Carbon pools and fluxes in a Tibetan alpine *Kobresia pygmaea* pasture partitioned by coupled eddy-covariance measurements and $^{13}CO_2$ pulse labeling

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HIGHLIGHTS

- We lack understanding of the carbon cycling of Tibetan alpine pastures.
- We measured the turnover of recent assimilates within plant soil atmosphere system.
- Absolute fluxes were assessed by coupling eddy-covariance and CO_2 pulse labeling.
- We identify the root turf as the major part for carbon turnover in this ecosystem.
- Grazing cessation didn't affect carbon allocation and fluxes in one growing season.

ARTICLE INFO

ABSTRACT

The Tibetan highlands host the largest alpine grassland ecosystems worldwide, bearing soils that store substantial stocks of carbon (C) that are very sensitive to land use changes. This study focuses on the cycling of photoassimilated C within a *Kobresia pygmaea* pasture, the dominating ecosystems on the Tibetan highlands. We investigated short-term effects of grazing cessation and the role of the characteristic *Kobresia* root turf on C fluxes and belowground C turnover. By combining eddy-covariance measurements with $^{13}CO_2$ pulse labeling we applied a powerful new approach to measure absolute fluxes of assimilates within and between various pools of the plant-soil-atmosphere system. The roots and soil each store roughly 50% of the overall C in the system (76 Mg C ha^{-1}), with only a minor contribution from shoots, which is also expressed in the root:shoot ratio of 90. During June and July the pasture acted as a weak C sink with a strong uptake of approximately 2 g C m^{-2} d^{-1} in the first half of July. The root turf was the main compartment for the turnover of photoassimilates, with a subset of highly dynamic roots (mean residence time 20 days), and plays a key role for the C cycling and C storage in this ecosystem. The short-term grazing cessation only affected aboveground biomass but not ecosystem scale C exchange or assimilate allocation into roots and soil.

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1. Introduction

Soils of grassland ecosystems store large amounts of carbon (C) (Scurlock and Hall, 1998) and their C sequestration potential has attracted a lot of attention in recent years (IPCC, 2013). In alpine environments the sensitivity of grasslands to external influences is very pronounced (e.g. Fang et al., 2010a; Lin et al., 2011; Ni, 2002; Wohlfahrt et al., 2008). This is especially the case for the *Kobresia* pastoral ecosystem of the Tibetan highlands (Atlas of Tibet Plateau, 1990; Miehe et al., 2008a,b; Chen et al., 2013, 2014; Sun and Zheng, 1998), which is among the ecosystems most sensitive to climate change and anthropogenic activities (Cui and Graf, 2009; Miehe et al., 2011; Qiu, 2008; Yang et al., 2014).

Although the Tibetan Plateau only accounts for approximately 1.0% of the global terrestrial land area (Fang et al., 2010b), the C stored in its soil makes up 2.5% of the global soil C storage (Wang et al., 2002). It is therefore important to understand and to quantify the C budget as well as to estimate C fluxes and identify their drivers in these remote highland pastures with in situ studies (Hafner et al., 2012; Wang et al., 2007; Wu et al., 2010).

The Tibetan highlands in general are mainly above the tree line at about 3800 m a.s.l. in the north and above 4800 m a.s.l. in the southeast (Miehe et al., 2007) and are thus characterized by alpine steppe and *Kobresia pygmaea* dominated pastures (Wang et al., 2006). *K. pygmaea*, a cyperaceae, extends approximately 450,000 km² along an altitudinal range of nearly 3000 m a.s.l., between the montane belt (around 3000 m in the northeast and around 4000 m in the eastern and southern declivity to nearly 6000 m (Miehe et al., 2008b)). It grows no more than a few centimeters tall while developing a very extensive rooting system. These roots form a very dense felty turf layer, consisting of roots, root remains, amorphous humus and minerogenious matter which covers and protects the soil from wind and water erosion as well as trampling damage by large herbivores (Kaiser, 2004; Miehe et al., 2011).

It is assumed that the major driver for the vegetation composition and structure of this *K. pygmaea* ecosystem is grazing by herbivores, namely traditional pastoral livestock and small mammals (Miehe et al., 2008b; Wu et al., 2009). Therefore, the state of the *K. pygmaea* ecosystem is strongly dependent on the grazing practices and livestock husbandry by the local Tibetan population (Miehe et al., 2014). These human activities have changed dramatically since the 1950s, for reasons including increasing livestock numbers, concentration of grazing close to settlements and fencing due to sedentarization programs (Du et al., 2004; Goldstein and Beall, 1991; Harris, 2010; Lu et al., 2009; Sheehy et al., 2006). As a reaction to overgrazing and subsequent degradation, rangeland policies of recent years included the regulation of livestock numbers and the implementation of grazing exclosures (Han et al., 2008). However, the effects of altered grazing intensity on C budgets of the alpine pastures in the highlands are not sufficiently understood yet (Gao et al., 2007). Grazing is considered to be one of the key factors for C budget and turnover of *K. pygmaea* pastures. It indirectly affects C allocation in the ecosystem by controlling species composition and functional diversity of the vegetation on the time scale of years (Cao et al., 2004; Gao et al., 2007; Klein et al., 2004; Miehe et al., 2008a,b; Wei et al., 2012; Wu et al., 2009; Zhao and Zhou, 1999). Grazing has been shown to have positive effects on the overall C storage of the *Kobresia* ecosystem (Gao et al., 2007; Hafner et al., 2012; Shi et al., 2013). The crucial role of the turf layer within this ecosystem is emphasized by the findings of Hafner et al. (2012). They report that the change from a Cyperaceae to Poaceae dominated montane grassland in the northeastern highlands (3400 m a.s.l.), induced by cessation of grazing, had the greatest effect within the turf layer, with a decrease of C fluxes and lower plant-derived C stocks within the upper layer of the soil. Since all mentioned studies have been conducted in already established grazing exclosures, no short-term effects of grazing cessation on the *Kobresia* pastures have been investigated yet, although direct physiological effects on the C allocation of plants have been observed on short time scales as well in other ecosystems (Bardgett and Wardle, 2003; Holland et al., 1996; Schmitt et al., 2013).

Two of the most commonly used methods in C studies are turbulent flux measurements with the eddy covariance (EC) method (Aubinet et al., 2012) and pulse labeling with ^{13}C or ^{14}C enriched CO_2 (see reviews by Kuzyakov and Domanski (2000) and Kuzyakov (2001)). EC measurements are a micrometeorological approach used to estimate C net ecosystem exchange (NEE) on the ecosystem scale (Baldocchi, 2003; Wohlfahrt et al., 2012). They provide absolute values for the C exchange with a high resolution and over a long time for a detailed overview of the exchange between the ecosystem and the atmosphere (Foken, 2008a). Only few studies with EC have been conducted on the Tibetan Plateau e.g. by Kato et al. (2004, 2006) and Zhao et al. (2005) in the northeast of the Plateau and by Fu et al. (2009) in the southern highlands. $^{13}CO_2$ pulse labeling enables tracking of the allocation of assimilated C to the various C pools within the plant–soil system. Assimilates are used for metabolism by shoots, roots and rhizosphere microorganisms or become incorporated into soil organic matter. Thus, their distribution affects how long the assimilated C will remain in the ecosystem before returning to the atmosphere by root and microbial respiration (Carbone and Trumbore, 2007). Above- and belowground C budgets and C allocation within the plant–soil-system of the Tibetan Plateau estimated by $^{13}CO_2$ labeling have been presented by Wu et al. (2010), Hafner et al. (2012) and Unteregelsbacher et al. (2011), but only from the northeast part of the Plateau in about 3000 m a.s.l.

Furthermore, each of the two methods, EC measurements and CO_2 pulse labeling, has its shortcomings. EC measurements do not reveal C fluxes within single compartments of the ecosystem (Leclerc and Foken, 2014). $^{13}CO_2$ pulse labeling only provides a relative distribution of assimilates, yet mass units and absolute fluxes are important in in situ studies related to C balance and turnover (Kuzyakov and Domanski, 2000). To close this gap, we apply a new approach proposed by Riederer (2014). We couple the relative distribution of photoassimilates, derived from a $^{13}CO_2$ pulse labeling experiment, with the ecosystem C uptake, derived from EC measurements. Thereby, we can determine the absolute fluxes of assimilates into the different plant and soil compartments of the ecosystem.

We chose our study site taking into account the general lack of in situ measurements of C cycling, especially in the core distribution of the *K. pygmaea* ecosystem at high altitudes (>4000 m a.s.l.). We consequently coupled EC measurements and $^{13}CO_2$ labeling to characterize the C allocation and turnover and to understand the role of the turf layer in terms of C storage and cycling. Furthermore, we investigated if grazing cessation affects C fluxes and stocks of alpine *K. pygmaea* pastures already within the first growing season after cessation. We expect that short-term effects of grazing cessation would quickly express in the allocation of recent assimilates and later on in above- and belowground C stocks.

2. Material and methods

2.1. Study site

Our study site is located on the Tibetan Plateau at 4410 m a.s.l. adjacent to the village Kema and the "*Naqu Ecological and Environmental Observation and Research Station*" (92°06′ E, 31°16′ N; established in 2007 as "*K. pygmaea Research Station Kema*" by the Marburg University and the Tibet University Lhasa with support of the Volkswagen foundation and since 2011 operated by the Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing).

The site itself is a typical alpine *Kobresia* pasture on a gentle slope, covered with *K. pygmaea* (Cyperaceae), accompanied by other graminoids (*Carex* spp., *Festuca* spp., *Kobresia pusilla*, *Poa* spp., *Stipa purpurea*) and to a minor degree by small rosette plants and cushion

plants. Thus, the site is representing one of the most common and important vegetation types on this ecosystem (Miehe et al., 2008b). The average vegetation height at the grazed plots of less than 2 cm is typical for the golf course-like Kobresia mats (Miehe et al., 2008b), and the characteristic turf layer has an approximate thickness of 7 cm overlying soils classified as stagnic Cambisols (humic, eutric) (Table 1, IUSS-ISRIC-FAO, 2006). The specific turf mats of K. pygmaea grasslands are designated as Afe horizons according to Kaiser et al. (2007) and Kaiser et al. (2008) throughout this study. Most of the pasture (65%) is covered by dense vegetation and an intact turf layer. 16% of the surface is covered by turf patches with crusts of lichens and algae, and only few grass bunches and cushion plants or rosettes turf (Unteregelsbacher et al., 2011). The remaining 19% of the surface is bare soil, with only few plants occurring and the characteristic turf layer missing. The distribution of the surfaces was surveyed in 2012 (Biermann et al., 2013). Grazing with a stocking rate of about 2.5 yaks per hectare is restricted to one month in winter or spring due to a governmental pasture health program started in 2006.

The nearest weather station of the Chinese weather service in Naqu (4507 m a.s.l.) recorded for the period 1971–2000 an annual precipitation of 430 mm as well as a mean maximum temperature for the warmest month of 15.6 °C and an annual average temperature of −0.9 °C (http://www.weather.com.cn). Precipitation falls mainly as rain during the summer months from May to August, but heavy snow events can occur in winter and spring. In contrast to the typical pattern, the spring and summer month in 2010 were comparably dry with only 40 mm of precipitation recorded at the study site in July.

2.2. Grazing treatments

At the research site a pasture area of 100 × 250 m was fenced in 2009, excluding grazing livestock such as yak, sheep and goat. In addition, four subplots (15 × 15 m) were established inside the livestock exclosure to additionally exclude the only surviving wild herbivore, an endemic small soil-dwelling mammal, the Plateau Pika (Ochotona curzoniae).

All three grazing treatments were investigated within the labeling experiment: normal grazing (G), a partial exclosure, with exclusion of livestock but allowing for grazing by Pikas (P) and ungrazed plots (U), with exclusion of livestock and pikas. EC measurements were only possible over G and P, but not over U, because maintaining an exclosure of pikas of the size necessary for EC measurements was not possible. Thus, effects of livestock grazing correspond to the difference between G and P, whereas the combined grazing effects of livestock and pikas are reflected by the difference between U and G.

During the experimental period from June to August 2010 the pasture was stocked with 2.5 yaks per hectare additionally to the governmental management, which is within the range of stocking rates applied in the Naqu prefecture (from 0.1 to 3.4 yaks per hectare; Wei and Chen (2001)) However, most of this stocking is beyond the carrying capacity and thus pastures in this region are overgrazed (Wei and Chen;, 2001).

Table 1
Horizons and texture of the stagnic Cambisol (humic, eutric) according to WRB (IUSS-ISRIC-FAO, 2006). The turf mat is designated as Afe following Kaiser et al. (2008) (Suffix fe from felty according to Kaiser (2004)).

Horizon	Depth [cm]	Texture	Description
Afe	0–7	Ls2	Felty Kobresia pygmaea turf mats consisting of woody roots
Ah1	7–15	Ls3	K. pygmea turf mats with decreasing root density and woody roots
Ah2	15–23	Ls3	Accumulation of organic carbon in mineral soil
Sg-Bw	23–49	Tl	Redoximorphic features, carbonate content 0.003%
Ck	>49		Diffuse CaCO$_3$

2.3. Eddy-covariance measurements

2.3.1. Data acquisition

Turbulent atmospheric fluxes, additional energy balance components and meteorological parameters were measured from 8 June to 2 August 2010, inside (EC-P) and outside (EC-G) the livestock exclosure. Eddy-covariance fluxes were determined with an ultrasonic anemometer (CSAT3, Campbell Sci. Inc.) and an open path infrared gas analyzer (IRGA, LiCOR 7500, LiCOR Bioscience Inc.). Further energy balance components were estimated with a net radiometer (CNR1, Kipp & Zonen) and soil temperature profiles beneath bare soil, grazed and ungrazed Kobresia mats. Meteorological reference data was also measured on site (HMP45, & PTB210, Vaisala; rain gauge, Ott). Detailed setup information is given in Table A1 or by Biermann and Leipold (2011).

2.3.2. Post processing

The turbulent fluxes, averaged for 30 min, were calculated from the high frequency raw data with the well-tested software package TK3 (Department of Micrometeorology, University of Bayreuth; Mauder and Foken, 2011). Furthermore a footprint analysis was performed to ensure representativeness of the measurements (Göckede et al., 2006). It showed that the source areas for both eddy-covariance stations were dominated by K. pygmaea mats. Furthermore, towers were separated far enough so that the measurements can be considered to be independent from each other and can be attributed to either G or P. This analysis also ensures the comparability between the $^{13}CO_2$ pulse labeling experiment and the EC measurements, as recommended in Reth et al. (2005). Since heterogeneity within the roughness or thermal properties of the underlying surface might result in large-scale turbulent structures not measured with EC, gaps can be found in the energy balance closure (EBC) (Foken, 2008b). Investigation of the EBC for the 2010 experiment at Kema showed that 73% of the energy balance is closed for observations from EC-G and EC-P. The here presented NEE measurements are not corrected for this missing energy in the turbulent exchange as it is not applicable (Foken et al., 2011) while it is a standard procedure for the latent and sensible heat flux. Due to malfunction of the measurement devices or the above-mentioned quality assessment and consequent rejection of data with poor quality, gaps are found within the time series of turbulent fluxes and C exchange measurements. To ensure a continuous time series of NEE, which is necessary for the estimation of C budgets, the data gaps were filled with a widely used technique as described in Ruppert et al. (2007) and Appendix A3.

2.4. $^{13}CO_2$ pulse labeling

2.4.1. Experimental setup and sampling

The $^{13}CO_2$ pulse labeling was conducted on the 1st of July 2010 (for details on selection of this date see 3.1) with four replicates of each of the three treatments (G, P, U), grouped in four blocks (in detail described in Biermann and Leipold (2011)). The labeling procedure itself is presented in detail in Appendix B1 and by Hafner et al. (2012).

The ^{13}C was chased in the plant–soil–atmosphere system over a period of two months with increasing sampling intervals (0, 1, 4, 8, 15, 23, 29, 36, 48 and 64 days after the labeling). The first sampling (0) was conducted immediately after the labeling. The following pools were sampled: plant shoots, roots and soil organic matter in two layers (0–5 cm and 5–15 cm) and soil CO_2 efflux. Shoots were sampled by clipping and belowground pools were sampled with a soil corer. Total belowground CO_2 efflux and its $\delta^{13}C$ signature were measured with the static alkali absorption method (Hafner et al., 2012; Lundegardh, 1921; Singh and Gupta, 1977). We are aware that this method is often described as inaccurate for the determination of the soil CO_2 efflux. However, it has been shown that this method can give reasonable

estimates for sufficiently long deployment times (Rochette and Hutchinson, 2005). It was the only means at this remote location of obtaining measurements of soil CO_2 efflux and its isotopic signature. The sampling is described in detail in Appendix B2.

2.4.2. Data analysis

To investigate the C distribution in the ecosystem and to compare C sequestration in the grazing treatments, C stocks (Mg C ha^{-1}) of the plant and soil pools were calculated on the basis of the pool mass and the C content determined by the IRMS (Appendices B2, B3).

The distribution of photoassimilates in the system is calculated based on the enrichment of ^{13}C in each sample achieved by the $^{13}CO_2$ pulse labeling. Briefly, this enrichment can be calculated as a product of the increment of ^{13}C ($^{13}C_{t\ atom\%excess}$) and the amount of C in the corresponding pool at a specific time after the labeling. For an inter-comparison between different plots all amounts of recovered ^{13}C in a pool at a given sampling time are expressed as percentage of the reference recovery. The reference recovery is defined for each plot, as the sum of all excess ^{13}C recovered in shoots, roots and soil organic carbon (SOC) at the first sampling, directly after opening the labeling chamber. The details of the calculation are given in Hafner et al. (2012) and Appendix B3. The figures and tables present means and standard errors of the mean (SEM).

Soil respiration measurements were distorted by the admixture of atmospheric CO_2 in the traps, which became apparent from a shifting towards higher values of the δ^{13}C signature of the non-enriched reference measurements of soil respiration. Therefore, Keeling Plots (Keeling, 1961) were used to account for this admixture and to obtain the natural abundance isotope signature of the soil CO_2 efflux.

2.5. Coupling of eddy-covariance flux measurements and $^{13}CO_2$ labeling

The $^{13}CO_2$ pulse labeling reveals the relative fraction of recently assimilated C that is transported into various pools of the plant–soil system after a given time. The EC technique measures absolute values of C fluxes on ecosystem scale. By coupling these two techniques, we assume that the fraction of recovered ^{13}C in a specific pool after a defined allocation period represents the ratio between the flux into this pool and the overall assimilation. Therefore, we use the following equation, adapted from Riederer (2014) to estimate absolute fluxes into the different pools within the ecosystem for the defined allocation period:

$$F(C)_i = R\left(^{13}C_i\right) * \overline{GPP}_{daily} \tag{1}$$

with $F(C)_i$ being the absolute flux into a specific pool i, $R\ (^{13}C_i)_t$ the fraction of recovered ^{13}C within pool i at the end of the defined allocation period and $\overline{GPP}_{daily}$ being the mean daily assimilation estimated with EC during the allocation period.

Although this approach is simple, it is essential that meteorological conditions and assimilation on ecosystem scale don't vary strongly since this would affect the transport of C within the plant–soil system, needs to be stable throughout the allocation period of the ^{13}C. Furthermore, it is difficult to estimate the length of this allocation period, which should not be confused with the end of the chase period. However, this period is critical for the interpretation of the distribution of the assimilated tracer (Wang et al., 2007). Allocation of ^{13}C to various pools in the plant–soil system is considered to be complete when the metabolic plant components are depleted of ^{13}C (Saggar et al., 1997). This point is difficult to identify, but numerous studies report that allocation is finished within 3–4 weeks (Hafner et al., 2012; Keith et al., 1986; Riederer, 2014; Swinnen et al., 1994; Wu et al., 2010).

3. Results

3.1. Carbon exchange on ecosystem scale

The observed matter and energy fluxes observed by the EC stations as well as temperature, humidity and precipitation measurements for the period 9 June to 2 August (Fig. 1) enable us to characterize the overall exchange conditions between the *K. pygmaea* ecosystem and the atmosphere. In general, the dynamics of the C fluxes measured at both EC stations were very similar. When averaged over the whole period, the NEE resembled a weak sink for both stations (Table 2). However, the observations can be divided into three periods with different characteristics. At the beginning of the observation period, the NEE did not show a clear daily cycle with mainly respiration and only weak assimilation. Starting from 24 June assimilation increased which resulted in a negative NEE during the day, leading to the decline of the cumulated NEE after this date. This can be explained by onset of rain, rise in soil water content and a rise in air temperature in June. For a period that lasted until 24 July fluxes showed a constant behavior. After 24 July till the end of the EC measurements the NEE was again characterized by a weaker assimilation during overall drier conditions. This was also apparent in the ratio between the sensible and latent heat flux, the Bowen ratio, for these periods, which was greater than one, since the sensible heat flux dominated over the latent heat flux (data not shown). Based on the in situ calculated fluxes and the so gained knowledge about the C dynamic, the start of the $^{13}CO_2$ pulse labeling experiment was scheduled on 1 July.

A comparison of the measured NEE fluxes from the two stations using the geometric mean regression (Dunn, 2004) – the method of choice to account for random errors in both time series – shows only a 3% difference. This small difference in mean NEE measurements on ecosystem scale cannot be considered as relevant and, additionally, cannot be attributed to any differences in grazing. Rather, existing differences between individual half-hour values of the two EC stations were related to differences in the distribution of vegetation and bare soil within the actual footprint of these flux estimates, or free convection events which were not captured with the EC measurements. This also propagated into the cumulated and mean daily fluxes (Fig. 1) and explained the small divergence within the dynamics of the fluxes from the two sites.

3.2. Carbon distribution within the ecosystem

Averaged over all grazing treatments, the total C stored aboveground and in the upper 15 cm of the soil made up 76.1 ± 1.6 Mg C ha^{-1}. The aboveground biomass had only a very marginal contribution (~0.6%) to the overall C stocks whereas equal C amounts (ca. 50%) were stored in roots and soil organic carbon (SOC) of the upper 15 cm (Fig. 2a). The mean root:shoot (R:S) ratio was 90.

The grazing treatment had a significant effect on the C stocks of the shoots ($F_{2,59} = 4.81$, $p_{adj} = 0.046$). The post-hoc test revealed that the shoot C of the livestock exclosure (P) was significantly lower than that of the ungrazed (U) treatment (difference 0.11 ± 0.03 Mg ha^{-1}, $z = -3.096$, $p_{adj} = 0.03$). The grazing treatment had no effect on belowground C stocks or the R:S ratio.

3.3. Dynamics of assimilate allocation

Tracing the distribution of ^{13}C in the plant–soil–atmosphere system over the course of the chase period allowed assessment of the dynamics of allocation of recent assimilates. In general, the grazing treatments did not reveal any difference in the recovery of ^{13}C in the C pools. The total uptake of ^{13}C during the labeling was not differing between treatments. On average, the total ^{13}C recovered right after the labeling was 0.54 ± 0.02 g ^{13}C m^{-2}. Additionally, the overall tracer dynamics in the different investigated pools were very similar between the treatments. The data was therefore pooled for further analysis to increase sample size.
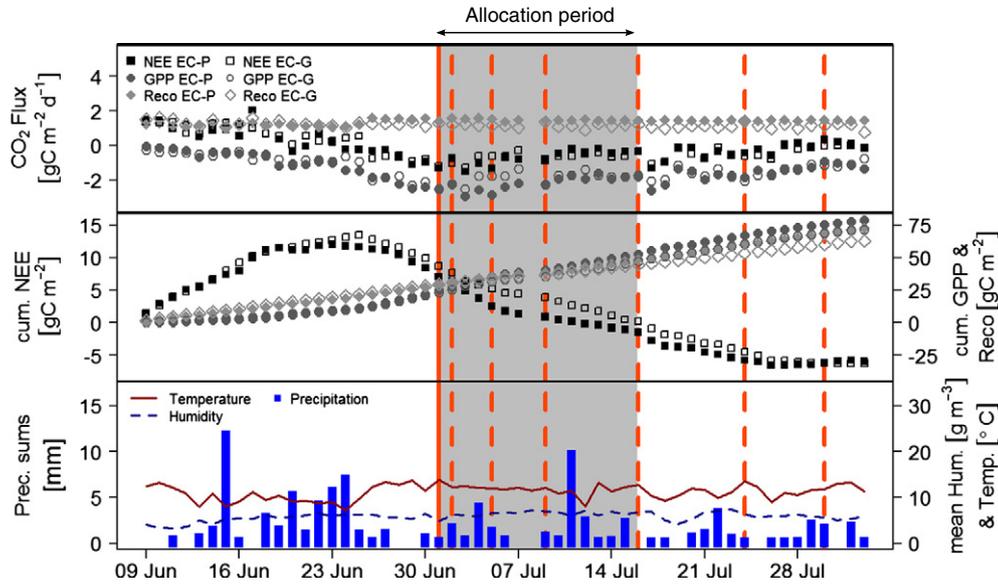
Fig. 1. CO_2 fluxes from 9 June to 2 August 2010 including the EC measured Net ecosystem exchange (NEE, black square) as well as the partitioned fluxes; gross primary production (GPP, dark grey circle) and total ecosystem respiration (R_{eco}, light grey diamond). Closed symbols represent the partially grazed site EC-P and open symbols represent the grazed site EC-G. The upper panel shows daily mean values and the middle panell shows the cumulated C-fluxes. Additionally, the lower panel shows sums of daily precipitation (blue bars), mean daily temperature (dark red line) and humidity (dark blue dashed line) characterizing the weather conditions for the duration of the labeling experiment. The ^{13}C labeling event on 1 July is marked by the vertical red line; ^{13}C sampling dates are indicated by vertical dashed red lines, the estimated allocation period by the grey shaded area.

In all pools, ^{13}C was significantly enriched after the labeling compared to its natural abundance, except for the SOC 5–15 cm. In this pool the $^{13}C_{at\%excess}$ was solely significantly different from zero for the first two samplings and days 36 and 64 after the labeling.

The percentage of recovered ^{13}C in the shoots decreased rapidly within the first days after the labeling and stabilized below 10% of recovered ^{13}C after 4 days (Fig. 3a). Afterwards the ^{13}C recovery in the shoots did not change significantly anymore.

The ^{13}C recovery in the CO_2 efflux from soil reflects root respiration and the belowground mineralization of recent assimilates. The highest rate of ^{13}C efflux in the belowground CO_2 efflux was detected within the first 24 h after the labeling (Fig. 3b). Afterwards, the contribution of ^{13}C to the CO_2 efflux declined rapidly. The decline can be described by the sum of two exponential functions. This provides turnover rates for two metabolic stages, one for root respiration and a rapid use of rhizodeposits by microorganisms ($TR_1 = 0.66 \pm 0.08$ days^{-1}) and a second, slower, stage of utilization of transformation products and dying roots ($TR_2 = 0.05 \pm 0.02$ days^{-1}). This corresponds to mean residence times (MRT) of 1.5 days (MRT_1) and 20 days (MRT_2). Due to the uniform behavior of the efflux from the three grazing treatments it can be stated that, on average, 36.8 ± 1.4% of recovered ^{13}C was released as belowground CO_2 efflux during two months.

The majority of the ^{13}C (58%) was already allocated belowground at the first sampling immediately after the labeling (day 0, roughly 4 h after the start of the $^{13}CO_2$ labeling), which reflected a fast allocation of assimilates to belowground pools. Most assimilates were recovered in roots of the layer 0–5 cm (Fig. 4a). Recovered ^{13}C peaked 15 days after the labeling and declined during the second half of the chase period between several sampling steps. The ^{13}C dynamic in the SOC of both layers was very low. In the soil of the upper layer, ^{13}C incorporation increased during the chase period (Fig. 4c). This increase of ^{13}C in SOC corresponded to the ^{13}C decline in the roots (Fig. 4a, b), reflecting their transformation to SOC. No clear trend could be obtained for the soil of 5–15 cm (Fig. 4d), because the mean ^{13}C enrichment was not significantly higher than in the unlabeled soil at several sampling times.

3.4. Absolute fluxes within the K. pygmaea ecosystem

Absolute C fluxes within the plant–soil–atmosphere continuum were calculated according to Eq. (1) using the relative distribution of ^{13}C at the end of the allocation period and the mean daily GPP of this period derived from a partitioning of the NEE measured with EC. The end of the allocation period is defined as the time when ^{13}C in the roots of the top layer reached a maximum, in our case 15 days after the labeling (Fig. 4a). The C fluxes estimated with the EC showed a fairly strong and constant assimilation during this period. Weather conditions were also quite stable with no relevant changes in temperature or available moisture between the days (Fig. 1). The relative distribution of assimilates as well as the resulting absolute fluxes derived from the coupling, are presented for each pool in Fig. 2b. It is clearly visible that most of the

Table 2
Mean daily CO_2 fluxes and standard errors measured at the EC Stations P and G, estimated for the whole period and the main vegetation period in July as well as the allocation period and the labeling day of the CO_2 labeling experiment.

| Station	Flux [gC m^{-2} d^{-1}]	Observation period 8 Jun–2 Aug 10	Constant flux period 24 Jun–24 Jul 10	Allocation period 1 Jul–16 Jul 10	Labeling day 1 Jul 10
EC-P	NEE	-0.12 ± 0.09	-0.66 ± 0.01	-0.71 ± 0.10	-1.24
	GPP	-1.51 ± 0.10	-2.1 ± 0.01	-2.18 ± 0.10	-2.52
	R_{eco}	1.38 ± 0.02	1.48 ± 0.00	1.47 ± 0.02	1.32
EC-G	NEE	-0.12 ± 0.09	-0.65 ± 0.01	-0.68 ± 0.08	-1.22
	GPP	-1.37 ± 0.08	-1.84 ± 0.01	-1.87 ± 0.10	-2.53
	R_{eco}	1.19 ± 0.02	1.15 ± 0.00	1.16 ± 0.03	1.30
Mean both	NEE	-0.12 ± 0.09	-0.65 ± 0.01	-0.69 ± 0.09	-1.23
	GPP	-1.44 ± 0.09	-1.97 ± 0.01	-2.02 ± 0.10	-2.53
	R_{eco}	1.28 ± 0.02	1.32 ± 0.00	1.32 ± 0.03	1.31
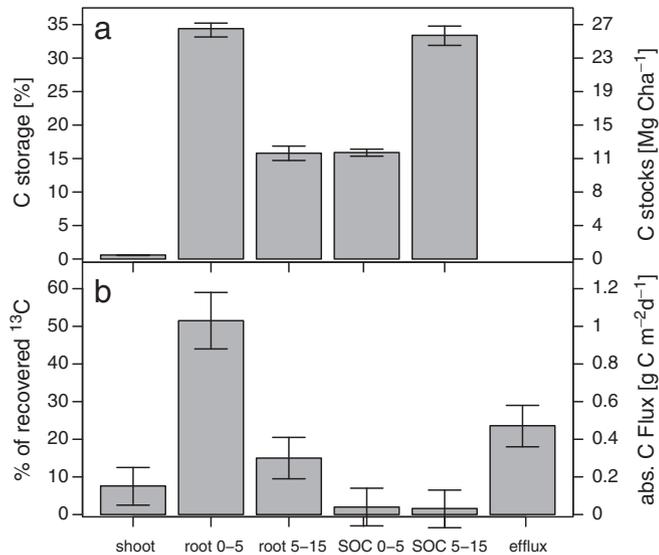
Fig. 1. (a) Relative distribution and absolute C stocks within the different compartments of the system. (b) Partitioning of assimilates (as % of recovered ^{13}C) at the end of the allocation period (15 days after the labeling) and the corresponding mean daily fluxes of C into the different C pools, based on the combination of eddy covariance measurement and pulse labeling.

assimilates were recovered within the roots of the first 5 cm resulting in an absolute flux of recent assimilates of 1.04 g C m^{-2} d^{-1} into this pool during this period of the growing season. The belowground CO$_2$ efflux represented the second largest flux with 0.48 g C m^{-2} d^{-1} while the flux of recent assimilates into aboveground biomass only accounted for 0.15 g C m^{-2} d^{-1}.

4. Discussion

4.1. Grazing effects on C fluxes and C budget

One of the aims of our study was to test whether grazing cessation already affected C fluxes and stocks of the alpine *K. pygmaea* ecosystem within the first growing season after grazing cessation. Therefore, we
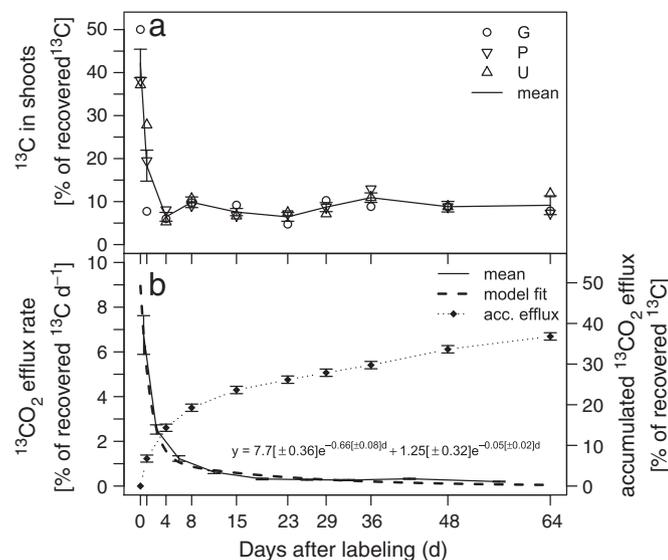
Fig. 3. (a) Dynamic of ^{13}C (±SEM) in the shoots, (b) mean ^{13}CO$_2$ efflux-rates (±SEM) from soil with a fitted biexponential model and accumulated amount of ^{13}CO$_2$ efflux (±SEM) during the chase period. The model fit is given by the formula. Open symbols indicate mean values of the different grazing treatments.

investigated ecosystem C fluxes, C allocation in the plant–soil-system and C stocks of this ecosystem in a grazing experiment. As grazing has been shown to affect belowground C allocation on a short time scale for several grassland species (Bardgett et al., 1998; Holland et al., 1996; Kuzyakov et al., 2002; Paterson and Sim, 2000; Schmitt et al., 2013) we expected that short-term effects of grazing would quickly express in the allocation of recent assimilates.

However, only the aboveground C stocks were affected by grazing cessation. It is intuitive that aboveground grazing affects the aboveground biomass. However, it is remarkable, that neither the allocation of recent assimilates nor the NEE on ecosystem scale were affected. This suggests that grazing cessation did not influence the C cycling, at least during the first half of the first growing season after grazing cessation. The very large R:S ratio of our study site (R:S = 90) is even higher than in other studies conducted in the alpine pastures of the Tibetan Plateau (52, Fan et al. (2008; 35.7), Yang et al. (2009)). It is conceivable that the high belowground biomass enables *K. pygmaea* to buffer aboveground effects of grazing in terms of C cycling, thus making the ecosystem resistant against short-term changes in the grazing regime. This emphasizes the importance of belowground plant compartments in this ecosystem and the need to increase knowledge of belowground C cycling of this extraordinary grassland ecosystem.

The lowest aboveground biomass was not found in the full grazing treatment (G), but in the livestock exclosure (P), where only small mammals – mainly pika – were grazing. We assume that pikas were attracted by the fenced area, due to fewer disturbances by livestock and herders, which increases overall pika density. This might actually have resulted in an overall higher grazing pressure on the livestock exclosure. We cannot verify this, because we lack data of pika density on the study site during the season of our experiment. But high pika density has been shown to negatively affect aboveground biomass (Liu et al., 2013). Additionally, pikas can graze vegetation completely down to the turf surface due to their smaller body size and more suitable teeth (Retzer, 2007).

We found no effects of grazing cessation on belowground C stocks. After several years of grazing exclosure Hafner et al. (2012) observed a decrease of belowground C stocks in a *Kobresia humilis* grassland (~3000 m a.s.l.) in the northeastern highlands. However, due to the large size of the belowground C stocks and the low productivity of these alpine ecosystems, such changes in the C stocks can rather be expected to be a long-term effect of grazing on the scale of years.

Unfortunately, we were not able to conduct EC measurements over the whole growing season due to logistical restrictions. Therefore, we were not able to test, if the grazing treatments started to affect ecosystem C exchange later in the growing season. Additionally, it was not possible to measure C fluxes on the ungrazed site (U) with EC, because maintaining a suitable area free of pikas is not feasible. Thus, the influence of the pika grazing on ecosystem scale remains uninvestigated in this study.

4.2. Distribution of C within K. pygmaea pastures

In the following section we discuss the C distribution within the plant–soil–atmosphere continuum of an alpine *K. pygmaea* pasture ecosystem for the main vegetation period in summer 2010. We present the relative distribution of C within the compartments of the ecosystem revealed by a ^{13}CO$_2$ pulse labeling experiment. Furthermore, we are able to present absolute estimates of these fluxes through the relatively new combination of labeling results and EC flux measurements (Riederer, 2014). For the better introduction of the new approach, we will start out with general remarks and explanations. Absolute fluxes were estimated by the pooled data from the ^{13}CO$_2$ pulse labeling experiment and a mean daily GPP value was estimated from both EC measurements for the allocation period. Due to lack of differences between the grazing treatments, the discussion will be grazing-independent.

Partitioning patterns of assimilates can vary greatly depending on the climatic conditions (Meharg and Killham, 1989; Palta and Gregory, 1997)
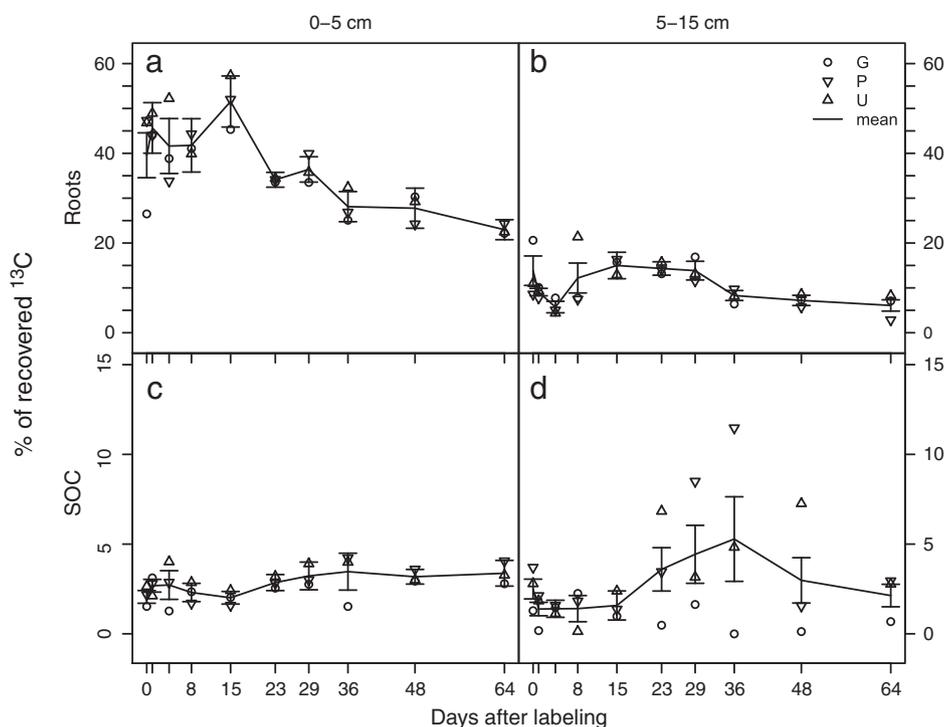
Fig. 4. Dynamic of recovered ^{13}C in roots and SOC in the two soil layers (±SEM, solid line) in (a) roots 0–5°cm (b) roots 5–15°cm, (c) SOM 0–5°cm, (d) SOM 5–15°cm). Open symbols indicate mean values of the different grazing treatments.

and change over the course of the growing season (Swinnen et al., 1994). This usually makes it impossible to extrapolate the partitioning of a single ^{13}C pulse labeling to the whole growth period (Kuzyakov and Domanski, 2000; Swinnen et al., 1994). Therefore, extrapolating partitioning patterns and fluxes over a longer period needs to be done with caution. The EC measurements provide a valuable constraint to judge whether C fluxes undergo strong changes within the allocation period. The labeling experiment was conducted in a period with a strong assimilation signal and overall constant fluxes (Fig. 1), which was only possible to identify through the simultaneous EC measurements and represents a great advantage of the new coupling approach. We therefore considered partitioning from the labeling experiment to be representative for the whole allocation period, since EC data showed constant C fluxes and comparable weather conditions (Fig. 1).

During the two months experiment the alpine *K. pygmaea* pasture acted as a weak C sink with a mean NEE of −0.1 g C m^{-2} d^{-1}. The estimated mean ecosystem assimilation of 1.36 ± 0.09 g C m^{-2} d^{-1} is in good agreement with values from another study over alpine *Kobresia* pastures in about 4000 m a.s.l. (Fu et al., 2009). However, it is roughly 1–2 g C m^{-2} d^{-1} smaller than the values from studies over montane *K. humilis* pastures at altitudes lower than 4000 m a.s.l. (e.g. Hirota et al., 2009; Kato et al., 2004, 2006; Zhao et al., 2006).

In the investigated alpine *K. pygmaea* ecosystem, the majority of assimilated C was allocated into belowground pools (Fig. 2b). This was reflected in the rapid decline of recovered ^{13}C in the shoots during the first days after labeling (Fig. 3). Leake et al. (2006) report ^{13}C losses in shoots of 32–70% in upland grassland within one day. Wu et al. (2010) observed a decline of fixed C in the shoots of 36.7% within 24 h after the labeling in a secondary *K. humilis* pasture (3250 m a.s.l.) in the northeastern highlands on the QTP. The slower decline of ^{13}C in shoots of a *Kobresia* pasture shown by Hafner et al. (2012) is associated with their definition of the reference recovery and differences in the vegetation itself. In contrast to our study, they relate the recovered ^{13}C to the amount of ^{13}C found one day after the labeling.

The shoot respiration, however, was of minor importance for the decline due to the small aboveground biomass and the high R:S ratio of the

Kobresia ecosystem. The photoassimilates remaining in the shoots were likely incorporated into structural shoot tissue. However, this remains speculative, because we do not have compound specific measurements of ^{13}C incorporation.

The total ^{13}C recovered belowground and in soil CO$_2$ efflux after 15 days accounts for 93.7% of recovered ^{13}C. According to the EC fluxes it corresponds to 1.87 g C m^{-2} d^{-1}. This is more than the 59% reported for *K. humilis* pasture (Wu et al., 2010) and the observed 40% for a *Kobresia* pasture (Hafner et al., 2012). This emphasizes the importance of belowground C allocation and cycling in these alpine *K. pygmaea* pastures. In our study, 23.6% of the ^{13}CO$_2$ allocated belowground was recovered in CO$_2$ efflux from soil (root exudates and root-derived CO$_2$), which is in good accordance with values reviewed by Kuzyakov and Domanski (2000). The roots acted as the largest sink of ^{13}C in the system (Fig. 2). This high incorporation of assimilates can be related to the very large rooting system maintained by the perennial plant *K. pygmaea* as adaptation to trampling und grazing (Miehe et al., 2008b).

The high ^{13}C recovery in roots and the low recovery in SOC are in contrast to the results observed for a montane *Kobresia* pastures in Qinghai by Hafner et al. (2012), who report only minor ^{13}C allocation into roots, but already very high amounts in the SOC one day after the labeling. Their ^{13}C pulse labeling was conducted later in the growing season. They argue that the rooting system was already developed and assimilates were invested mainly aboveground in vegetative and generative organs and shoot tissue and belowground into root exudation. In our study assimilates were mainly invested into the build-up of roots, leading to a longer turnover time of this C to become SOC. This might not only be an effect of the growing season, but could additionally be a response of the plant to the relatively dry growing season. However, we lack data from other years to estimate effects of this dry season.

In general, belowground pools have the largest contribution to C turnover within *K. pygmaea* pastures. The roots within the turf layer acted as the greatest sink for recently assimilated C, which is in good agreement with Fan et al. (2008) who found the highest C density in

the uppermost centimeter of alpine soils on the southeastern highlands. For the allocation period of the ^{13}C labeling experiment, which was also the period with the greatest C uptake during the observation period, this sums up to 28 g C m^{-2}. The further fate of these assimilates, e.g. their turnover in the roots or a possible incorporation into SOC, is of major importance to understand the role of recent assimilates for the overall C sequestration within this ecosystem.

4.3. Rapid turnover of assimilates in the root turf

Tracing ^{13}C of the pulse labeling in the soil CO_2 efflux gives valuable information about belowground metabolism and turnover of recent assimilates (Unteregelsbacher et al., 2011). By following the ^{13}C incorporation in roots and SOC we gain an overall picture of the role of the root turf for the fate and turnover of assimilates in this ecosystem.

During the first days after the labeling the recovery of tracer in soil CO_2 efflux was high, which was associated with root and rhizomicrobial respiration of assimilates. Its MRT of 1.5 days is well in accordance with (Kuzyakov, 2006), who reports that in grasses a maximum of 1–2 days is necessary for most of the C allocated to root respiration to return to the atmosphere as CO_2.

After approximately two weeks, the amount of tracer recovered in roots peaked (Fig. 4a,b). In contrast to other pulse labeling studies on the northeastern highlands of the Tibetan Plateau (Hafner et al., 2012; Wu et al., 2010), the long chase period and the high number of replicates after pooling the grazing treatments allows us to follow tracer dynamics precisely over a time scale of several weeks. The decline after two weeks was accompanied by a simultaneous slight but steady $^{13}CO_2$ efflux from soil (Fig. 3). This might partly be caused by metabolic turnover of assimilates from storage pools. Lehmeier et al. (2008) showed that stores play a central role for respiratory C metabolism, but also that these stores are quite short lived. Additionally, we also observed an increase in the recovery of ^{13}C in SOC (Fig. 4c). This suggests that labeled root material, i.e., roots that had been built up by recent assimilates, started to be decomposed, which contributed to soil CO_2 efflux, and partly transformed to soil organic matter. The mean residence time of recently assimilated C in these Kobresia roots is approximately 20 days, as described by the slower decay rate of the biexponential decline fitted to the CO_2 efflux rate (Fig. 3b). Thus, a subset of roots in the root turf, probably fine roots, had a rapid turnover, as it has also been reported by Wu et al. (2011) for a K. humilis pasture of the northeastern highlands and others for forest and grassland ecosystems (Gill et al., 2002; Hendrick and Pregitzer, 1993). Roots that become lignified have a much longer lifespan, which we can't estimate with our two months study.

The decomposition of fine roots partially leads to a stabilization of root C in SOC due to the chemical recalcitrance of root compounds (Rasse et al., 2005), however, this will be of minor importance for these fine roots, which are poor in lignin and suberin. The two other mechanisms important in temperate ecosystems (physico-chemical protection through interaction with minerals and physical protection from decomposition by aggregation) are of minor importance in Kobresia ecosystems. Interaction with minerals is hardly possible because most of the Ah horizon consists of dead roots, and the minerals are mainly quartz crystals of a medium and large silt size without any relevant sorption places. The further common mechanism—protection by aggregation, is also of minor importance because the aggregate structure is not well presented in these soils. Therefore, C stabilization mechanisms (cold temperatures and short period of microbial activity) in soils under Kobresia root mats may be different from that under temperate grasslands.

5. Conclusions

By combining two commonly used methods, pulse labeling and EC, we present a new and more powerful approach to understand C cycling in the plant–soil–atmosphere system compared to singular plot- or ecosystem scale approaches. It enabled us to estimate absolute C fluxes into

various pools of the K. pygmaea pastures and to identify C dynamics on various spatial scales.

Within the first growing season after grazing cessation we observed effects on aboveground C stocks of the alpine K. pygmaea pasture, whereas recent C fluxes were not influenced. This was shown for the partitioning and turnover of recently assimilated C on plot scale as well as the overall C budget at ecosystem scale by combining $^{13}CO_2$ pulse labeling with eddy-covariance flux measurements. We conclude that the high belowground biomass, expressed in the very large R:S ratio of 90, enables K. pygmaea to buffer aboveground effects of short term changes in the grazing regime.

The K. pygmaea root turf makes up roughly 50% of the overall C stocks. However, besides its huge size in terms of relative as well as absolute C storage, it is a highly dynamic component of the C cycle in this ecosystem. A more detailed investigation of C fluxes identified the root turf as major sink for recent assimilates. Our study showed that a subset of roots is highly dynamic, with a mean residence time of 20 days. Carbon input into the soil is controlled by root turnover and not rhizodeposition.

Overall, we conclude that the living roots of the turf layer represent the most active part in terms of C cycling and play a key role in the turnover of recent assimilates. As the turf stores a very high amount of C its destruction through environmental or anthropogenic factors, e.g. overgrazing-induced degradation or changes of vegetation could lead to a great release of CO_2 to the atmosphere.

This unique ecosystem requires further studies on the role of grazing, especially on longer time scales, for C stabilization and a more in-depth understanding of the development, age and structure of the turf layer as well as its protective role for the ecosystem. This knowledge is necessary in order to evaluate and mitigate the effects of climate and land use change on the Tibetan Plateau.

Table A1

Setup specification for the eddy covariance stations, EC-P and EC-G.

Measured quantity	EC-station	Device	Height [m]
Wind components	P and G	CSAT3 (Campbell Sci., Inc.)	2.20
CO_2 and H_2O Concentration	P and G	LICOR 7500 (LI-COR Biosciences)	2.20
Reference temperature and humidity	P and G	HMP45 (Vaisalla).	2.20
Precipitation	P	Tipping rain gauge	1.00
Radiation components	P and G	CNR1 (Kipp & Zonen)	2.00
Soil temperature "Kobresia" mat"	P and G	Pt100	−0.025, −0.075, −0.125 (−0.200 only at P)
Soil water contend "Kobresia" mat"	P and G	TDR probes (IMKO)	P:−0.10,−0.20 G: −0.15
Soil temperature "bare soil"	Only P	Pt100	−0.025, −0.075, −0.125
Soil water contend "bare soil"	Only P	TDR probes (IMKO)	−0.15

Appendix A. Eddy covariance

A1. Instrumentation EC stations

Table A1 lists the devices used at the two stations EC-P and EC-G. It describes the measured quantity, manufacturer and measurement height.

A3. Post processing of turbulent fluxes

The internationally compared software TK3 (Mauder et al., 2008) includes all necessary data correction and provides tools for the quality control of data. Therefore, calculated fluxes match up-to-date micrometeorological standards (Foken et al., 2012; Rebmann et al., 2012). Wind data was rotated according to the planar-fit rotation method considering terrain effects on the measurements (Wilczak et al., 2001). Quality of the derived fluxes is indicated with a quality-flagging scheme after Foken and Wichura (1996), accounting for development of turbulence as well as stationarity. It enables to be distinguish between data of high quality (flag 1–3), intermediate quality (flag 4–6) and poor quality (flag 7–9) (Foken et al., 2004).

The utilized footprint analysis is based on a Lagrangian stochastic forward model, providing a two dimensional representation of the contributions of source areas (Rannik et al., 2000). Nevertheless, it needs to be considered that, depending on the wind direction, the distribution of IM, DM and BS within the footprint for single half-hour values might differ from the overall distribution within the research area.

A3. Gap filling and partitioning of turbulent C fluxes

Gap filling of NEE measurements and also the partitioning of this flux in C uptake and respiration is a common procedure (e.g. Desai et al., (2008); Falge et al., (2002); Lasslop et al., (2010); Reichstein et al., (2012)). Therefore, gross primary production (GPP) was estimated with a light response function following Michaelis and Menten (1913) using in situ solar radiation measurements. This technique also enables estimation of the C uptake of the *Kobresia* pastures from the measured NEE. The approach is described in Ruppert et al. (2007) follows Falge et al. (2001):

$$GPP = \frac{aRgNEE_{sat,day}}{aRg + NEE_{sat,day}} + R_{eco,day} \tag{A1}$$

with a the initial slope of the function, the global radiation Rg, the saturated NEE rate $NEE_{sat,\ day}$ and the respiration rate during daytime $R_{eco,day}$.

Ecosystem respiration (R_{eco}) is parameterized from in situ measured night-time NEE and temperature measurements following Lloyd and Taylor (1994) as used in Falge et al. (2001):

$$R_{eco} = R_{eco10}e^{E_0\left[\left(\frac{1}{(283.15-T_0)}\right) - \left(\frac{1}{(T-T_0)}\right)\right]} \tag{A2}$$

with R_{eco10} being the respiration rate at 10 °C and E_0 the sensitivity of the respiratory fluxes at a constant T_0.

The fitting of the parameters for GPP and R_{eco} was done with high quality data (flag 1-3) for two periods due to the strong differences in the diurnal cycle. Respiratory fluxes dominated within the first period and no daily cycle existed from 9 to 23 June, while assimilation became more dominant leading to a daily cycle in the second period from 24 June to 8 August. The NEE time series selected for intermediate data quality was gap–filled with estimated values, where missing values due to instrument failure or rejection of data due to inappropriate data quality made this necessary. The time series of GPP and R_{eco} are entirely made up of parameterized values originating from the measured NEE.

Appendix B. $^{13}CO_2$ pulse labeling

B1. Labeling procedure

Chambers of the size 60 cm × 60 cm × 10 cm were erected with transparent plastic foil. The chambers were carefully sealed by burying the foil in the soil and additionally sealing with wet soil. Prior to the closing, a vial with 2 g of ^{13}C enriched (99 atom-%) Na_2CO_3 dissolved in water was placed inside each chamber. The label was released into the chamber atmosphere by injecting an excess of 5 M sulphuric acid with a syringe into the vial. To facilitate a uniform distribution of the tracer inside the chamber, the chambers were agitated from time to time. The labeling started at noon; chambers were opened after 4 h of labeling.

B2. Sampling procedure

Plant shoots were cut from a small circular area (diameter 6.5 cm). Belowground samples (soil and roots) were taken with a soil corer (diameter 2.6 cm) from two layers (0–5 cm and 5–15 cm), which contain the vast majority of roots and soil organic matter. Except for the first sampling, all samples from each compartment were taken as mixed samples of two soil cores from each plot. The samples were dried at 50 °C and belowground samples were separated into roots and soil afterwards. All samples were weighed and homogenized in a ball mill prior to further analysis. To make sure that the soil samples were free of carbonates, they were decalcified with hydrochloric acid (HCl).

Total belowground CO_2 efflux and its $\delta^{13}C$ signature were measured as follows. CO_2 originating from the soil was captured in a sodium hydroxide solution (NaOH). After clipping of the shoots an opaque aluminum chambers, with a diameter of 6.5 cm, was placed on the bare soil. A graduated beaker with a defined amount of 1 M NaOH was placed inside the chamber. The NaOH captures the CO_2 flowing out from the soil into the chamber. Clipping of the shoots is necessary to avoid the additional CO_2 originating from shoot respiration. The beakers were changed on the sampling days, and thus measured the cumulative CO_2 efflux in the periods between the sampling days. The amount of NaOH was adjusted between 20 to 30 ml according to the length of these trapping periods to ensure that NaOH was not neutralized. The amount of CO_2 captured in the NaOH in the measurement periods was quantified by titration against 0.1 M HCl to the color change of phenolphthalein (pH = 8.2). To determine the $\delta^{13}C$ signature of the CO_2 efflux, 2 M $SrCl_2$ was added to precipitate the carbonate captured in the NaOH as $SrCO_3$. The precipitation was neutralized by repeated addition of purified water and dried afterwards.

The natural abundance of ^{13}C in the different plant and soil pools, as well as of the soil CO_2 was measured by doing the identical sampling and analysis procedure on unlabeled spots at the field site. Carbon content and the $\delta^{13}C$ signature of enriched and nonenriched (reference) samples were determined by an isotope ratio mass spectrometer coupled with an elemental analyzer at the laboratory of Isotope Biogeochemistry, Bayreuth Center of Ecology and Environmental Research (BayCEER) (IRMS: Delta Plus, Thermo Fisher Scientific, Bremen Germany; EA: NC 2500, CE Instruments, Milano, Italy) and at the Centre for Stable Isotope Research and Analysis, University of Göttingen (IRMS: Delta C, Finnigan MAT, Bremen, Germany; EA: NA1108, Fisons-Instruments, Rodano, Milano, Italy). With the exception of the samples from the first sampling, a subset of three replicates per treatment and sampling day were analyzed.

B3. Calculations

The belowground C stocks were calculated for both layers (0–5 cm, 5–15 cm):

$$C\left(Mg\ ha^{-1}\right) = z \cdot \rho \cdot C \tag{B1}$$

where z (cm) is the thickness of each layer, ρ (g cm^{-3}) is the bulk density and C (%) is the C content.

The soil CO_2 efflux rate (mol C m^{-2} d^{-1}) was calculated by:

$$CO_2\ efflux = \frac{m(C)}{A\Delta t} \tag{B2}$$

where $m(C)$ represents the amount of C absorbed in the trap, A is the area of the soil under the chamber and Δt is the length of the trapping period.

The enrichment of ^{13}C ($^{13}C_{t\ atom\%excess}$, % of total C atoms) in each sample achieved by the pulse labeling is calculated by subtracting the amount of ^{13}C in the natural abundance samples ($^{13}C_{atom\%\ of\ NA}$, % of total C atoms) from the amount of ^{13}C in the sample ($^{13}C_{t\ atom\%\ of\ sample}$, % of total C atoms):

$$^{13}C_{atom\%excess} = {}^{13}C_{atom\%\ of\ sample} - {}^{13}C_{atom\%\ of\ NA}. \tag{B3}$$

The amount of ^{13}C in the C pools at a specific time t after the labeling ($^{13}C_t$, g m^{-2}) is the product of the increment of ^{13}C at that time ($^{13}C_{t\ atom\%excess}$) and the amount of C in the corresponding pool ($C_{t\ pool}$, g m^{-2}) and can be calculated as such:

$$^{13}C_t = \frac{^{13}C_{t\ atom\%excess}}{100} \cdot C_{pool}. \tag{B4}$$

To make the ^{13}C incorporation into the investigated pools comparable between the plots, the amounts of ^{13}C in a pool at time t ($^{13}C_t$) are expressed in percentage of the reference recovery at day 0 ($^{13}C_{t0\ rec}$) of the corresponding plot:

$$^{13}C_{rec} = \frac{^{13}C_t}{^{13}C_{t0rec}} \cdot 100\% \tag{B5}$$

The reference recovery $^{13}C_{t0\ rec}$ is defined as the total amount of $^{13}C_{atom\%excess}$ found in all investigated plant and soil C pools at the first sampling (day 0), directly after opening the labeling chamber. A time delay of 12 h was assumed between the clipping and the complete stop of metabolic processes by drying. These ^{13}C losses during the drying of soil and plant samples were corrected.

The statistical analysis was done in R 2.10.1 (R Development Core Team, 2009). To test for treatment effects in the five investigated pools we used linear mixed effect models (R-package nlme, Pinheiro et al., 2011) with 'Treatment' (U, P, G) as fixed effect and 'Block' (1–4) and 'sampling date' as random effects. To account for the multiple testing of the treatment effect in the five C pools p-values were adjusted according to Holm's procedure (n = 5). In case of a significant treatment effect within a C pool ($p_{adj} < 0.05$) we used a post-hoc Tukey test (R-package multcomp, Hothorn et al., (2008), p-adjustment by Holm's procedure), to test which treatments show differences in the respective pool. A non-parametric Mann–Whitney-U test was applied to evaluate differences between the grazing treatments in ^{13}C partitioning at every sampling step of the chase period. Differences in the percentage of recovered ^{13}C between time-steps were tested with the non-parametric Wilcoxon matched pair test (significance level p = 0.05).

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