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Livestock enclosure with consequent vegetation changes alters photo-assimilated carbon cycling in a *Kobresia* meadow

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Received: 22 September 2013 – Accepted: 1 November 2013 – Published: 12 November 2013

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Livestock enclosure has been widely used as an approach for grassland restoration. However, the effects of enclosure on grassland 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 ecosystem function in response to livestock enclosure in a *Kobresia humilis* meadow under six years grazing enclosure on the Qinghai-Tibetan plateau. We focused on two ecosystem functions: plant community structure and ecosystem carbon cycling. The plant above-ground 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 the short-term.

The results showed that the plant community structure was changed after being fenced for six 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 4 days after labeling. A higher proportion of ^{13}C amount recovered in the plant–soil system were migrated into soil as root exudates immediately after labeling at both fenced and control grazed sites, with significantly lower proportion in the fenced site, coinciding with the lower loss of ^{13}C in soil respiration. Thirty-two days after labeling, 37% of recovered ^{13}C remained in the soil of the fenced plots, with significant differences compared to 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 d.

Overall, our study suggested that livestock enclosure had negative effects on the two ecosystem functions investigated, and the effects on ^{13}C cycling and sequestrations in the soil were in response to variations in community structures, especially the suppression of forbs and legumes in the fenced site.

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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, plants removed by grazing were suggested to decrease the carbon migration into below 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 enclosures have a potential value in assessing the effects of grazing upon vegetation and C sequestration in grasslands (Bock et al., 1984; Cheng et al., 2011; He et al., 2011; Li et al., 2012; Su et al., 2003). Enclosure appears to favor higher community diversity and productivity compared with grazing in arid grasslands (Bock et al., 1984; Cheng et al., 2011). Furthermore, grazing enclosure is 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 outcomes from enclosure 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 enclosure (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; De Deyn

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et al., 2011). 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 $1.5 \times 10^6 \text{ km}^2$ (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 yr BP (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 enclosures were widely used as an approach to restore the degraded grassland on the Qinghai-Tibetan plateau (Yeh, 2005). However, the policy of completely eliminating domestic grazing from the grassland 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 allocated into below 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 the 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).

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In order to investigate how livestock enclosure affects the grassland ecosystem function, we focused on the assessment of vegetation properties and ecosystem services as C storage of a 6 yr grazing enclosure meadow on the Qinghai-Tibetan plateau. 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 fencing, (2) the effects of enclosure on the cycling of the newly assimilated ^{13}C in the plant–soil system, 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 northeast Tibet ($37^{\circ}29'–45' \text{ N}$, $101^{\circ}12'–23' \text{ E}$) 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°C , with the coldest monthly temperature of -18°C recorded in January, and the warmest of 10°C 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 most important vegetation communities, *Kobresia humilis* meadow, *Dasiphora fruticosa* shrub, *Kobresia pygmaea* meadow, and *Kobresia tibetica* swamp meadow. 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 humilus*, *Stipa aliena*, *Festuca ovina*, and so on.

At the experimental site, a total area of 100 × 100 m was fenced for ecological research in 2005 to exclude yaks, sheep and goats. The grassland outside the fenced area exposed to moderate grazing in winter was used as the control site in the experiments.

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 × 50 cm.

The point-intercept method was carried out to assess the percentage vegetation coverage of the recorded species (Walk, 1996). In each quadrate, a 50 cm × 50 cm frame with 100 squares divided by nylon strings, each square measuring 5 cm × 5 cm, was placed over the vegetation. We used a short, thin metal rod to vertically insert from the canopy top of the vegetation down to the ground in each square. The species hit by the rod were recorded in the square, and 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 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 material 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 °C for 48 h before weighing.

2.3 ¹³C pulse labeling

We carried out the ¹³C pulse labeling experiment on 22 July in 2011, which was a clear day. Four replicates were selected in the fenced and in the grazed sites. Each plot

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replicate was pulse-labeled in a closed chamber consisting of a stainless steel base (1 m × 1 m, 10 cm height) with a channel on the top and a PVC cover (1 m × 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 in the channel on the bases. All the plots were labeled in the $^{13}\text{CO}_2$ atmosphere simultaneously between 10:00 and 12:00 LT, with several minutes difference. The $^{13}\text{CO}_2$ was released by carefully injecting 10 mL 10 % H_2SO_4 into the container holding the solution of 2.0 g $\text{Na}_2^{13}\text{CO}_2$ 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 $^{13}\text{CO}_2$ in the chambers.

2.4 Sampling

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

At each sampling occasion, shoot samples were harvested in 10 cm × 10 cm squares by clipping the aboveground plant parts of all species. The shoot samples were separated into live and dead and the live 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 $^{13}\text{CO}_2$ 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 h, 6 h, 1 d, 4 d, 11 d, 18 d, 32 d after labeling, the containers holding alkali were well-sealed until laboratory analysis. To estimate total CO_2 efflux, the CO_2 trapped in NaOH solu-

tion was precipitated with a 2 M barium chloride (BaCl_2) solution and the NaOH was titrated with 0.1 M hydrochloric acid (HCl) against phenolphthalein indicator (Zibilske, 1994; Werth and Kuzyakov, 2008). 10 mL SrCl_2 was added into 10 mL NaOH of each sample to produce SrCO_3 precipitation. The SrCO_3 precipitation 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 cm, 5–15 cm 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, carbonates were removed from the soil samples by washing in 0.1 M HCl for 24 h (Midwood and Boutton, 1998), the samples neutralized by adding deionized water and dried at 40°C for ^{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 measurement. Only data from living roots are mentioned in this work.

2.5 Measurement and calculations

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

The isotopic ratio ($^{13}\text{C}/^{12}\text{C}$) of each sample R_{sample} was calculated:

$$R_{\text{sample}} = \left(\frac{\delta^{13}\text{C}}{1000} + 1 \right) \cdot R_{\text{PDB}}.$$

$R_{\text{PDB}} = 0.011237$ is the isotopic ratio of $^{13}\text{C}/^{12}\text{C}$ in Pee Dee Belemnite. 17640

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

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

For the existence of natural abundance of $\delta^{13}\text{C}$ (‰) 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 excess (at %) = ^{13}C of samples (at %) – ^{13}C of unlabeled samples (at %).

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

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

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.

$$\% \text{ of recovered } ^{13}\text{C} = \frac{^{13}\text{C}_t \text{ amount}}{^{13}\text{C}_0 \text{ amount}} \cdot 100$$

was calculated to determine the partition (%) of the amount of ^{13}C incorporated into C pools at a special time t after the labeling. $^{13}\text{C}_0 \text{ amount}$ represented the weight (mg m^{-2}) of ^{13}C in pools at 0 h after the labeling.

2.6 Statistical analyses

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

3 Results

3.1 Vegetation composition

6 yr without grazing has led to remarkable alterations in the vegetation composition of the *Kobresia humilis* meadow.

More litter (219.00 gm^{-2}) and less productivity (351.76 gm^{-2}) of the vegetation were estimated in the fenced plot compared with the control grazed plots (litter of 104.08 gm^{-2} and productivity of 403.35 gm^{-2}) (Table 1). The significant differences ($P < 0.05$) indicated that the fenced grassland had a lower productivity.

In addition, the plant diversity was reduced in the fenced plots (Table 1), with 29 recorded species, while 36 species were represented in the grazed plots. The missing species were legumes and forbs and there was no variation in grasses and sedges.

The biomass variations of the four plant functional groups did not always predict plant productivity. The biomass of legumes (1.57 gm^{-2}) and forbs (56.59 gm^{-2}) in the fenced plot was significantly lower compared with the grazed plot (42.58 gm^{-2} , 116.29 gm^{-2} , $P < 0.05$). As for grasses, the biomass increased from 198.30 gm^{-2} to 264.43 gm^{-2} after 6 yr enclosure, and this difference was statically significant ($P < 0.05$). Sedges showed no significant variations between the two sites, although the biomass of sedges was lower in the fenced sites (29.17 gm^{-2} vs. 46.18 gm^{-2} , $P > 0.05$).

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

During the chase period, C stocks in the aboveground and belowground C pools of the plant–soil systems were significantly different ($P < 0.05$) between the fenced and grazed sites in the shoot and soil pools at 0–5 cm, 15–30 cm.

C stock in the aboveground shoot pools of the fenced site was 1.46 Mgha^{-1} , significantly lower ($P < 0.05$) than that found in the grazed site (2.12 Mgha^{-1}), as shown in Table 2. In the root pool, the pool sizes indicated a rank order of the depth $\approx 0\text{--}5 \text{ cm} > 5\text{--}15 \text{ cm} > 15\text{--}50 \text{ cm}$. C stocks were greater in the root pool of the fenced site

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at each depth, but the differences were not statistically significant compared with the grazed site. Soil had more C distributed at the depth of 5–15 cm with a minimum at 0–5 cm in both sites. C stocks in the soil of 0–5 cm and 15–30 cm were significantly different between the two sites ($P < 0.05$). Interestingly, we found that enclosure leads to more C distribution in the top-surface of the soil. In addition, there were higher C stocks in soil at 0–30 cm depth in the fenced site but the difference was not statistically significant (Table 2).

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

At the beginning of the chase period, 495.43 mg and 370.36 mg ^{13}C were labeled as total amounts of ^{13}C in the plant–soil systems of the fenced and control grazed plots, respectively. The allocation of ^{13}C in shoots was 53 % in the fenced plots and 42 % in the grazed plots, a statistically significant difference ($P < 0.05$). Then, the amount of ^{13}C decreased following exponential decay within the chase period in both plots (Fig. 2a). The recovery of ^{13}C in shoots declined from 53 % to 43 % ($P < 0.05$) during the first 24 h in the fenced plots; this was lower than that observed in the grazed grassland site where we observed a decrease of 16 % in ^{13}C recovery in shoots. A slower rate of ^{13}C decay in shoots was observed in the first 4 d after labeling in the fenced plots compared with the grazed plots. This was followed by a nonsignificant decrease until the end of the chase period in the grazed plots (Fig. 2a). The decreasing trend of ^{13}C recovered with no plateau period was apparently due to shoots in the fenced plots during the chase period.

A larger recovery of ^{13}C was detected in soil during the chase period in both land types, with a significantly lower value in the fenced plots (Fig. 2c). However, the allocation of ^{13}C in roots was lower during the chase period (Fig. 2b). The allocation of ^{13}C in roots was effected by the import of ^{13}C in shoots, the export of ^{13}C into soil, and CO_2 in soil respiration. There were no significant differences in ^{13}C found in roots between the fenced and grazed grassland types at any sampling time during the chase period, probably as a result of the higher variability among the plots (Fig. 2b). It was obvious

that less ^{13}C migrated to the soil through roots in the fenced plots immediately after labeling (44 %, $P < 0.05$). A higher rate of ^{13}C decline in soil was found in the fenced plots during the first 24 h after labeling, while there were nonsignificant variations at the grazed site. Thereafter (from 24 h to the end of the chase period), the allocation of ^{13}C in the soil of the fenced plots reached stable values with nonsignificant differences. In the grazed plots, a minimum was reached 18 d after labeling. The results correlated with the ^{13}C variations in shoots and the $^{13}\text{CO}_2$ efflux rates from soil respiration. During the first 24 h after labeling, there was less ^{13}C loss from shoots (10 %), with a lower rate at the fenced site. Coupled with a high rate of ^{13}C loss from soil respiration, this resulted in the significant decrease observed in the amounts of ^{13}C in soil at the fenced grassland (Fig. 2a and d). A significant reduction in ^{13}C amounts in shoots was observed in the grazed plots. However, the ^{13}C variations in soil were not significant during the first 24 h, indicative of significantly higher rates of $^{13}\text{CO}_2$ efflux from soil respiration than what occurred in fenced site (Fig. 2d).

At the end of the chase period (32 d after labeling), significantly less ^{13}C (14 %) was left in shoots in the fenced plots and 18 % was left in the grazed plots ($P < 0.05$). However, the allocation of ^{13}C into below ground at the fenced sites (53 %) was significantly lower than that of the grazed plots (61 %, $P < 0.05$). The reduced distribution of ^{13}C into below ground at the fenced plots resulted from the significantly lower allocation of ^{13}C both in soil (37 %, $P < 0.05$) and soil respiration (5 %, $P < 0.05$). These values were 47 % and 8 % for ^{13}C allocated in soil and soil respiration at the grazed plots, respectively. We found a greater allocation of ^{13}C in roots at the fenced plots in comparison with the grazed sites. However, this did not influence the unequal below ground ^{13}C allocation observed in the two land types. As shown in Fig. 3, the allocation of ^{13}C in roots was not significantly different between the two sites.

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

The ^{13}C recovery in roots varied according to depths at both land use types. It decreased gradually from the highest in the surface layer to the lowest values obtained in the deepest layer (Fig. 4a). The ^{13}C in roots at 0–30 cm was mainly allocated in the shallow depth of soil (0–5 cm) and the recovery of ^{13}C at 0–5 cm determined the amounts of ^{13}C in roots for the whole surface layer (0–30 cm), as shown in Fig. 4a.

The ^{13}C allocated in the soil was not consistent with the rank order of the depth. In both land use types, more ^{13}C was recovered in the depths of 5–15 cm and 15–30 cm with the lowest in the shallow layer (Fig. 4b). After being fenced for 6 yr, there was lower ^{13}C recovery in the enclosure soil at 5–15 cm and 15–30 cm than that observed in the grazed site. At the end of the chase period, significantly lower ^{13}C was allocated into the depths of 5–15 cm and 15–30 cm in the fenced plots. However, the ^{13}C allocation at 0–5 cm showed a nonsignificant difference between the two sites (Fig. 4b).

4 Discussion

Livestock enclosure alters 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 enclosure as an effective approach for restoring vegetation and improving C storage of the grassland (Li et al., 2012; Su et al., 2003), while others have demonstrated that enclosure 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 enclosure on the grassland are community-specific.

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4.1 Effect of exclosure on vegetation structure

In the *Kobresia* meadow, the peak biomass and plant coverage was assessed (Table 1). The results indicated that elimination of livestock from grassland lead to more accumulation of litter (219.00 g m^{-2}) than what was observed in the grassland with grazing (104.08 g m^{-2}). In contrast, the productivity of live plants in the fenced grassland (351.76 g m^{-2}) was significantly lower than that in the grazed grassland (403.35 g m^{-2}). These results are not consistent with several works that have demonstrated exclosure has had 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 the involved grazing (Qian, 1979; Guo et al., 2006). For a winter grazing pasture in our research, 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 (Table 1), with livestock exclosure promoting the growth of grasses while suppressing legumes and forbs. In addition, exclosure reduced the plant diversity, especially that of forbs (Table 1). 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 are palatable for livestock and it was shown that grasses had a stronger competition for light than the 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,

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1996). After suppression of livestock feeding, the increased growth of grasses and the accumulated litter had negative effects on the productivity and diversity of legumes and forbs through light limitation. The *Kobresia humilis* meadow was therefore found to be nutrient-limited. Thus, nutrient level may be another important factor (in addition to light) cooperating with grazing to affect the community composition of the grassland.

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

To investigate the effects of enclosure on C cycling in the ecosystem, stable C-isotope analysis was used to track carbon movement in the fenced grassland as well as the grazed sites (Fig. 1). The chase period to determine the cycling of ^{13}C newly incorporated by photosynthetic was approximately 32 d in our study (Hafner et al., 2012; Wu et al., 2009). However, a different chase period has been reported as well due to the steady state of ^{13}C in the plant–soil system after labeling in their experiments (Wang et al., 2007). Four replications were used to evaluate the cycling and allocation of ^{13}C in each land use type. The carbon stocks (g m^{-2}) of the different pools in the plant–soil systems were assumed to be constant during the chase period of 32 days (Wu et al., 2009). We used an average $\delta^{13}\text{C}$ of the four replications to assess the dynamics and allocation of ^{13}C in the plant–soil system during the chase period (Wang et al., 2007).

Immediately after pulse labeling, 53 % of ^{13}C assessed in the plant–soil system was recovered in shoots in the fenced plots, which was significantly higher than the 42 % obtained in the grazed plots. During the first 24 h after labeling, 19 % of ^{13}C was estimated to loss or export from shoots in the fenced plots, and this was twice lower than in the grazed plots (38 %) (Fig. 2a). These results suggest that ^{13}C is lost or exported from shoots at a lower rate in the grassland after enclosure. The lower rate of ^{13}C migrating to the soil in the fenced plots during the first 24 h confirmed the restricted ^{13}C dynamics from shoots into below ground in the grassland under enclosure (Fig. 2c). This is probably due to the variations in vegetation structure. It is known that plant diversity has positive effects on C accumulation in soil (Steinbeiss et al., 2008; De Deyn et al., 2011). This was confirmed by our results with reduced plant richness in the fenced

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grassland. Indeed, the loss of legumes in the fenced grassland may be an important factor affecting C sequestration (Fornara and Tilman, 2008) (Table 1).

The ^{13}C in shoots continually declined during the chase period in the fenced plots, while in the grazed plots, the recovered ^{13}C (%) diminished to a constant value during the first days, followed by no significant variations from 4 days after labeling until the end of the chase period (Fig. 2a). These findings suggest that a part of ^{13}C was transformed into more stable structural carbon in shoots in the grazed plots, in accordance with previous works (Wu et al., 2009). The data were consistent with the lower peak biomass of vegetation as lower ANPP (annual aboveground net primary productivity) was obtained in the grassland under enclosure (Table 1). Less ^{13}C was allocated to shoots for growth in the fenced plots. The lower ^{13}C allocation in shoots at the end of the chase period in the fenced plots (Fig. 3) is likely caused by lower productivity due to the light or nutrient limitation.

Generally, roots are recognized as a major sink in the plant–soil system, and more C migrate in soil by means of roots than exudates (Wu et al., 2009). However, our results showed that ^{13}C recovered (%) in living roots was much less than that in soil at both land use types (Fig. 2b and c), consistent with another study using stable C labeling (Hafner et al., 2012). It has been suggested that the plant development stage during the chase period influences the ^{13}C allocation in roots (Kuzyakov et al., 1999; Palta and Gregory, 1997). In an earlier *Kobresia humilis* meadow study, many plants such as *Kobresia humilis*, *Elymus nutans*, and many forbs species were in the state of flowering and fruit-bearing (August) (Shi et al., 1988). It is possible that less ^{13}C was found in roots because the plants first attributed ^{13}C to produce assimilates for generation instead of root growth during the chase period in our experiments (Hafner et al., 2012). There were no significant differences of ^{13}C recovered (%) in roots between the two land use types at any sampling time. However, the ^{13}C recovered in roots tended to increase during the chase period in the fenced plots (Fig. 2b). Lower productivity of shoots in the fenced grassland favored more ^{13}C migration to roots, although higher spatial variability obscured the differences of ^{13}C in roots between the two sites. Fur-

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thermore, the evidence from root C stocks in the two land use types confirmed these results. Indeed, higher but not statistically significant C stocks were assessed in roots in the fenced grassland in comparison with the grazed site (Table 2).

Our data suggest that at low levels, ^{13}C is firstly shifted into soil by means of exudates from roots. This process took place immediately after labeling. Indeed, less ^{13}C was allocated in soil in the grassland under enclosure, in addition to significantly lower $^{13}\text{CO}_2$ efflux rate of soil respiration (Fig. 2c and d). It is likely that the plant diversity of the vegetation influences the ^{13}C dynamic migration from plant to soil with major influences on the microorganism activity in our study (Steinbeiss et al., 2008; Wardle et al., 1999; Hooper et al., 2000; Stephan et al., 2000). The reduced rate of CO_2 efflux in the fenced grassland may indicate a decrease of microorganism activity in soil compared with the grazed site. There have been complementarities effects that promote the nutrient cycling existing in the grassland with high plant diversity (Oelmann et al., 2007; Temperton et al., 2007). Additionally, the composition of the functional groups, especially the variations in legumes, has been suggested to influence ^{13}C allocation in soil (Fornara and Tilman, 2008; De Deyn, 2011).

We found that enclosure management has negative effects on ^{13}C allocated in deeper layers (Fig. 4b). Less ^{13}C migrated from roots to soil at deeper soil of the fenced plots compared with the grazed grassland during the chase period. Probably the characteristics of different root types and structures affected the vertical distributions of ^{13}C input into soil. Indeed, legumes and forbs species have deep root systems. The suppressed growth of legumes and forbs in the fenced grassland had therefore negative effects on ^{13}C exudation into deeper soil. In addition, a weak leaching effect in the fenced grassland as a result of accumulated litter on the above ground constitutes another factor influencing the vertical distribution of ^{13}C allocated in soil.

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Our results demonstrated that livestock enclosure changed the vegetation community structure. We also found that enclosure decreased the ^{13}C dynamic rate in the plant–soil system, suggesting that more ^{13}C is allocated into roots in the fenced grassland. However there was less ^{13}C migration into soil under enclosure. There were relations between the variations of vegetation community structure and C cycling. The decreased productivity of legumes, forbs and the accumulated aboveground litter after fencing may be responsible for the difference observed in C cycling in the short-term. However, long-term experiments should be carried out in order to better understand the effects of enclosure on the *Kobresia humilis* meadow. In this study, considering the negative effects of enclosure, we found evidence that livestock enclosure 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 enclosure practice to the grassland management should be community specific.

Acknowledgements. We acknowledge the support of this study by the Key Program of National Natural Science Foundation of China (41030105) and the Special Program of Carbon Sequestration of Chinese Academy of Sciences (XDA05070000). We gratefully acknowledge Zhou Huakun for his advice during the study. Many thanks also go to Cao Hui, Wang Jiheng, Ge Shidong, Li Bing and Li Chunli for their help in the field sampling work of the study.

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Table 1. Species diversity, mean (\pm SD) vegetation aboveground biomass, and vegetation cover in the fenced and control grazed meadow.

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

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

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Table 2. Mean (\pm SD) C stocks (Mg ha^{-1}) during the chase period in aboveground and below-ground C pools of the fenced and grazed meadow.

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

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

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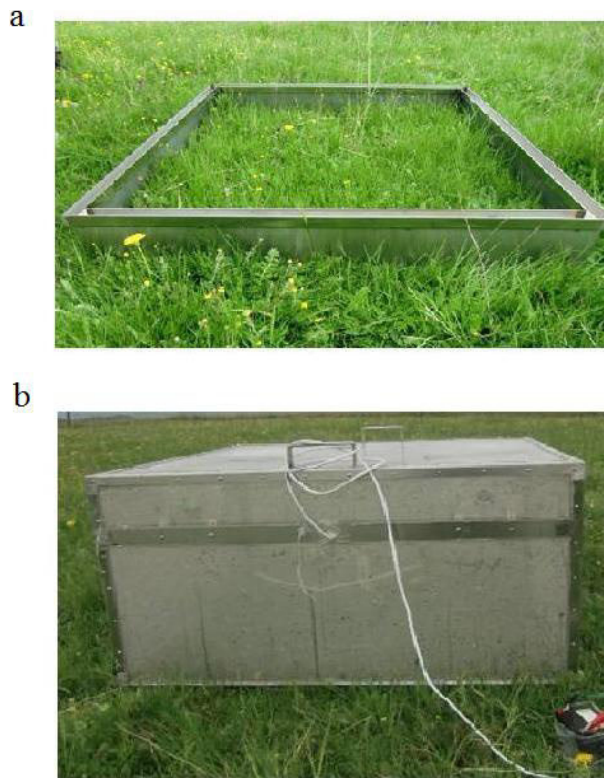


Fig. 1. Experimental chamber setup for ^{13}C pulse labeling. The steel base (a) was installed in the soil before labeling. At the beginning of labeling, a PVC cover was sealed to the base to form a chamber (b). The plant in the chamber was labeled by ^{13}C through photosynthesis with $^{13}\text{CO}_2$. The $^{13}\text{CO}_2$ was released by injecting H_2SO_4 into the container holding Na_2CO_3 in the chamber.

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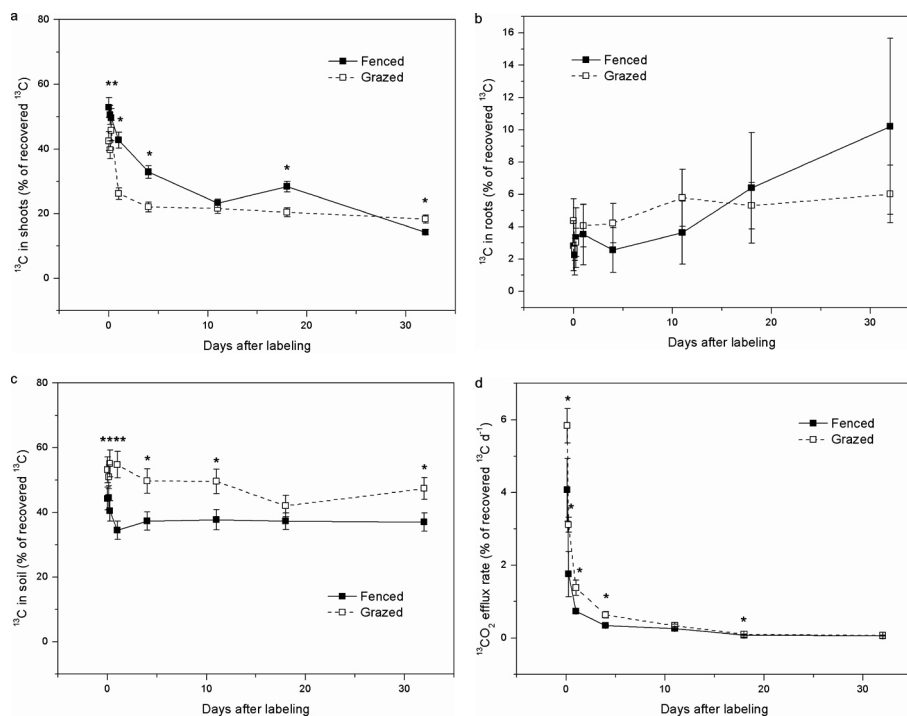
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Fig. 2. The dynamics of ^{13}C allocation (% of recovered ^{13}C) in shoots (a), roots (b), and soil (c) in the fenced and control grazed meadow during the 32 day chase period. The last figure shows the dynamics of $^{13}\text{CO}_2$ efflux rate (% of recovered $^{13}\text{C} \text{ d}^{-1}$) by soil respiration (d) during the chase period. * Indicates significant differences at $P < 0.05$ between the fenced and grazed meadow for each time step. Data are means \pm standard deviation ($n = 4$).

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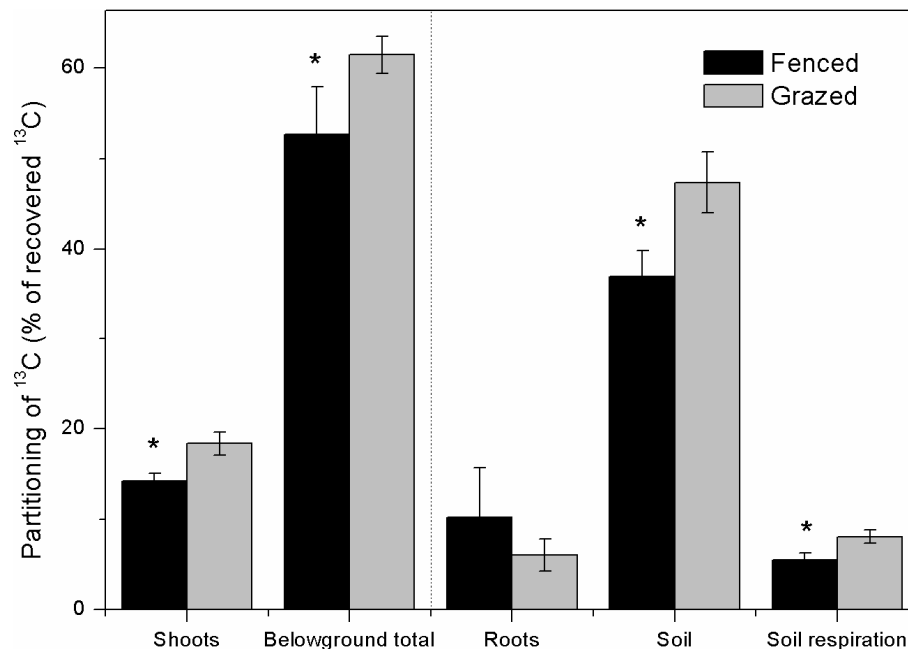


Fig. 3. Partitioning of ^{13}C (% of recovered ^{13}C) in shoots, below ground of the fenced and control grazed meadow at 32d of the chase period. The partitioning of ^{13}C (% of recovered ^{13}C) in belowground stocks was divided into three parts, including roots, soil stocks and loss by soil respiration (right panel in the figure). * Indicates significant differences at $P < 0.05$ between the fenced and grazed meadow. Data are means \pm standard deviation ($n = 4$).

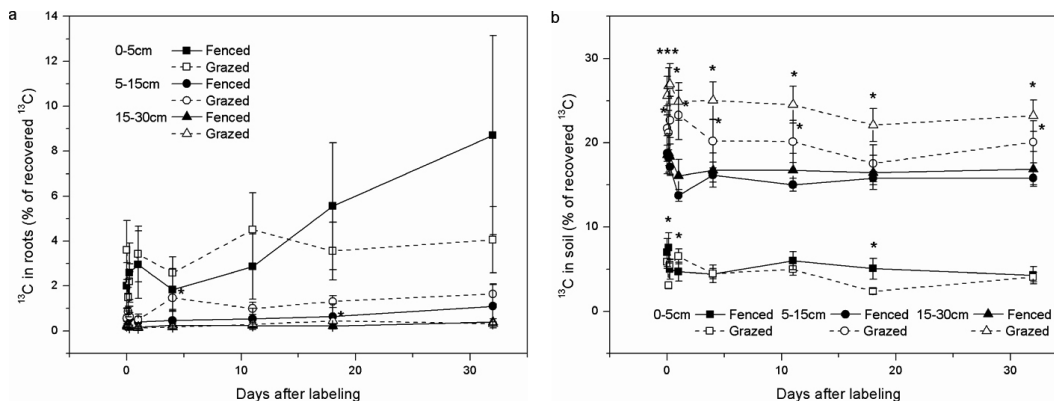


Fig. 4. The vertical distribution dynamic of ^{13}C allocation (% of recovered ^{13}C) in roots (**a**) and soil (**b**) at layers 0–5, 5–15 and 15–30 cm in the fenced and control grazed meadow during the 32 day chase period. * Indicates significant differences at $P < 0.05$ between the fenced and grazed meadow for each time step at each soil layer. Data are means \pm standard deviation ($n = 4$).

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