Biogeosciences

Field $^{13}CO_2$ pulse labeling reveals differential partitioning patterns of photoassimilated carbon in response to livestock exclosure in a *Kobresia* meadow

J. Zou[1,3]**, L. Zhao**[1]**, S. Xu**[1]**, X. Xu**[2]**, D. Chen**[1]**, Q. Li**[1]**, N. Zhao**[1]**, C. Luo**[1]**, and X. Zhao**[1]

[1]Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Plateau Institute of Biology, Chinese Academy of Sciences, Xining 810001, China
[2]Key Laboratory of Ecosystem Network Observation and Modelling, Institute of Geographical Sciences & Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China
[3]University of Chinese Academy of Sciences, Beijing 100049, China

Correspondence to: X. Zhao (xqzhao@nwipb.cas.cn)

Abstract. Livestock exclosure has been widely used as an approach for grassland restoration. However, the effects of exclosures on grasslands are controversial and can depend on many factors, such as the grassland ecosystem types, evolutionary history and so on. In this study, we conduct field experiments to investigate the variations of the ecosystem function in response to livestock exclosure in a *Kobresia humilis* meadow with 6 years of grazing exclosure on the Qinghai–Tibetan Plateau. We focused on two ecosystem functions: plant community structure and ecosystem carbon cycling. The plant aboveground productivity, plant diversity and the composition of plant functional groups of the meadow were addressed as the indicators of the plant community structure. The ^{13}C isotope pulse labeling technique was applied to evaluate the alterations of ecosystem carbon cycling during a short term. The results showed that the plant community structure was changed after being fenced in for 6 years, with significantly decreased aboveground productivity, species loss and varied composition of the four plant functional groups (grasses, sedges, legumes and forbs). Using the pulse labeling technique, we found a lower cycling rate of ^{13}C in the plant–soil system of the fenced plots compared with the grazed sites during the first 24 h after labeling. A higher proportion of recovered ^{13}C in the plant–soil system migrated into the soil as root exudates immediately after labeling at both fenced and control grazed sites, with a significantly lower proportion in the fenced site, coinciding with

the lower proportion of ^{13}C lost from soil respiration. Thirty-two days after labeling, 37 % of the recovered ^{13}C remained in the soil of the fenced plots, with significant differences compared to in the grazed plots (47 %). In addition, less ^{13}C (5 vs. 7 %) was lost by soil respiration in the fenced plots during the chase period of 32 days. Overall, our study suggests that livestock exclosures have negative effects on the plant community structure and partitioning patterns of the photoassimilated carbon in the *Kobresia* meadow, and the effects on photoassimilated carbon cycling are likely to result from the variations of community structures in the ecosystem.

1 Introduction

In the grazing ecosystem, livestock is a major force in the determination of grassland productivity (McNaughton, 1979, 1983). Many studies have revealed the positive effects of grazing on grassland productivity with plant compensatory mechanisms (McNaughton, 1985; Kotanen and Jefferies, 1989). Moreover, grazing can increase the plant diversity and indirectly change the competitive relationships among species (Collins, 1987; Denslow, 1980; Knapp et al., 1999). However, the effects of grazing on the grassland ecosystem were shown to be controversial in different ecosystems or with variable intensity (Waser and Price, 1981). In addition to the contribution of palatable plants consumed by livestock,

the grassland also helps the ecosystem with C storage. In grazed grasslands, the removal of plants by grazing was suggested to decrease the migration of carbon into the ground (Morris and Jensen, 1998). Nevertheless, other works have suggested that grazing has positive effects on the community structure resulting in an increase of C sequestration (Reeder and Schuman, 2002; Derner et al., 2006).

Livestock exclosures have a potential value in assessing the effects of grazing upon vegetation and C sequestration in the grasslands (Bock et al., 1984; Cheng et al., 2011; He et al., 2011; Li et al., 2012; Su et al., 2003). Exclosures appear to favor higher community diversity and productivity compared with grazing in the arid grasslands (Bock et al., 1984; Cheng et al., 2011). Furthermore, grazing exclosures are widely used as a management practice to restore degraded grasslands (Li et al., 2012; Su et al., 2003). However, recent studies on a fenced *Leymus chinensis* grassland in northern China demonstrated that the outcomes from exclosure were related to the community types of the grasslands, with responses to litter accumulation dependent on plant density (He et al., 2011). Generally, there were cascade effects on C sequestration in the plant–soil system from variations of the community structure and other factors related to exclosure (Li et al., 2012; Su et al., 2003). Many studies demonstrated that plant diversity and the interactions among different species or plant functional groups had major effects on C sequestration (Fornara and Tilman, 2008; Steinbeiss et al., 2008). In addition, litter accumulation as a result of lack of grazing was suggested to suppress C cycling in the plant–soil system (Reeder and Schuman, 2002; Schuman et al., 1999).

On the Qinghai–Tibetan Plateau, one-third of the total area is occupied by grasslands at 1.5×10^6 km^2 (Sun and Zheng, 1998). The grasslands of the Tibetan Plateau are one of the most extensive grazing systems in the world (Schaller, 1998). Much evidence indicates that grazing has been a widespread land use of the grasslands on the Qinghai–Tibetan Plateau since 10 000 years BP (before present; Qian, 1979; Guo et al., 2006). The plants of the Tibetan Plateau have evolved with grazing. The long history of grazing has had important effects on the community structure and ecosystem function of the grasslands on the Tibetan Plateau (Klein et al., 2004, 2008). It has been shown that grazing increases productivity of the grassland (Klein et al., 2007). However, conflicting findings suggest that grazing decreases the productivity of the grassland, especially overgrazing associated with privatization and sedentarization, which leads to land degradation (Zhao and Zhou, 1999; Miller, 1999). Livestock exclosures were widely used as an approach to restore the degraded grasslands on the Qinghai–Tibetan Plateau (Yeh, 2005). However, the policy of completely eliminating domestic grazing from grasslands may not be suitable for the grasslands with different vegetation types, degrees of degradation and evolutionary histories.

Large quantities of carbon are stored in the soil of grasslands, especially on the Qinghai–Tibetan Plateau, and, due to long cold winters, the C sequestration in soil has been shown to be stable (Kuzyakov and Domanski, 2000). The *Kobresia* pastures are characterized by productive vegetation with a dense root system (Miehe et al., 2008). Its high root/shoot biomass results in 90 % of the carbon assimilation being allocated into the ground of the pastures. It has been suggested that the *Kobresia* pastures may be a moderate C sink as a result of a neutral net ecosystem CO_2 exchange (Ni, 2002; Shi et al., 2006). However, this C sink is vulnerable to land use and grassland management, which have been suggested to be decisive factors for a C sink and source switch in the *Kobresia* pastures (Wang et al., 2005).

In order to investigate how livestock exclosure affects the grassland ecosystem function, we focused on the assessment of vegetation properties and ecosystem services as C storage of a 6-year grazing exclosure meadow on the Qinghai–Tibetan Plateau. A stable C-isotope analysis was carried out to track the newly assimilated carbon for C sequestration. We were interested in (1) the variations of the vegetation community structure after exclosure, (2) the cycling of the newly assimilated ^{13}C in the plant–soil system in response to exclosure, and (3) if plant community structure influences ^{13}C cycling in the plant–soil system.

2   Materials and methods

2.1   Site description

The study was conducted at the Haibei Alpine Meadow Ecosystem Research Station, located in northeastern Tibet (37°29′–45′ N, 101°12′–23′ E) at an altitude of 3250 m. The station has a continental monsoon-type climate, characterized by long, cold winters and short, cool summers. The annual average temperature is $-2°$, with the coldest monthly temperature of $-18°$ recorded in January, and the warmest of 10° in July. The mean annual precipitation ranges from 426 to 860 mm, with more than 80 % precipitation occurring in the short summer from May to September. The annual average sunlight is 2462.7 h, 60 % of which is available for plants to grow. This provides advantages for the photosynthesis of herbage. The research area is dominated by four of the most important vegetation communities: *Kobresia humilis* meadows, *Dasiphora fruticosa* shrubs, *Kobresia pygmaea* meadows and *Kobresia tibetica* swamp meadows. Plants grow from May to September.

The experiments were carried out at the alpine *Kobresia humilis* meadow. The soil of the *Kobresia humilis* meadow is classified as Mat Cry-gelic Cambisols according to the Chinese National Soil Survey and Classification System (Chinese Soil Taxonomy Research Group in Institute of Soil Science of CAS, 2001). The vegetation is mainly dominated by *Kobresia humilis*, *Stipa aliena*, *Festuca ovina*, and so on.

Our experimental site is situated along a valley floor. And the meadow was characterized by a long winter grazing history, from 1 January to 30 March each year. The grazing intensity was 3.51 sheep ha^{-1} season^{-1}, identified as a moderate grazing practice. The fenced meadow with an area of 50 m $\times$ 50 m was established in 2005 in the experiment site. It excluded yaks, sheep and goats during the whole year. The grazed meadow with an area of more than 50 $\times$ 50 m to the side of the fenced meadow was used as the control site. Before exclosure, the vegetation and other environmental conditions inside and outside the fence were homogeneous, and this homogeneity can reduce or eliminate the effects of potential bias from variable sources on the differences between treatments. Four independent quadrates in each treatment were selected to investigate the vegetation composition, while four independent plots were selected to carry out the stable ^{13}C isotopic labeling experiment. All the replications in the experiments were dispersed at random with about 10 m of spacing between the experimental areas. One quadrate for vegetation investigations corresponded to one adjacent ^{13}C labeling plot. The distance between the quadrate and the adjacent labeling plot was about 3 m. In our study, the experimental quadrates and plots in each treatment were in a segregated area, and the differences between the meadows under exclosure and under grazing might possibly be due to factors other than the treatment effects during the 6-year exclosure; however, the identical environmental conditions between the treatments during exclosure decreased this possibility. Therefore, all the differences between the meadows under exclosure and grazing were assumed to be due to the exclosure effects.

2.2 Vegetation structure analysis

We investigated the vegetation structure in the fenced and control grazed sites in late August during the experiment period. Four quadrates were selected randomly in each site. The size of each quadrate was 50 cm $\times$ 50 cm.

The point-intercept method was carried out to assess the percentage of vegetation coverage of the recorded species (Walk, 1996). In each quadrate, a 50 cm $\times$ 50 cm frame with 100 squares divided by nylon strings, each square measuring 5 cm $\times$ 5 cm, was placed over the vegetation. We vertically inserted a short, thin metal rod from the canopy top down to the ground in each square. The species hit by the rod were recorded in the square, and the species diversity of each site was the sum of species found in the four quadrates. The ratio of total hits of each species in the quadrates to the 100 squares was recognized as the relative coverage of the species. Then, the aboveground biomass was harvested from each quadrate to evaluate the productivity of the grassland. Living and dead materials were separated and living species were divided into four functional groups: grasses, sedges, legumes and forbs. The biomass of each functional group

was assessed and the samples oven-dried at 70° for 48 h before weighing.

2.3 ^{13}C pulse labeling

We carried out the ^{13}C pulse labeling experiment on 22 July 2011, which was a clear day. Four replicates were selected in the fenced and grazed sites, respectively. Each plot replicate was pulse-labeled in a closed chamber consisting of a stainless steel base (1 $\times$ 1 m, 10 cm height) with a channel on the top and a PVC (polyvinyl chloride) cover (1 $\times$ 1 m, 45 cm height). The bases were installed in the soil at 10 cm depth on the day before the pulse labeling. When the pulse labeling experiment began, the PVC covers were sealed to the bases using air-tight water seals in the channel on the bases. All the plots were labeled in the $^{13}CO_2$ atmosphere simultaneously between 10:00 and 12:00 LT, with several minutes of difference between pairs of plots. The $^{13}CO_2$ was released by carefully injecting 10 mL of 10 % H_2SO_4 into the container holding the solution of 2.0 g $Na_2^{13}CO_3$ in each chamber. The containers were connected to the chambers by tubing and were mounted in the center of the plots before the chambers were sealed. The air in each chamber was circulated by the fans mounted on the PVC cover to guarantee a uniform air environment. The chambers were removed after 2 h. Before opening the chambers, the chamber air was injected into 1M NaOH using syringes to absorb the unassimilated $^{13}CO_2$ in the chambers.

2.4 Sampling

After pulse labeling, samples were collected at 0, 3, and 6 h, and at 1, 4, 11, 18, and 32 days in each replicate pot at the two experiment sites.

At each sampling occasion, shoot samples were harvested in 10 cm $\times$ 10 cm squares by clipping the aboveground plant parts of all species. The shoot samples were separated into living and dead and the living shoots were oven-dried and ground (< 0.25 mm) for ^{13}C measurement.

Immediately after shoot sampling, the static alkali absorption method was used to assess the amount of CO_2, including $^{13}CO_2$, released from soil respiration (Hafner et al., 2012; Singh and Gupta, 1977). Briefly, CO_2 samples of the soil respiration were absorbed in alkali (NaOH) in a closed chamber (10 cm diameter, 10 cm high) on the soil surface where the shoot samples were clipped. At the sampling occasions of 3 and 6 h, and 1, 4, 11, 18, and 32 days after labeling, the containers holding alkali were well-sealed until laboratory analysis. To estimate total CO_2 efflux, the CO_2 trapped in the NaOH solution was precipitated with a 2 M barium chloride ($BaCl_2$) solution and the NaOH was titrated with 0.1 M hydrochloric acid (HCl) against a phenolphthalein indicator (Zibilske, 1994; Werth and Kuzyakov, 2008). A total of 10 mL of $SrCl_2$ was added to 10 mL of NaOH of each sample to produce $SrCO_3$ precipitation. The $SrCO_3$ precipitation

Table 1. Species diversity, mean ($\pm$ SD – standard deviation) vegetation aboveground biomass, and vegetation cover in the fenced and control grazed meadows.

Plant functional group	Species diversity		Biomass (g m^{-2})		Vegetation cover (%)	
	Fenced	Grazed	Fenced	Grazed	Fenced	Grazed
Grasses	6	6	264.43 ($\pm$28.11)	198.30 ($\pm$39.60)*	109.5 ($\pm$5.07)	81.5 ($\pm$9.88)*
Sedges	3	3	29.17 ($\pm$11.46)	46.18 ($\pm$16.08)	8.5 ($\pm$3.70)	17.25 ($\pm$12.66)
Legumes	2	5	1.57 ($\pm$1.71)	42.58 ($\pm$14.79)*	6.5 ($\pm$4.43)	41.5 ($\pm$11.45)*
Forbs	18	22	56.59 ($\pm$25.12)	116.29 ($\pm$19.17)*	61.5 ($\pm$19.82)	97.25 ($\pm$7.50)*
Total	29	36	351.76 ($\pm$5.84)	403.35 ($\pm$41.29)*	186 ($\pm$22.99)	237.5 ($\pm$16.82)*
Litter			219.00 ($\pm$82.57)	104.08 ($\pm$5.39)*		

* Indicates significant differences at $P < 0.05$ between the fenced and grazed meadows ($n = 4$).

in the NaOH solution was neutralized with degassed water and oven-dried for ^{13}C measurement.

Soil cores of 8 cm in diameter were taken from three layers, 0–5, 5–15 and 15–30 cm, immediately after air sampling. All roots and soil in the cores were carefully extracted and sieved with a 2 mm screen. The soil samples that passed through the sieve were air-dried and ground (< 0.15 mm). For ^{13}C measurement in soil organic C (SOC), carbonates were removed from the soil samples by washing in 0.1 M HCl for 24 h (Midwood and Boutton, 1998), the samples were then neutralized by adding deionized water and dried at 40° before the ^{13}C measurement. The roots were carefully washed with river water and rinsed with deionized water through a 0.15 mm screen to remove attached soil and dark-brown/black debris. The roots were further separated into living and dead components based on their color and texture. The living roots were treated in the same way as the living shoots for ^{13}C measurements. Only data from living roots are mentioned in this work.

2.5 Measurement and calculations

The carbon contents in the samples were measured with an elemental analyzer; and the natural abundance in samples, which was expressed as δ^{13}C (‰), was determined with a MAT 253 stable isotope ratio mass spectrometer system coupled to an elemental analyzer.

The isotopic ratio (^{13}C / ^{12}C) of each sample R_{sample} was calculated as

$$R_{sample} = (\frac{\delta^{13}C}{1000} + 1) \times R_{PDB}.$$

$R_{PDB} = 0.011237$ is the isotopic ratio of ^{13}C / ^{12}C in Pee Dee Belemnite.

The ^{13}C in the total C in the samples as ^{13}C (at %) was calculated as

$$^{13}C(at \%) = \left(\frac{R_{sample}}{R_{sample} + 1} \right) \times 100.$$

Because of the existence of natural abundance of δ^{13}C (‰) in the unlabeled samples, the isotopic ratio in the total C in the

unlabeled samples should be subtracted from that in the samples to assess the ^{13}C (at %) derived from the pulse labeling in the samples.

$$^{13}C \text{ excess (at \%)} = {}^{13}C \text{ of samples (at \%)}$$
$$- {}^{13}C \text{ of unlabeled samples (at \%)}$$

Finally, the following equation was used to determine the amount of ^{13}C incorporated in the samples from pulse labeling:

$$^{13}C \text{ amount (mg m}^{-2}) = {}^{13}C \text{ excess (at \%)}$$
$$\times C \text{ pool size (g m}^{-2}) \times 10.$$

C pool size (g m^{-2}) is the carbon content in samples, which was assumed to be constant in shoots, roots and soil during the chase period.

$$\% \text{ of recovered } {}^{13}C = \frac{{}^{13}C_{t \text{ amount}}}{{}^{13}C_{0 \text{ amount}}} \times 100$$

was calculated to determine the partition (%) of ^{13}C recovery incorporated into C pools at a special time t after the labeling. $^{13}C_{t \text{ amount}}$ represented the ^{13}C mass incorporated into the carbon pools at a special time t, and $^{13}C_{0 \text{amount}}$ represented the ^{13}C mass incorporated into the plant–soil system by summation of ^{13}C amounts measured in shoots, roots and soil at 0 h after the pulse labeling.

2.6 Statistical analyses

All statistical analyses were performed using SPSS 19.0 software. Data were analyzed by ANOVA (analysis of variance). The only factor was the land use type: fenced and grazed. The statistical analyses of ^{13}C recovery (%) in carbon pools at each sampling time between the fenced and grazed meadows during the chase period were performed. $P < 0.05$ was considered statistically significant for differences between the fenced and grazed meadows.

Table 2. Mean ($\pm$SD) C stocks ($Mg\,C\,ha^{-1}$) aboveground and belowground C pools, and mean ($\pm$SD) soil respiration rate ($Mg\,C\,ha^{-1}\,d^{-1}$) during the chase period in the fenced and grazed meadows.

	Depth	Fenced	Grazed
Shoot		1.46 ($\pm$0.23)	2.12 ($\pm$0.25)*
Roots	0–5	5.45 ($\pm$3.03)	2.89 ($\pm$1.11)
	5–15	1.80 ($\pm$1.66)	1.09 ($\pm$0.32)
	15–30	0.72 ($\pm$0.28)	0.42 ($\pm$0.10)
	0–30	7.96 ($\pm$4.85)	4.40 ($\pm$1.28)
Soil	0–5	26.30($\pm$4.41)	18.72 ($\pm$2.33)*
	5–15	44.64 ($\pm$5.41)	43.10 ($\pm$5.49)
	15–30	38.29 ($\pm$1.19)	41.79 ($\pm$2.07)*
	0–30	109.23($\pm$4.01)	103.61 ($\pm$5.15)
Soil respiration rate		0.025 ($\pm$0.002)	0.035 ($\pm$0.002)*

* Indicates significant differences at $P < 0.05$ between the fenced and grazed meadow ($n = 4$).

3 Results

3.1 Vegetation composition

A total of 6 years without grazing has lead to remarkable alterations in the vegetation composition of the *Kobresia humilis* meadow.

The fenced meadow had a lower aboveground biomass and a larger aboveground litter mass than the grazed meadow (Table 1). In addition, the composition of the shoot biomass was changed after exclosure (Table 1). The relative biomass of each of the four functional groups to the total shoot biomass in the fenced meadow was 75, 8, 0.4 and 16 % corresponding to grasses (Gramineae species), sedges, legumes and forbs, respectively, and different from those of the grazed meadow (49, 11, 11 and 29 %, respectively). The uniformity in the composition of the functional groups was lower in the fenced meadow than in the grazed meadow. The biomass of Gramineae species was significantly higher in the fenced meadow than in the grazed meadow, but the biomass of legumes and forbs were significantly lower in the fenced meadow. However, the biomass of sedges had no significant differences between the fenced meadow and the grazed meadow (Table 1).

The total coverage of the meadow decreased significantly in the fenced meadow compared to the grazed meadow (Table 1). The coverage was significantly lower in the legumes and forbs of the fenced meadow, while the opposite response occurred in the grasses. The coverage of sedges had no significant differences between the fenced meadow and the grazed meadow (Table 1).

The plant diversity was reduced in the fenced plots (Table 1). The missing species were legumes and forbs and there was no variation in grasses and sedges.

3.2 Carbon stocks in the plant–soil system during the ^{13}C chase period

The carbon stocks in the meadow under exclosure changed significantly only in shoots and soil organic C pools at 0–5 and 15–30 cm compared to the meadow under grazing (Table 2), based on the data during the chase period. The carbon stock in shoots was significantly lower in the fenced meadow than in the grazed meadow (Table 2). The carbon stock in roots at 0–30 cm increased in the fenced meadow compared to the grazed meadow, but the differences were not significant at each depth interval. The carbon stocks in roots decreased significantly with increasing soil depth in the two treatments. Soil organic C stocks at 0–5 and 15–30 cm were significantly different between the two treatments. SOC stocks at 0–5 cm were higher in the fenced meadow compared to in the grazed meadow, but it was lower at 15–30 cm. SOC stocks at 5–15 cm were not changed significantly after exclosure. SOC stocks at 0–30 cm depth were higher in the fenced meadow than in the grazed meadow, but the difference was not statistically significant. However, the C loss rate from belowground in soil respiration was significantly lower in the fenced meadow than in the grazed meadow (Table 2).

3.3 ^{13}C allocation and dynamics in the plant–soil system

At the beginning of the chase period, the total amount of fixed ^{13}C which was recovered by summation of ^{13}C estimated in shoots, roots and soil (per m^2), was assumed to be 100 % of the net plant ^{13}C fixation during the 2 h labeling time either in the fenced meadow or in the grazed meadow. The ^{13}C losses from shoot respiration occurring concurrently with partitioning were not estimated. The recovery of ^{13}C in shoots was significantly higher in the fenced plots (53 %) compared to the grazed plots (42 %) at this time (Fig. 1a). Conversely, the recovery of ^{13}C in soil was significantly lower in the fenced plots (44 %) than in the grazed plots (53 %) (Fig. 1c). The recovery of ^{13}C in roots had no significant difference between the fenced plots (3 %) and the grazed plots (4 %) (Fig. 1b).

The ^{13}C recovery decreased following exponential decay in shoots within the chase period in both the fenced and grazed plots (Fig. 1a). The fixed ^{13}C was exported from the shoots mainly by shoot respiration and belowground transport into the roots and soil. The partition of recovered ^{13}C in shoots (14 %) and belowground carbon pools (53 %) in the plots at the end of chase period was significantly lower in the fenced meadow compared to that in the grazed meadow (Fig. 2). Accordingly, the ^{13}C recovered in shoots and belowground carbon pools was 18 and 61 % in the grazed plots. Being estimated from the recovery of ^{13}C in shoots and belowground during the chase period, a higher ^{13}C recovery was lost from shoot respiration in the fenced plots than in the grazed plots.
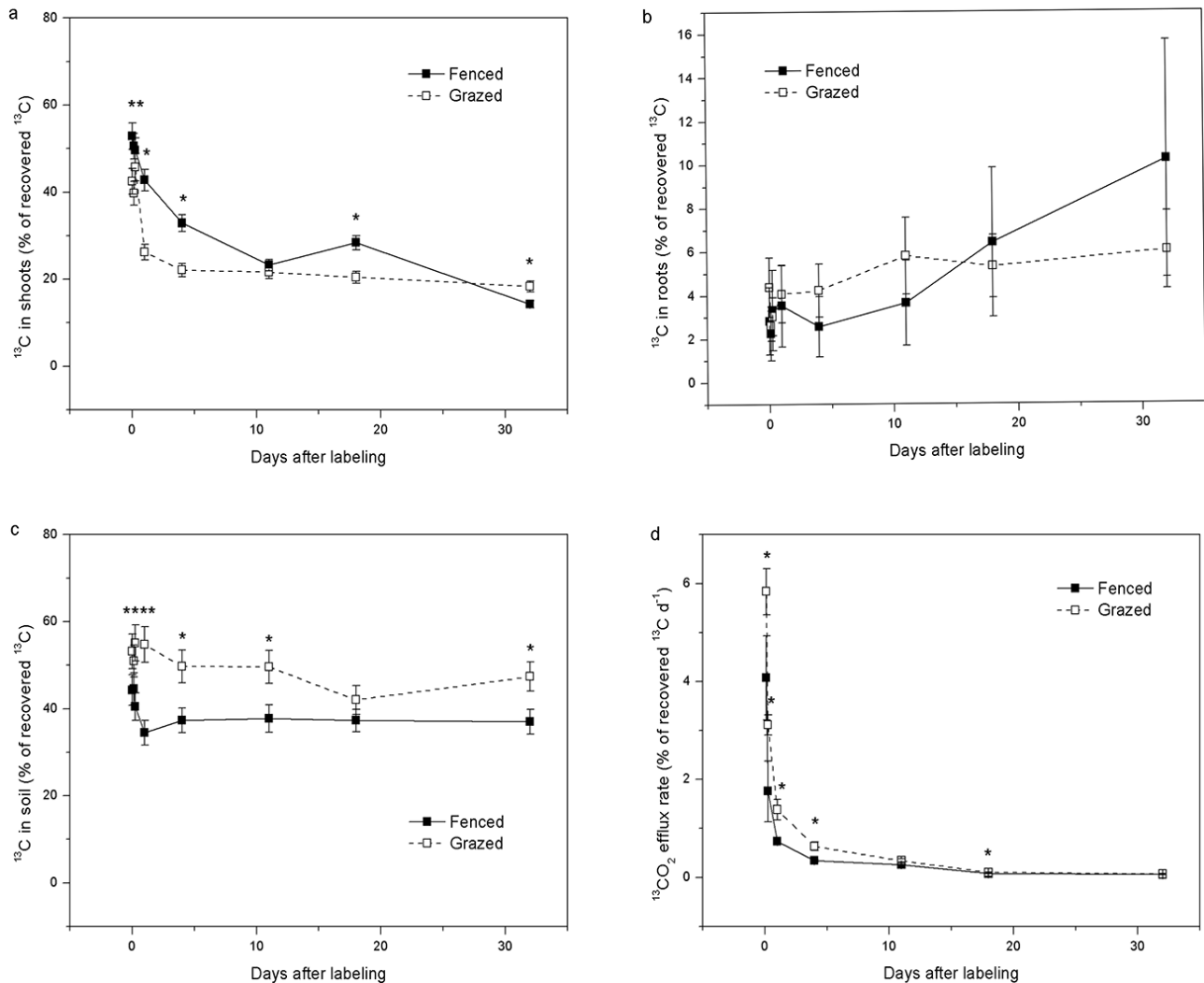
**Figure 1.** The dynamics of ^{13}C allocation (percentage of recovered ^{13}C) in shoots **(a)**, roots **(b)**, and soil **(c)** in the fenced and control grazed meadows during the 32-day chase period. The last figure shows the dynamics of the $^{13}CO_2$ efflux rate (percentage of recovered $^{13}C\,d^{-1}$) by soil respiration **(d)** during the chase period. * Indicates significant differences at $P < 0.05$ between the fenced and grazed meadows for each time step. Data are means $\pm$ standard deviation ($n = 4$).

Exclosure had effects on the trend of ^{13}C exported from shoots in the plots (Fig. 1a). The recovery of ^{13}C declined in a rapid process from 53 to 23 % in the fenced plots during the 11-day period after labeling, and then it decreased to 14 % at the end of chase period. The recovery of ^{13}C in the grazed plots decreased in a rapid process from 42 to 26 % during the 1-day period after labeling. Thereafter, it decreased to 22 % at day 4 and was followed by a slow decrease until the end of the chase period (Fig. 1a). The decline of recovered ^{13}C in shoots was lower during the first 24 h after labeling in the fenced plots (10 %) than in the grazed plots.

Small proportions of fixed ^{13}C were recovered in roots after 2 h of labeling both in the fenced plots and in the grazed plots (Fig. 1b). No significant differences in the recovery of ^{13}C in roots were found between the fenced plots and grazed

plots at all sampling times during the chase period, probably as a result of the higher variability between the four plots (Fig. 1b). The recovery of ^{13}C in roots reached its maximum at 32 days (10 %) in the fenced plots and at 11 days (6 %) in the grazed plots.

Belowground, ^{13}C was mainly distributed in the soil of the fenced plots and the grazed plots (Fig. 2). The proportions of fixed ^{13}C recovered in soil were significantly lower in the fenced plots compared to the grazed plots at all sampling times except 18 days after labeling (Fig. 1c). The recovery of ^{13}C in soil declined at a higher rate during the first 24 h in the fenced plots than in the grazed plots (Fig. 1c). It reached its minimum (35 %) on day 1 and increased to 37 % on day 4 followed with nonsignificant differences until the end of
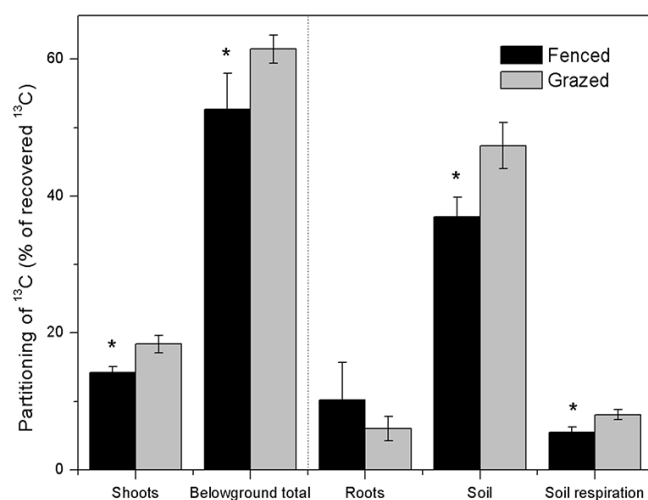
Figure 2. Partitioning of ^{13}C (percentage of recovered ^{13}C) in shoots and belowground of the fenced and control grazed meadows at day 32 of the chase period. The partitioning of ^{13}C (percentage of recovered ^{13}C) in belowground stocks was divided into three parts, including roots, soil stocks and loss by soil respiration (right side of figure). * Indicates significant differences at $P < 0.05$ between the fenced and grazed meadows. Data are means ± standard deviation ($n = 4$).

the chase period in the fenced plots. In the grazed plots, a minimum (42 %) was reached 18 days after labeling.

Exclosures decreased the ^{13}C recovery in total CO_2 efflux from soil respiration during the chase period in the fenced plots (5 %) compared to the grazed plots (8 %) (Fig. 2). The $^{13}CO_2$ efflux rate declined exponentially during the chase period both in the fenced and grazed plots. A higher $^{13}CO_2$ efflux rate from soil respiration occurred during the first 24 h after labeling, thereafter, it declined gradually and slowly until the end of the chase period. The $^{13}CO_2$ efflux rate from soil respiration during the first 24 h was significantly lower in the fenced plots compared to the grazed plots (Fig. 1d).

3.4 Vertical–spatial variations of belowground ^{13}C allocation

The ^{13}C recovery in roots decreased with depth in the fenced plots and in the grazed plots (Fig. 3a). The percentage of ^{13}C in the top 5, 5–15 and 15–30 cm relative to the 30 cm depth averaged about 78, 15 and 7 %, respectively, in the fenced plots compared to 72, 23 and 6 % in the grazed plots during the chase period. The dynamics of ^{13}C recovery in roots mainly occurred in the top 5 cm in the fenced plots, and there was a gradual and slow increase of the ^{13}C recovery in the 5–15 cm depths. In the grazed plots it reached its maximum 11 days after labeling in the top 5 cm, similar to that in the total 30 cm; however, it reached its maximum on day 4 in the 5–15 cm depths. The recovery of ^{13}C in the third layer

remained constant during the chase period in the two treatments (Fig. 3a).

The ^{13}C recovery in the soil was not consistent with the rank order of the depth (Fig. 3b). The percentages of ^{13}C recovery in the top 5, 5–15 and 15–30 cm relative to the total 30 cm averaged 13.9, 41.7 and 44.2 % in the fenced plots, respectively, compared to 9.1, 41.4 and 49.5 % in the grazed plots during the chase period. No significant changes in ^{13}C recovery in the top 5 cm occurred during the whole chase period except at several sampling times in the soil between the fenced plots and the grazed plots; however, significantly lower ^{13}C recoveries in the second and third layers were found in the fenced plots than in the grazed plots (Fig. 3b). Similar dynamics of ^{13}C recoveries in the top 5, 5–15 and 15–30 cm were suggested both in the fenced plots and in the grazed plots. As the dynamics in total 30 cm, the ^{13}C recoveries at all three layers in the soil reached their minimum in the first 24 h in the fenced plots and at day 18 in the grazed plots (Fig. 3b).

4 Discussion

Livestock exclosure alters the structure of grassland communities as well as the cycling of materials in the grassland ecosystem (Morris and Jensen, 1998; Reeder and Schuman, 2002; Derner et al., 2006; Altesor et al., 2005). Some field studies have proposed exclosure as an effective approach for restoring vegetation and improving C storage of the grassland (Li et al., 2012; Su et al., 2003), while others demonstrated that exclosure has had negative effects on C sequestration in grasslands (Reeder and Schuman, 2002). This apparent contradiction can be explained by the different evolutionary processes, degrees of degradation and grazing history in these grassland communities. Indeed, the effects of exclosures on grasslands are community-specific.

4.1 Effect of exclosure on vegetation structure

Our results indicated that the aboveground plant biomass, coverage and richness had significant decreases associated with the changes in functional group composition in *Kobresia humilis* meadows under exclosures compared to the meadows under grazing, where the grass (Gramineae species) increased in abundance compared to the decrease for the sedges, legumes and forbs (Table 1). These results are not consistent with several works that have demonstrated exclosures having positive effects on the growth of the vegetation (Morris and Jensen, 1998; Derner et al., 2006; Bock et al., 1984; Cheng et al., 2011). However, other studies have shown that exclosure is detrimental to the vegetation because of the lack of livestock grazing (McNaughton, 1983; Knapp and Seastedt, 1986).

The *Kobresia humilis* meadow is productive and is well known to evolve with grazing (Qian, 1979; Guo et al., 2006).
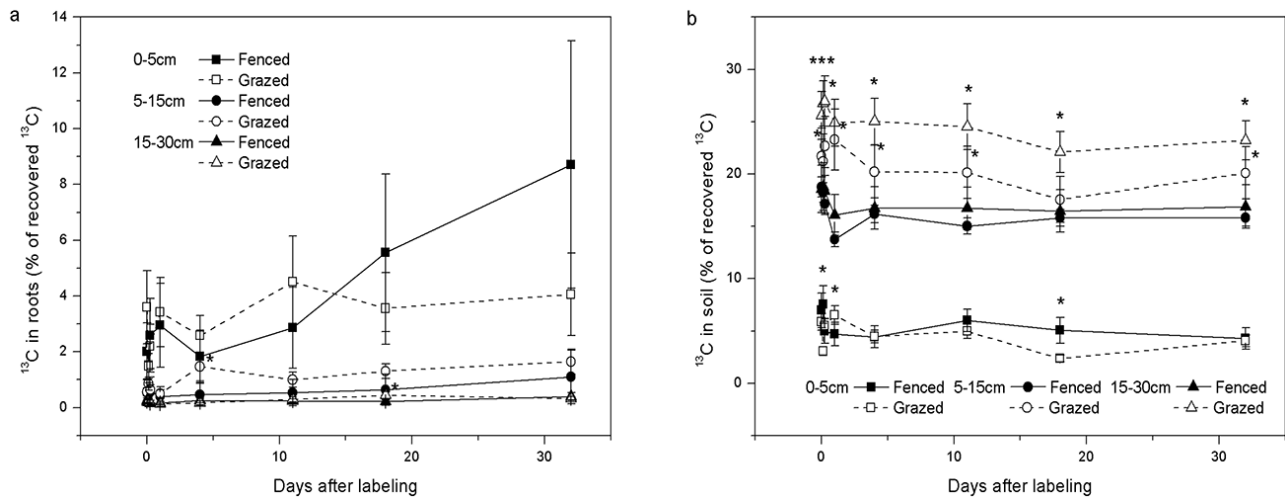
Figure 3. The vertical distribution dynamic of ^{13}C allocation (percentage of recovered ^{13}C) in roots **(a)** and soil **(b)** at layers of 0–5, 5–15 and 15–30 cm in the fenced and control grazed meadows during the 32-day chase period. * Indicates significant differences at $P < 0.05$ between the fenced and grazed meadows for each time step at each soil layer. Data are means $\pm$ standard deviation ($n = 4$).

For a winter-grazing pasture in our research, the elimination of livestock from grassland caused more accumulation of aboveground litter, leading to a decrease of the bare ground area for the extension and reproduction of the vegetation in spring. Furthermore, and importantly, the litter on the ground may alter the productivity by reducing the absorption efficiency of radiation due to self-shading (Altesor et al., 2005; Knapp and Seastedt, 1986).

We showed that the composition of the four functional groups was changed after fencing of the grassland. The different characteristics of the functional groups and the aboveground accumulated litter may be important factors affecting the composition of the functional groups (Klein et al., 2004). Grasses dominating the canopy top of the meadow had a stronger competition for light than other functional groups in the grassland community (Kull and Aan, 1997). Many studies have demonstrated that light is one of the most important resources that determine plant production (Altesor et al., 2005; Knapp and Seastedt, 1986; Semmartin and Oesterheld, 1996). Self-shading due to the accumulated litter was detrimental to the growth of legumes and forbs, and lead to the biodiversity loss in the two functional groups (Grime, 1979, 1998; Huston, 1994). The growth of grasses was enhanced concurrently with the suppressed growth of legumes and forbs.

4.2   Effect of exclosure on ^{13}C dynamic and allocation

The ^{13}C flux rate transported from shoots was lower in the meadow under exclosure. Immediately after labeling, a significantly larger recovery of ^{13}C in shoots was found in the fenced plots compared to the grazed plots (Fig. 1a). A lower proportion of recovered ^{13}C (10 %) is lost from shoots by shoot respiration and belowground transport in the fenced

plots than that in the grazed plots (16 %) during the first 24 h after labeling. These estimations in the two treatments were much lower than the value of 36.7 % reported by Wu et al. (2010) and 77 % found by Ostel et al. (2000).

Exclosure limited the ^{13}C allocation into the ground compared to moderate grazing. Significantly lower recovery of ^{13}C in soil was found in the fenced plots immediately after labeling (Fig. 1c), as a response of the lower ^{13}C flux rate transported from shoots. The rapid decline of the recovery of ^{13}C in soil under exclosure during the first 24 h confirmed the restricted ^{13}C dynamics from shoots into soil as compared to that under moderate grazing. The lowest proportions of recovered ^{13}C were allocated to roots both in the fenced plots and in the grazed plots immediately after labeling. This result was consistent with the reports on *Lolium perenne* (Kuzyakov et al., 1999; Kastovska and Santruckova., 2007). In a ^{13}C labeling experiment on the alpine grassland, the results also indicated the amount of ^{13}C recovered in living roots was the smallest within the belowground pools (Hafner et al., 2012). We indicated that the roots provided a rapid transport and much ^{13}C fluxed into soil as root exudates. Also, it was supported by the slowly and gradually increasing of ^{13}C incorporated in root biomass during the chase period. However, no significant differences of the ^{13}C recovery in roots existed between the fenced plots and the grazed plots during the chase period. The $^{13}CO_2$ efflux rate in soil respiration decreased exponentially with time, which might be induced by the ^{13}C redistribution from shoots. Exclosure lead to a significantly decreased $^{13}CO_2$ efflux rate compared to grazing. Considering the nonsignificant differences of ^{13}C recovery in roots between the meadow under exclosure and grazing, the decrease might mainly result from the decrease in $^{13}CO_2$ released from soil. Decreased root exudates might

decrease the abundance and activity of the microorganisms with a decreased C turnover rate in soil (Uhlirova et al., 2005). At the end of chase period, a significantly lower recovery of ^{13}C in the fenced meadow (53 %) was transported into the ground than in the grazed meadow (61 %). The recovery of ^{13}C transported into the ground in the two treatments was within the range of 40–80 % of fixed C in perennial plants reported by Kuzyakov and Domanski (2000), and close to 58.7 % was transported into the ground reported in the similar *Kobresia* meadow (Wu et al., 2010).

The significantly lower ^{13}C allocation in soil under exclosure limited the vegetation productivity with significantly lower ^{13}C allocation in shoots. Less ^{13}C allocated in soil as root exudates under exclosure might decrease the ^{13}C turnover in soil. Blagodatskaya et al. (2007) demonstrated the relationships between root exudation and SOM turnover through the abundance and activity of microorganisms in the rhizosphere. This processes had important impacts on soil nitrogen mineralization, furthermore, the decreased soil nitrogen mineralization rate under exclosure was detrimental to the nutrient supply for plant growth (Hamilton and Frank, 2001; Ayres et al., 2004). The lower recovery of ^{13}C allocated in shoots at the end of the chase period might result from less nutrients available to absorb from the soil. However, the carbon stored in roots and the allocation of ^{13}C in roots were not significantly influenced with the decreased proportion of fixed ^{13}C in shoots under exclosure. The ^{13}C recovered in roots tended to increase during the chase period in the fenced plots (Fig. 2b). Although a higher recovery of ^{13}C was allocated in roots in the fenced plots than in the grazed plots, and higher spatial variability obscured the differences of ^{13}C allocation in roots between the two sites. Plants increased the recovery of ^{13}C in roots as a response to the shortage of nitrogen (Hamblin et al., 1990). We suggest that lower ^{13}C turnover in soil with lower nitrogen acquisition stimulated root growth for nitrogen absorption.

Exclosure affected the vertical distribution of ^{13}C in soil. Jobbagy and Jackson (2000) demonstrated that vegetation changes SOC distributions with depth in the soil through different carbon allocation in the system. Less ^{13}C migrated from the roots to the soil at deeper depths in the fenced plots than in the grazed grasslands during the chase period. We suggest that the lower allocation of ^{13}C in soil transported from shoots affected the vertical distribution of ^{13}C in soil.

Exclosure in *Kobresia humilis* meadows under moderate grazing had negative effects on the carbon cycling in the plant–soil system, by limiting recently assimilated carbon input from vegetation and the carbon turnover in soil with important consequences on nutrient cycling for plant growth and carbon allocations. Relating the significant change in vegetation structure to the carbon cycling under exclosure, we hypothesize that the vegetation structure is the principal driver linking exclosure to recently assimilated carbon cycling in the plant–soil system. The decrease of aboveground biomass has important implications for carbon cy-

cling by limiting the contribution of recently fixed plant photosynthate to ecosystem carbon cycling. The plant richness has been demonstrated impacting the aboveground biomass through complementary effects of light utilization from diverse plant canopy structures and other characteristics (Loreau and Hector, 2001; Tilman et al., 2001; Vojtech et al., 2008). Thus, the decrease of plant richness under exclosure could impact the carbon inputs by affecting the aboveground biomass in the community. Besides, several investigators demonstrated that the increased plant richness could affect the carbon cycling in soil by increasing microbial biomass and activity (Steinbeiss et al., 2008; Wardle et al., 1999; Hooper et al., 2000; Stephan et al., 2000). In addition, the decrease of legumes abundance in the fence meadow could decrease soil C sequestration as suggested by Fornara and Tilman (2008). The decreased allocation of recovered ^{13}C in shoots as a result from shortage of nutrients might be influenced by the lack of available nitrogen from N-fixed legumes.

5   Conclusions

Our results demonstrated that the vegetation community structure and the ^{13}C partitioning patterns were altered in response to livestock exclosure in the *Kobresia humilis* meadow. Exclosure limited the ^{13}C partitioning in soil with decreased carbon turnover in soil. The significant vegetation changes under exclosure may be responsible for the difference observed in C cycling in the short term. However, future experiments over long periods and on large spatial scales are required to better understand the effects of exclosure on the *Kobresia humilis* meadow. In this study, considering the negative responses of vegetation and photoassimilated carbon cycling in responses to exclosure, we found the evidence that livestock exclosure was detrimental to the *Kobresia humilis* meadow, which has evolved with a long history of grazing. Given different evolutionary processes, degrees of degradation and grazing histories of different grassland ecosystems, the application of the exclosure practice to the grassland management should be community specific.

Edited by: Z. Jia

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