., Wang Y.F. *et al.*: Short-term effects of sheep excreta on carbon dioxide, nitrous oxide and methane fluxes in typical grassland of Inner Mongolia. – New Zeal. J. Agr. Res. **49**: 285-297, 2006.
Monson R.K., Turnipseed A.A., Sparks J.P. *et al.*: Carbon sequestration in a high-elevation, subalpine forest. – Glob. Change Biol. **8**: 459-478, 2002.
Niu S.L., Wu M.Y., Han Y. *et al.*: Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. – New Phytol. **177**: 209-219, 2008.
Novick K.A., Stoy P.C., Katul G.G. *et al.*: Carbon dioxide and water vapor exchange in a warm temperate grassland. – Oecologia **138**: 259-274, 2004.
Rey A., Pegoraro E.P., Tedeschi V. *et al.*: Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. – Glob. Change Biol. **8**: 851-866, 2002.
Saito M., Kato T., Tang Y.H.: Temperature controls ecosystem CO_2 exchange of an alpine meadow on the northeastern Tibetan Plateau. – Glob. Change Biol. 15: 221-228, 2009.
Schmitt M., Bahn M., Wohlfahrt G. *et al.*: Land use affects the net ecosystem CO_2 exchange and its components in mountain grasslands. – Biogeosciences **7**: 2297-2309, 2010.
Wohlfahrt G., Anderson-Dunn M., Bahn M. *et al.*: Biotic, abiotic and management controls on the net ecosystem CO_2 exchange of European mountain grasslands. – Ecosystems 11: 1338-1351, 2008.
Wohlfahrt G., Anfang C., Bahn M. *et al.*: Quantifying nighttime ecosystem respiration of a meadow using eddy covariance, chambers and modelling. – Agr. Forest Meteorol. **128**: 141-162, 2005.
Wohlfahrt G., Bahn M., Newesely C. *et al.*: Canopy structure versus physiology effects on net photosynthesis of mountain grasslands differing in land use. – Ecol. Model. **170**: 407-426, 2003.
Wolf S., Eugster W., Potvin C. *et al.*: Strong seasonal variations in net ecosystem CO_2 exchange of a tropical pasture and afforestation in Panama. – Agr. Forest Meteorol. **151**: 1139-1151, 2011a.
Wolf S., Eugster W., Potvin C. *et al.*: Carbon sequestration potential of tropical pasture compared with afforestation in Panama. – Glob. Change Biol. **17**: 2763-2780, 2011b.
WRB. World Reference Base for Soil Resources. FAO/ISRIC/ISSS, Rome 1998.
Xu L.K., Baldocchi D.D.: Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. – Agr. Forest Meteorol. **123**: 79-96, 2004.
Yashiro Y., Shizu Y., Hirota M. *et al.*: The role of shrub (*Potentilla fruticosa*) on ecosystem CO_2 fluxes in an alpine shrub meadow. – J. Plant Ecol. 3: 89-97, 2010.
Zhang Z.H., Duan J.C., Wang S.P. *et al.*: Effects of land use and management on ecosystem respiration in alpine meadow on the Tibetan plateau. – Soil Till. Res. **124**: 161-169, 2012.
Zhao X.Q., Zhou X.M.: Ecological basis of alpine meadow ecosystem management in Tibet: Haibei alpine meadow ecosystem research station. – Ambio **28**: 642-647, 1999.