

Response of long-, medium- and short-term processes of the carbon budget to overgrazing-induced crusts in the Tibetan Plateau

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Abstract The *Kobresia* pastures of the Tibetan Plateau represent the world's largest alpine grassland ecosystem. These pastures remained stable during the last millennia of nomadic animal husbandry. However, strongly increased herds' density has promoted overgrazing, with unclear consequences for vegetation and soils, particularly for cycles of carbon (C), nutrients and water. Vegetation-free patches of dead

root-mat covered by blue-green algae and crustose lichens (crusts) are common in overgrazed *Kobresia* pastures, but their effect on C turnover processes is completely unknown. We tested the hypothesis that the crusts strongly affect the C cycle by examining: (i) the long-term C stock measured as soil organic matter content; (ii) medium-term C stock as dead roots; (iii) recent C fluxes analyzed as living roots and CO₂ efflux; and (iv) fast decomposition of root exudates. Up to 7.5 times less aboveground and 1.9 times less belowground living biomass were found in crust patches, reflecting a much smaller C input to soil as compared with the non-crust *Kobresia* patches. A lower C input initially changed the long-term C stock under crusts in the upper root-mat horizon. Linear regression between living roots and CO₂ efflux showed that roots contributed 23% to total CO₂ under non-crust areas (mean July–August 5.4 g C m⁻² day⁻¹) and 18% under crusts (5.1 g C m⁻² day⁻¹). To identify differences in the fast turnover processes in soil, we added ¹³C labeled glucose, glycine and acetic acid, representing the three main groups of root exudates. The decomposition rates of glucose (0.7 day⁻¹), glycine (1.5 day⁻¹) and acetic acid (1.2 day⁻¹) did not differ under crusts and non-crusts. More ¹³C, however, remained in soil under crusts, reflecting less complete decomposition of exudates and less root uptake. This shows that the crust patches decrease the rates of medium-term C turnover in response to the much lower C input. Very high ¹³C amounts recovered in plants from non-crust areas as well as the two times

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lower uptake by roots under crusts indicate that very dense roots are efficient competitors with microorganisms for soluble organics. In conclusion, the altered C cycle in the overgrazing-induced crustose lichens and blue-green algae crusts is connected with strongly decreased C input and reduced medium-term C turnover.

Keywords Overgrazing · Land-use changes · *Kobresia* pasture · Root exudates · ^{13}C pulse labeling · CO_2 efflux from soil · Soil organic carbon · Soil respiration

Introduction

The Tibetan Plateau (TP), with an average altitude of more than 4000 m above sea level and an area of $2.5 \times 10^6 \text{ km}^2$, is the largest and highest plateau on Earth (Lu et al. 2004). Over 60% of the plateau is covered by grasslands (Zhang et al. 2007), representing a very important part of the global grassland ecosystems. Grassland soils in the TP store a huge amount of organic carbon (C) (33.52 Pg C in the upper 0.75 m of topsoil), which represents approximately 2.5% of the global soil C stock (Ni 2002; Wang et al. 2002). Therefore, C dynamics in grasslands in the TP—C stocks, C turnover and CO_2 fluxes—play a very important role in regional and global C cycles (Zhang et al. 2007; Zhao et al. 2005). The response of these C stocks and processes to recent land use changes remains unknown.

The *Kobresia* pastoral ecosystem of the eastern Tibetan highland is crucial in determining the C and water balance of the TP and is highly susceptible to climate and land-use changes. The *Kobresia* pastures form a dense vegetation cover of *Cyperaceae* turf named “*Kobresia* turf” (“Rhizomull”, Afe horizon, Kaiser et al. 2007), with a very dense root system in the top 15 cm of soil. This makes the *Kobresia* pastures very durable and resistant to trampling by yaks and sheep (Cao and Long 2009). The *Kobresia* pastoral ecosystem is grazing-dependent, induced and maintained by herders and their livestock (Miehe et al. 2008a). Intact *Kobresia* pastures probably have a neutral net ecosystem CO_2 exchange (Shi et al. 2006). They may even represent a moderate C sink

(Ni 2002; Wu et al. 2010; Zhao et al. 2006), mainly in the aboveground plant parts that are removed by grazing. Although this ecosystem has been quite stable during the last centuries or millennia of nomadic animal husbandry (Miehe et al. 2008a), minor changes in internal or external drivers may significantly alter the soil organic C pool. This, in turn, influences the atmospheric CO_2 concentration and the global climate (Cui and Graf 2009).

Strongly increased density of herding animals and sedentarisation programs enforced in the TP since the early 1980s (Gad 2005) induced strong land-use and vegetation changes, with drastic consequences for C, N and water cycles. The concentration of grazing around the villages leads to overgrazing and land degradation (Zhao and Zhou 1999). In the worst stages of degradation the *Kobresia* turf cover is completely removed; the exposed silt (Bkc or even Ck horizons) is prone to deflation and water erosion (Wang and Cheng 2000; Miehe et al. 2011). Overgrazing also changes the vegetation (Ning and Richard 1999) and its pattern. The present structure of many overgrazed *Kobresia* pastures is characterized by open turf/root-mat covered only by blue-green algae and crustose lichens (termed ‘crust’ in this study); this closely adjoins pastures dominated by graminoids and *Kobresia* species. On the adjacent plots we found that there are no crusts in grazing exclosure older than 8 years (Hafner et al. 2011 under review) and in those pastures without heavy grazing. This indicates that strong overgrazing increases the percentage of the crust area and thus decreases ecosystem productivity and grassland quality. Many dead and partly decomposed *Kobresia* roots (root-mat, frequently termed “root-felt”) are present under such crusts. Based on the obvious differences between crust and *Kobresia* grassland (non-crust) in living biomass, both above- and belowground, we hypothesized that root exudates have a different fate (microbial decomposition and remaining in the soil) and thus, reflect short- to medium-term C turnover processes. Correspondingly, we hypothesized that decreased C input under crusts reduces the medium- and long-term organic C stock, turning this ecosystem part into a C source. This can be traced by comparing CO_2 efflux with C input. Recognizing and evaluating possible changes in the C cycle of this ecosystem requires determining the C fluxes between C pools along with the related storage and internal turnover.

To investigate the effects of overgrazing on processes of C turnover, we investigated C dynamics in soil under the two contrasting patches of vegetation: (i) blue-green algae and crustose-lichens (crust) and (ii) grass composed predominantly of *Kobresia* and *Stipa* species (non-crust), in a montane-alpine grassland (*Kobresia-Stipa* pasture) on the TP. Based on the predicted different response of C stocks and turnover processes depending on the characteristic residence times and rates, we evaluated (i) the long-term C stock (decades) by the soil organic matter content; (ii) the medium-term C stock (years) by the amount of dead roots; (iii) recent C stock and C input (months) by the amount of living roots, whereby the C fluxes were measured as CO₂ efflux from soil, as well as remaining ¹³C from exudates; and (iv) fast C turnover based on ¹³C labeled substances representing root exudates.

Materials and methods

Field sites and soil

The experimental site is located in Qinghai province in the northeastern Tibetan Plateau, approximately 200 km southwest of Xining, about 15 km south of Xinghai city (longitude 35°32'N, latitude 99°51'E). The montane-alpine grassland has developed on a

loess-covered (~1.2 m) terrace of the Huang He River (3417 m a.s.l.). The grassland is classified as *Kobresia humilis/pygmaea-Stipa* pasture and used as a winter pasture for yaks and sheep for 6–7 months of the year (Miehe et al. 2008b). About 20% of the pasture at the experiment site is completely covered with blue-green algae and crustose-lichens (crust) (Fig. 1).

Due to the East Asian monsoon, almost all of the precipitation falls in the summer months from May to September, most frequently in the form of torrential rain during afternoon thunderstorms. The annual precipitation (Xinghai climate station) averaged 353 mm, ranging from 214 to 483 mm during 40 years from 1961 to 2001. The rain gauge nearest to the study site recorded 448 mm a⁻¹ (2002–2007). Winter snowfall is irregular and rare (Miehe et al. 2008b). In Xinghai, mean monthly temperatures lie above 5°C between May and September, and above 10°C from June to August. During the wintertime, the north-east of the TP is subject to the Siberian high pressure system. Mean monthly temperatures for December and January in Xinghai lie below –10°C. The mean monthly temperature for the coldest month is –20.8°C, and the absolute low was –33.5°C (Miehe et al. 2008b).

The soil is classified as a Haplic Kastanozem (WRB 2006) with three characteristic horizons. The upper horizon consists of a high quantity of fine

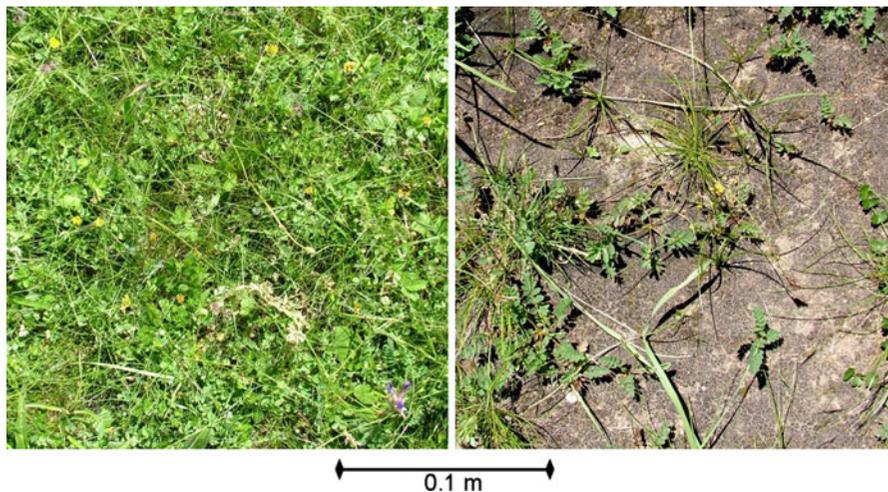


Fig. 1 Two contrasting patches of vegetation at the study site (Qinghai province) common for the Tibetan Plateau: **a** Grassland with 100% vegetation cover with predominant *Kobresia* and *Stipa* species (*left*), and **b** Blue-green algae and crustose

lichens above the dead *Kobresia pigmea* turf (*right*). The cover of crust patches is less than 30% with the predominance of the same species

sedge-roots (*Kobresia*) and generates a felty turf known as “*Kobresia* turf” (Kaiser et al. 2007).

Labeling procedure

In July 2009 we conducted a field ^{13}C labeling experiment with representatives of typical root exudates (Krafczyk et al. 1984; Fischer et al. 2010a, b): glucose (representative for sugars), glycine (for amino acids) and acetic acid (for carboxylic acids) were added in situ to the two contrasting patches of vegetation (Fig. 1):

- i) Grassland (vegetation cover approximately 100%) with predominant *Kobresia* and *Stipa* species (non-crust).
- ii) The same species cover <50% of the soil. More than 50% of the surface is covered by root felt with blue-green algae and crustose-lichens (crust).

Twelve plots (0.3×0.3 m) were set up for three substances in either of patches. There were four replicates for each substance. In total, there were 24 plots for the labeling experiment. All the three substances were labeled by 99 atom% ^{13}C (Campro Scientific GmbH). A total amount of 12.6 mg C was applied to each plot, equaling to 334 mg glucose, 415 mg glycine and 334 mg acetic acid per square meter, respectively. The labeled substances (glucose, glycine, acetic acid) were dissolved in 150 ml water, and then uniformly sprayed on the respective plots using a small watering can. After the substances were added, additional distilled water (300 ml) was slowly sprayed to each plot to ensure that no labeled substances remained on the leaves of vegetation.

CO₂ efflux from soil

CO₂ efflux from soil was analyzed by two approaches. The first approach was focused on sampling CO₂ for further ^{13}C analyses. After the labeling, at each plot a small part of vegetated area (if present) was cut close to the soil surfaces and a round aluminum chamber (diameter 5.2, height 4.0 cm) was pushed 5 mm into the soil of the plots and sealed with wet silt to avoid CO₂ loss. The NaOH solution was placed inside the chamber to trap CO₂ for estimation of ^{13}C loss via soil respiration. The NaOH solution was exchanged on days 1, 4, 9, 18 and 29 after the labeling. Increasing

amount of NaOH solution was used for the intervals so that the NaOH solution was enough to trap all CO₂ released from soil. The data of CO₂ efflux measured by this approach was related to the amount of living roots separated from soil sampled at the same time and locations, where the CO₂ efflux was measured. This allows to evaluate the contributions of root respiration and soil organic matter derived CO₂ to the total CO₂ by the linear regression approach (Kucera and Kirkham 1971).

The second approach was focused on evaluation of diurnal dynamics of CO₂ fluxes. CO₂ efflux from soil was determined by closed round chambers (diameter 12 cm and height 10 cm). This was done in adjacent plots including non-crust and crust patches. The increase of CO₂ concentration (ppm) inside the chamber was measured by a CO₂-meter (VAISALA Hand-held CO₂ Meter GM70, Helsinki, Finland) every 20 s during 300 s. The diurnal dynamics of CO₂ fluxes from soil with and without crusts were measured by the same closed chamber approach.

When the NaOH solution was exchanged, shoots, roots and soil were collected from each plot. Plants were cut at the base and soil was divided in the layers 0–5 cm, 5–15 cm and 15–30 cm using a 2.1 cm diameter soil corer. The soil was sieved (2 mm) and roots were separated from bulk soil by handpicking. Roots were divided into living and dead according to color. All soil and plant samples were dried at 60°C and prepared for $\delta^{13}\text{C}$ analyses.

Sample preparation and analyses

Dried samples of soils, shoots and roots were weighed and then ground by a ball mill prior to $\delta^{13}\text{C}$ analysis. Carbonates in soil were completely destroyed during four days in an exsiccator with an atmosphere of concentrated HCl (37% HCl). To remove the remaining HCl before $\delta^{13}\text{C}$ analysis, distilled water was added and soil samples were frozen-dried until a pH of 7. All data on C stocks and fluxes were reported for organic C only (except CO₂ efflux from soil). We accepted that the possible changes of CaCO₃ in Ahk, Bkc and the parent loess (Ck) are too small to be measured because recrystallization periods of pedogenic carbonates take centuries to millennia (Kuzyakov et al. 2006; Gocke et al. 2011).

The total CO₂ trapped in the NaOH was analyzed in an aliquot by titration with 0.1 M HCl against phenolphthalein after adding strontium chloride (SrCl₂). The CO₂ trapped in NaOH was precipitated with 0.5 M SrCl₂ aqueous solution and the SrCO₃ precipitants were washed with deionized water to remove NaOH and to reach a pH of 7. After washing, the remaining water was removed from the vials and the SrCO₃ was dried for δ¹³C analyzes.

The relative ¹³C abundance, and total C and N contents in the samples of plants, soils and SrCO₃ were analyzed using a C–N analyzer (CE Instruments, Milano, Italy) coupled via a ConFlo III (Finnigan MAT, Bremen, Germany) to an isotope ratio mass-spectrometer Delta Plus (IRMS-a NA 1108, Finnigan MAT).

Calculations and statistics

CO₂ efflux rates were calculated using a linear increase of CO₂ concentration measured every 20 s during 300 s by a CO₂-meter. Partitioning of total CO₂ efflux for root-derived CO₂ and the sum of SOM-derived CO₂ and microbial decomposition of dead plant residues was estimated by a linear regression approach (Kucera and Kirkham 1971; Kuzyakov 2006). The linear relationship between root biomass and total CO₂ efflux rate was extrapolated to yield a Y-intercept value. This indicates the minimum microbial respiration in the absence of living roots, corresponding to the SOM-derived CO₂ and microbial decomposition of dead plant residues.

To calculate the decomposition rate of ¹³C labeled representatives of root exudates and their metabolites, a single first-order kinetics was fitted to the experimental data for CO₂.

$$^{13}\text{C}_{\text{tot}} = C_0 \cdot \exp(-k_{\text{CO}_2} \cdot t) + \text{Const} \quad (1)$$

$$^{13}\text{C}_{\text{tot}} = C_0 \cdot (1 - \exp(-k_{\text{CO}_2} \cdot t)) + \text{Const} \quad (2)$$

¹³C_{tot} is the amount of ¹³C label in a certain pool at a sampling time (*t*), C₀ is the maximum flux out of the pool at the beginning, *k*_{CO₂} describes the decomposition rate constant, and the parameter Const describes the remaining ¹³C label for which biodegradation cannot be described using the exponential decay approach during the 29 days. Equation 2 was used for all cumulative data.

A single first-order decay equation was also fitted to the ¹³C recovered from the soil to describe the remaining exudates and their metabolites (Eq. 3).

$$^{13}\text{C}_{\text{tot}} = C_0 \cdot \exp(-k_{\text{soil}} \cdot t) + \text{Const} \quad (3)$$

*k*_{soil} is the decline rate of the initial exudates and their metabolites remaining in soil. The half-lives (*t*_{1/2}) of ¹³C exudates and their metabolites were calculated as follows:

$$t_{1/2} = \ln(2)/k \quad (4)$$

Significant effects of crust vs. non-crust on soil organic C, aboveground biomass, living and dead roots was tested by ANOVA at *p* < 0.05 (Statistica ver. 7.0). Nonlinear regressions were used to fit the parameters of Eqs. 1–3. Means and standard errors are presented in Tables and Figures.

Results

Above- and belowground carbon stock

The presence of crust significantly affected the above- and belowground C pools (Table 1), i.e., strongly decreased aboveground biomass (*p* < 0.001) and living roots (0–5 cm) (*p* < 0.001), and increased the amount of dead roots (0–5 cm) (*p* < 0.01). In the non-crust area the shoot biomass was about 7.5 times higher than in the crusted area, while the C stored in the living roots (0–30 cm) was about two times higher than in the crusted area. Although the non-crust soil contained more organic C in the upper 5 cm (*p* < 0.05), the C stock in the upper 30 cm was not significantly different between crust and non-crust. When living and dead roots were also considered, more C was stored belowground in the non-crust patches. This data on changes of C stocks are highly representative as they are based on 120 replications for each treatment. The decrease of the total belowground C stock under crusts was mainly due to living roots, but also due to decreasing organic C content in the upper 5 cm.

CO₂ efflux from the soil

Although the above- and belowground living biomass (Table 1) was significantly smaller in crust patches,

Table 1 Organic carbon stocks above and below ground in the plant-soil system and CO₂ efflux from soil

Pool	Organic carbon stock (g C m ⁻²)		Ratio Non-crust/crust
	Non-crust	Crust	
Plant biomass total	517 ± 91.4 ^a	201 ± 47.6 ^b	2.6
Above ground (shoots)	176 ± 14.1 ^a	23.6 ± 5.9 ^b	7.5
Below ground (living roots ^A)	341 ± 77.3 ^a	177 ± 41.7 ^b	1.9
0–5 cm	125 ± 17.3 ^a	49.2 ± 11.1 ^b	2.5
5–15 cm	105 ± 12.4 ^a	70.9 ± 12.2 ^b	1.5
15–30 cm	111 ± 47.6 ^a	57.0 ± 18.4 ^b	1.9
Dead roots (0–5 cm)	46.6 ± 5.9 ^a	74.9 ± 7.1 ^b	0.6
Ratio: shoots/living roots (0–30 cm)	0.52 ^a	0.13 ^b	4.0
Ratio: living roots/dead roots (0–5 cm)	2.68 ^a	0.66 ^b	4.1
Soil organic C total	8712 ± 460	8715 ± 698	1.0
0–5 cm	2775 ± 93.6 ^a	2375 ± 96.8 ^b	1.2
5–15 cm	3405 ± 172	3444 ± 215	1.0
15–30 cm	2532 ± 195	2896 ± 386	0.9
CO ₂ efflux from soil ^B (g C m ⁻² day ⁻¹)	5.44 ± 0.21	5.09 ± 0.27	1.1

Organic carbon stocks represent means ± SE (n = 120). Small letters show significant differences between Non-crust and Crust. The significance of all differences except for soil C pools is at least with $p < 0.01$.

^A The amount of living roots may be underestimated because of very high amount of dead roots and very dense *Kobresia* root-mats hindering complete extraction of living roots.

^B CO₂ efflux from soil is an average for July–August 2009 calculated based on cumulative CO₂ trapping in NaOH.

there were no significant differences between the CO₂ efflux from soil under crust and non-crust ($p > 0.05$; Table 1). The soil CO₂ efflux rate averaged 21.2 ± 1.1 mg CO₂-C m⁻² h⁻¹ in crust patched and 22.7 mg CO₂-C m⁻² h⁻¹ in non-crust patches during 29 days (Table 1).

The CO₂ effluxes from crust and non-crust patches showed clear diurnal dynamics (Fig. 2). The minimum occurred at night and amounted to 6.88 ± 0.92 and 8.54 ± 0.67 mg CO₂-C m⁻² h⁻¹ in crust and non-crust patches, respectively. Sunlight after 9:00 am strongly increased the surface temperature, photosynthetic activity and soil respiration, increasing the soil CO₂ efflux rate accordingly. The maximum efflux occurred between 12:00 and 1:00 pm, with rates of 21.4 ± 2.3 and 27.6 ± 0.9 mg CO₂-C m⁻² h⁻¹ for crust and non-crust patches, respectively (Fig. 2).

A significant correlation was observed between living root biomass and total CO₂ efflux from soil ($p < 0.001$). This allowed us separating the CO₂ derived from living roots (root and rhizomicrobial respiration) from the sum of microbial decomposition of SOM and dead plant remains. The Y intercept of 17.5 mg CO₂-C m⁻² h⁻¹ (Fig. 3) indicates the microbial respiration

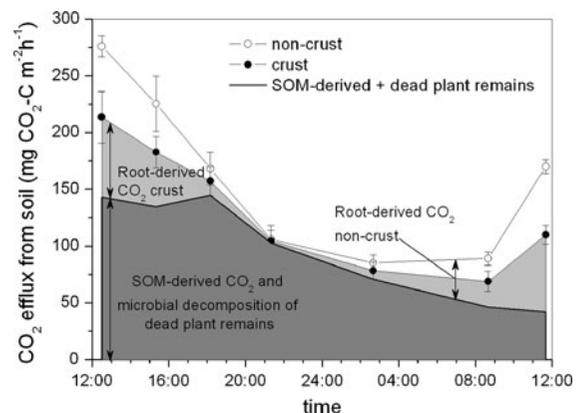


Fig. 2 Typical diurnal dynamics of CO₂ efflux from soil (±SE) in crust and non-crust vegetation patches (from 14. 08. 2009 12:00 to 15. 08. 2009 12:00 (n = 4)) and its partitioning based on the data of the regression approach. The arrows demonstrate CO₂ derived from SOM and microbial decomposition of dead plant remains, and of root-derived CO₂ in crust and non-crust vegetation patches

in the absence of living roots, representing the CO₂ efflux from the decomposition of dead roots and SOM. Based on the average values during 29 days (Table 1),

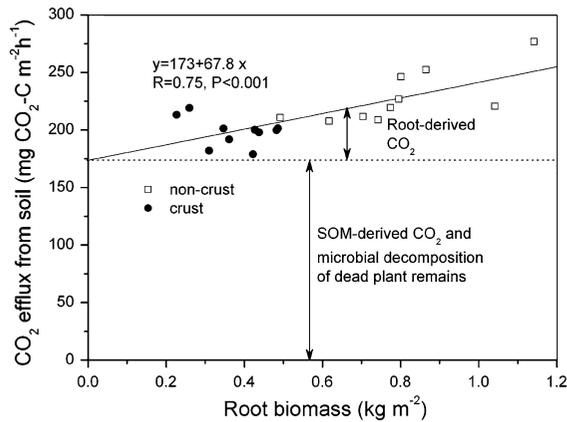


Fig. 3 Contribution of root-derived CO_2 and SOM-derived CO_2 to the total CO_2 efflux from soil calculated based on the linear regression between biomass of living roots and CO_2 efflux. Points represent means values ($n = 5$). Line represents linear correlation. Arrows demonstrate CO_2 derived from SOM and microbial decomposition of dead plant remains, and from living roots. Root-derived CO_2 is presented for crust versus non-crust plots. Black dots and empty squares indicates soil respiration measured in non-crust and crust patches, respectively

the contribution of root-derived CO_2 to total CO_2 efflux from soil was estimated to be 18 and 23% for crust and non-crust patches, respectively. During the nighttime the contribution of root-derived CO_2 to total CO_2 efflux

from soil ranged from 2 to 33% for crust patches and from 3 to 49% for non-crust patches.

Fate of root exudates in soil

The short-term (hours to days) and medium-term (days to weeks) processes in soil were examined based on the transformation of three ^{13}C labeled low molecular weight organic substances representing three main groups of root exudates. Short-term processes were described based on mineralization rates, and medium-term processes according to the residual ^{13}C remaining in soil. After ^{13}C labeled substances were added, a very rapid $^{13}\text{CO}_2$ efflux occurred and lasted for 3 days at an initial phase, indicating mineralization of initial substances. This pattern was similar for all treatments and organic substances. A single exponential decay equation with a constant (Eq. 1) fitted well to the measured data ($R^2 > 0.98$ in all treatments). The glucose decomposition rate ($0.73 \pm 0.23 \text{ day}^{-1}$ non-crust vs. $0.70 \pm 0.12 \text{ day}^{-1}$ crust) was significantly lower than that of glycine ($1.42 \pm 0.23 \text{ day}^{-1}$ non-crust vs. $1.53 \pm 0.25 \text{ day}^{-1}$ crust) for both treatments ($p < 0.01$). However, no significant differences ($p > 0.05$) in decomposition rates were found between crust and non-crust soils (Table 2).

Table 2 ^{13}C recovery from three LMWOS in various C pools in Tibetan grassland 29 days after the labeling (% of total added)

Sample	Glucose		Glycine		Acetic acid	
	Non-crust	Crust	Non-crust	Crust	Non-crust	Crust
Soil total (0–30 cm)	30.9 ± 2.68	38.2 ± 5.32	54.6 ± 6.04	65.7 ± 4.72	29.7 ± 6.75	39.6 ± 5.03
0–5 cm	16.8 ± 1.15	31.9 ± 4.41	28.7 ± 2.18	57.0 ± 2.89	26.0 ± 6.24	36.0 ± 4.94
5–15 cm	6.25 ± 0.87	6.21 ± 0.90	13.5 ± 3.12	2.49 ± 0.62	–	–
15–30 cm	7.89 ± 0.66	0.06 ± 0.01	12.4 ± 0.74	6.20 ± 1.21	3.65 ± 0.51	3.64 ± 0.09
Total living biomass	16.3 ± 1.76	6.70 ± 0.38	31.1 ± 0.99	14.6 ± 0.79	9.63 ± 0.74	4.60 ± 0.32
Above ground (shoots)	1.80 ± 0.60	0.24 ± 0.08	1.72 ± 0.05	0.23 ± 0.01	0.52 ± 0.21	0.07 ± 0.03
Living roots	14.5 ± 1.16	6.46 ± 0.30	29.3 ± 0.94	14.4 ± 0.78	8.84 ± 0.53	4.53 ± 0.29
0–5 cm	5.61 ± 0.45	1.51 ± 0.17	10.8 ± 0.01	4.39 ± 0.33	3.37 ± 0.12	1.31 ± 0.15
5–15 cm	4.59 ± 0.40	2.79 ± 0.11	10.9 ± 0.64	5.53 ± 0.27	2.81 ± 0.22	1.94 ± 0.03
15–30 cm	4.28 ± 0.31	2.16 ± 0.02	7.64 ± 0.29	4.43 ± 0.18	2.66 ± 0.19	1.28 ± 0.11
Dead roots	1.33 ± 0.22	3.11 ± 0.25	1.96 ± 0.08	3.49 ± 0.16	1.66 ± 0.11	3.05 ± 0.24
0–5 cm	0.49 ± 0.08	1.14 ± 0.09	0.72 ± 0.03	1.28 ± 0.06	0.61 ± 0.05	1.14 ± 0.09
5–15 cm	0.41 ± 0.07	0.96 ± 0.08	0.60 ± 0.03	1.07 ± 0.05	0.51 ± 0.04	0.93 ± 0.07
15–30 cm	0.43 ± 0.07	1.01 ± 0.08	0.64 ± 0.02	1.14 ± 0.05	0.54 ± 0.02	0.98 ± 0.08
$^{13}\text{CO}_2$ efflux from soil	25.4 ± 0.51	23.0 ± 1.08	24.9 ± 1.79	28.2 ± 7.50	29.2 ± 3.26	30.3 ± 2.18
Recovered	73.9 ± 5.17	71.0 ± 7.03	113 ± 8.90	112 ± 13.2	70.2 ± 10.9	77.6 ± 7.53

Values represent means ± SE ($n = 3$)

The rapid $^{13}\text{CO}_2$ emission was exchanged by slower evolution phase that was well described by the cumulative $^{13}\text{CO}_2$ efflux (Fig. 4). This phase was characterized by the decomposition of metabolites of the initial substances as well as the metabolites incorporated in microorganisms and temporarily absorbed to soil particles (and thus protected from fast microbial decomposition). The cumulative CO_2 efflux conformed well to a single exponential decay equation with constant ($R^2 > 0.98$ in all treatments; Eq. 2; Fig. 4). Decomposition rates of metabolites ($0.06\text{--}0.15\text{ day}^{-1}$) were about one order of magnitude slower than that of initial substances ($0.70\text{--}1.53\text{ day}^{-1}$). Slow decomposition rates for the

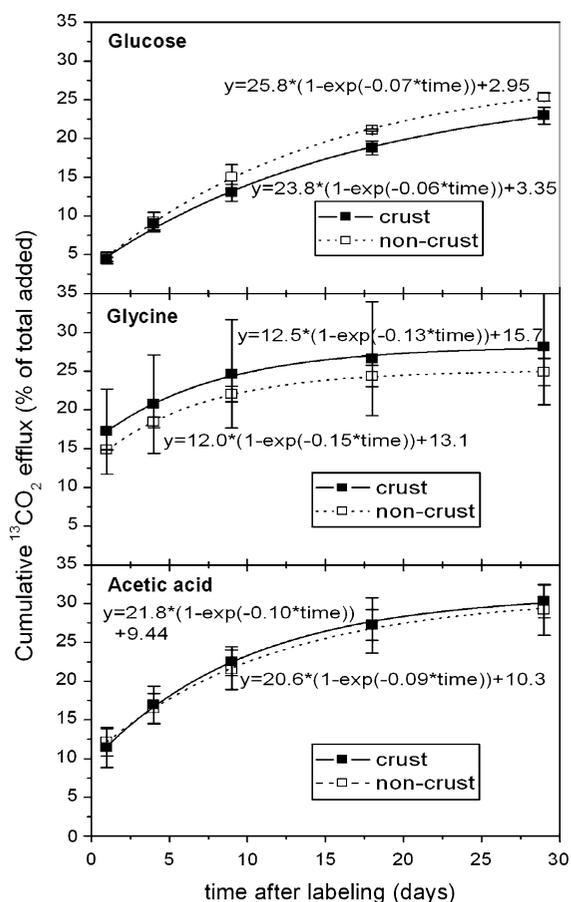


Fig. 4 Measured (filled square, open square) and fitted (lines) cumulative $^{13}\text{CO}_2$ efflux ($\pm\text{SE}$) from soil by decomposition of ^{13}C -labeled glucose, glycine and acetic acid; 29 day period ($n = 3$). Values represent the amount of ^{13}C recovered as a percentage of total ^{13}C added. Statistical significance for cumulative $^{13}\text{CO}_2$ efflux with increasing time for glucose, glycine and acetic acid is at $P < 0.01$ level, with $R^2 > 0.99$

second phase were reflected in long half-lives (Table 3). The decomposition rate of glucose metabolites was significantly lower than that of glycine and of acetic acid in both vegetation patches. However, no significant differences were observed between crust and non-crust ($p > 0.05$).

In contrast to the results obtained based on $^{13}\text{CO}_2$ fluxes, the ^{13}C remaining after 29 days in the soil (0–5 cm) differed significantly in the two vegetation patches (Fig. 5). The minimum amount of the added ^{13}C was found in the soil without crust (0–5 cm) after glucose addition (17% of total added) and the maximum after glycine addition in the soil under crust (57% of total added). With an exception of acetic acid under crust, the ^{13}C of the initial substances and metabolites were described well by a single exponential decay equation with a constant (Eq. 3, $R^2 > 0.77$; Fig. 5). The quantity of remaining ^{13}C was up to 2 times higher under crust ($p < 0.01$; Fig. 5), reflecting slower medium-term processes of C turnover as compared to the non-crust *Kobresia* patches and/or low plant uptake.

Much less ^{13}C from added exudates was found for all treatments at 5–15 and 15–30 cm depth compared with the upper layer (0–5 cm) (Table 2). Totally, about 31–38% of ^{13}C -glucose, 55–66% of ^{13}C -glycine and 30–40% of ^{13}C -acetic acid remained in the soil (0–30 cm) 29 days after labeling, with significantly greater amounts under crust (Table 2). This indicates much slower turnover and higher remains of root exudates under crust.

When evaluating the fate of exudates and ^{13}C budget, the uptake by plants should be considered. Already 1 day after addition, 5.2% of total ^{13}C added glucose, 10.8% of glycine and 3.7% of acetic acid were recovered in the roots (non-crust, depth 0–5 cm). This indicates an initial rapid uptake. However, most ^{13}C remained in the roots and was not transferred to the shoots even after 29 days (Table 2). Two times more ^{13}C was recovered in the living roots under non-crust versus crust, showing that roots play a very important role in the turnover of substances in this ecosystem. Up to 2% of total added ^{13}C was recovered in the dead roots under non-crust and about twice that amount was recovered in dead roots under the crust (Table 2). ^{13}C recovery under both patches clearly shows that the higher ^{13}C remaining in soil under the crust and a lower ^{13}C uptake by living roots.

Table 3 Half-lives ($T_{1/2}$) of ^{13}C labeled substances and metabolites in soil derived from single exponential decay equation fitted to $^{13}\text{CO}_2$ efflux

	$T_{1/2}$ of initial ^{13}C -substances (days)			$T_{1/2}$ of ^{13}C -metabolites and ^{13}C in microbial biomass (days)		
	Glucose	Glycine	Acetic acid	Glucose	Glycine	Acetic acid
Non-crust	0.95 ± 0.31	0.49 ± 0.08	0.52 ± 0.11	10.0 ± 0.53	4.67 ± 0.18	7.81 ± 0.75
Crust	0.99 ± 0.17	0.45 ± 0.07	0.64 ± 0.12	11.7 ± 0.31	5.26 ± 0.68	6.86 ± 0.60

Half-life is defined as $\ln(2)/k$. Values represent means \pm SE ($n = 3$)

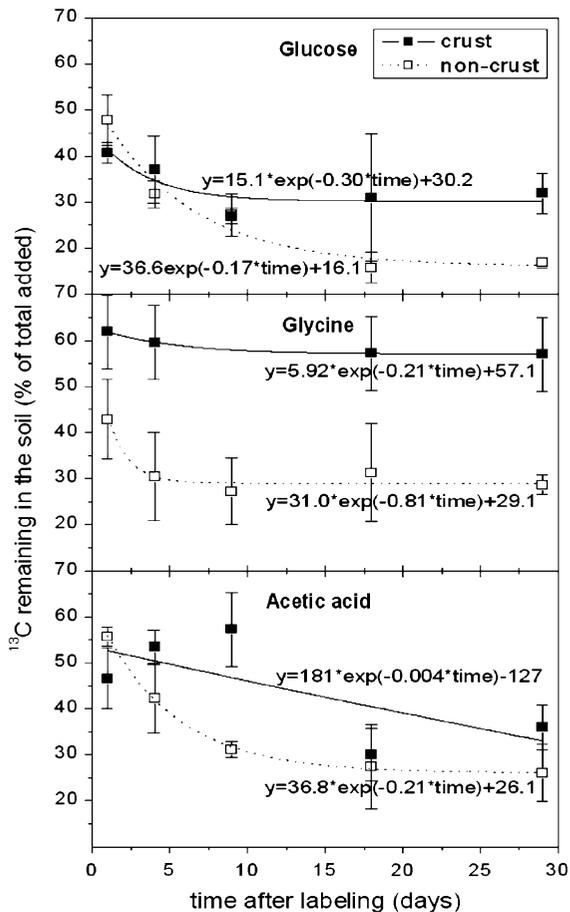


Fig. 5 Measured (filled square, open square) and fitted (lines) ^{13}C (\pm SE) remaining in soil (0–5 cm) after adding ^{13}C -labeled glucose, glycine and acetic acid; 29 day period ($n = 3$). Values represent the amount of ^{13}C recovered in soil as a percentage of total ^{13}C added. Statistical significance for ^{13}C remaining in the soil for glucose ($R^2 > 0.99$), glycine ($R^2 > 0.99$) and acetic acid ($R^2 = 0.65$) is at $P < 0.01$ level

Discussion

As a result of overgrazing, *Kobresia*, *Stipa* and other grasses are partly replaced by blue-green algae and crustose-lichen crusts (Kaiser et al. 2007). This

replacement changes the C cycle differently over long-, medium- and short-term processes.

Changes in carbon stocks

Grasslands play a very important role in the global biogeochemical C cycle (Hall et al. 1995; Sala et al. 1996; Tate et al. 1995). In these ecosystems, C is mostly stored in soils, where turnover-times of the bulk C are relatively long (Hall et al. 1995; Matthews 1997; Tate et al. 1995). Therefore, change in C stocks represents the long-term processes. Natural and anthropogenic changes (e.g., temperature and precipitation, atmospheric CO_2 concentration, land-use) in grassland ecosystems have great impact on the C cycle and may convert the system from a C sink to a C source or vice versa.

Heavy overgrazing in the Tibetan plateau have formed thick root mats with lichen and blue algae crusts that strongly protect the soil from further degradation because these structures are highly resistant against trampling by yaks and sheep and against erosion (Cao et al. 2010). The above- and belowground C stocks under *Kobresia* (non-crust) were close to those reported by Wu et al. (2010) for a comparable site at Haibei station with similar altitude and vegetation type. We showed, however, that the two contrasting patches of vegetation (non-crust vs. crust) differed significantly ($p < 0.01$) in both root and shoot biomass. Above- and belowground (shoots and roots) biomass was significantly ($p < 0.001$) smaller under crusts than under non-crust (23.6 g C m^{-2} crusts vs. $176 \text{ g C non-crust m}^{-2}$ for shoots and 177 g C m^{-2} crusts vs. 341 g C m^{-2} non-crust for roots, Table 1). This indicates that the annual C input by roots and rhizodeposits strongly decreased under crusts. Besides, microbial decomposition of dead plant remains and SOM, did not differ significantly in crust vs. non-crust ($p > 0.05$), indicating the same C output on crust patches. This means that crust formation will lead to

decreasing C sequestration or even increasing C loss over the long-term. This was further confirmed by significant differences ($p < 0.05$) in the C content of the upper soil layer (0–5 cm) between two different vegetation patches. We therefore conclude that long-term processes have just started to reflect the changes in C pools due to overgrazing.

It has been reported that intact *Kobresia* pastures are a neutral net ecosystem CO₂ exchange (NEE) on the annual scale (Shi et al. 2006; Zhao et al. 2006; Pei et al. 2009). However, the grazing-induced reduction of above- and belowground biomass, as well as the decline of C content in the upper soil layer, lead us to expect a decrease of the C stock under crust in the near future.

CO₂ efflux from soil

The CO₂ efflux from soil is the major pathway for C losses from terrestrial ecosystems. The SOM-derived CO₂ characterizes the long-term processes and reflects responses to land-use changes (Chen et al. 2009). In contrast, root-derived CO₂ contributes to an increased rate of total efflux, but has no influence on the long-term C stock (Kuzyakov 2006). The efflux rates in our study varied between 4.0 and 5.4 g C m⁻² day⁻¹, similar to the observation (3.3 and 4.6 g CO₂-C m⁻² day⁻¹ for heavily and lightly grazed sites, respectively) in an alpine *Kobresia humilis* meadow from mid-July to August (Cao et al. 2004). The linear regression approach showed low contribution of root-derived CO₂ to total CO₂ efflux (18% for crust vs. 23% for non-crust) in alpine grasslands. Despite some limitations of this approach (Kuzyakov 2006), these values fall within the range (17–40%) in grassland soils reported by Raich and Tufekcioglu (2000). The contribution of root-derived CO₂ are also comparable to that (26.5%) estimated by a root removal technique in another alpine *Kobresia humilis* meadow (Wu et al. 2005), but are less than

those (from 25 to 72%) observed in a temperate grassland in northern China (Wang et al. 2007).

Diurnal dynamics of CO₂ efflux from soil reflect an integrative effect of biotic and abiotic factors on various C turnover processes over a day scale (i.e., the difference between daytime and nighttime). Higher contribution of living roots to the total CO₂ during the daytime is explained by tight connection to photosynthesis (Kuzyakov and Gavrichkova 2010). Besides, the SOM-derived CO₂ was approximately three times higher at the start of measurement period than at the end of the measurement period (Fig. 3), indicating that decomposition rates of SOM vary greatly within few days. This is mainly connected with the interactions between soil temperature and moisture affecting microbial activity and consequently SOM decomposition.

This study was not designed to evaluate the contribution of crust to CO₂ efflux from soil. We assume however, that this contribution is relatively small, as lichens and algae cover only the upper 5–7 mm of soil surface and this is negligible as compared to the layer of 6 cm with living and dead roots (Table 4). Additionally, the CO₂ efflux from soil was not significantly different between crust and non-crust patches (5.4 g C m⁻² day⁻¹ non-crust vs. 5.1 g C m⁻² d⁻¹ crust). However, further experiments should be designed to evaluate the contribution of the algae and lichen crusts to CO₂ efflux from soil.

Crust patches are especially sensitive to climatic factors such as solar radiation, drought and heavy rain. Particularly solar radiation at high altitudes has a strong effect because it rapidly heats up the vegetation-free and darkish crust surface. This accelerates the SOM and root litter decomposition. At the same time, the surface occupied by lichens increases water run-off and hinders infiltration into the soil. Additionally, higher soil surface temperature and increased wind contact accelerate evaporation and

Table 4 Properties of soil horizons of the Haplic Kastanozem on the Tibetan Plateau near Xinghai

Depth (cm)	Horizon symbol	Soil structure	Bulk density (g cm ⁻³)	pH	C _{org} ^a (%)	Total N (%)	C/N ratio
0–6	Afe	Felty ^b	0.60 ± 0.01	6.64 ± 0.15	8.80 ± 0.20	0.68 ± 0.01	12.9 ± 0.60
6–25	Ahk	Granular	0.81 ± 0.01	6.96 ± 0.19	4.38 ± 0.15	0.46 ± 0.01	9.52 ± 0.54
25–90	Bkc	Angular	0.84 ± 0.01	7.62 ± 0.04	2.28 ± 0.19	0.25 ± 0.02	9.12 ± 1.62

^a dead and living roots were removed prior to C_{org} and total N analyses

^b Kaiser et al. (2007)

reduce soil moisture. Previous study showed that higher temperature enhances CO₂ efflux in *Kobresia* grasslands (Saito et al. 2009), but moisture is probably the major limiting factor for CO₂ efflux from soil (Yang et al. 2008) under the crust patches. Low moisture may also be responsible for more ¹³C remaining in the soil under crust after the exudate addition. Future work should therefore be devoted to evaluating the importance of individual climatic factors and their interactions as well as the response of these two contrasting vegetation patches.

Fate of root exudates in soil

The fate of root exudates and their metabolites in soil and plants reflects short- and medium-term processes. A large portion of ¹³C derived from glucose (about 31–38% of total ¹³C added), glycine (55–66%) and acetic acid (30–40%) was recovered in the 30 cm soil 29 days after labeling, with larger values for crusted soil. In contrast to the release of rhizodeposits after ¹³C plant labeling (Wu et al. 2010), directly adding ¹³C labeled substances to the soil resulted in a much higher percentage of remaining ¹³C. Based on decomposition rates, the calculated half-lives for exudates in soil were 0.86–4.05 days. These half-lives are similar to that of glucose (4 days) in a Brown Chernozemic soil (Shields et al. 1973) and are within the range of values for easily available organic substances as reviewed by Jones et al. (2005a, b). However, the half-lives were much shorter than those of organic substances incorporated in microorganisms, e.g., 0.25–2.5 years for various organics in forest soils (van Hees et al. 2005; Blagodatskaya et al. 2011), 56.8 days (glucose) for soil under ryegrass (Kouno et al. 2002) and 60 days (glucose) in soil from permanent grassland (Wu et al. 1993).

Numerous studies under field and controlled conditions have suggested that temperature strongly enhances decomposition of SOM and LMWOS (Kirschbaum 1995; Luo and Zhou 2006). To regret, we have not measured the soil temperature under crusted and non-crusted patches. We assume however, that because the dark crust surfaces were directly prone to solar radiation, their temperature was higher than under the non-crust patches. A clipping experiment in an alpine grassland showed that soil temperatures under non-vegetated areas may be up to 5°C higher compared to areas covered by

vegetation, resulting in an increase of respiratory activity for 20–50% (Bahn et al. 2006). This indicates that an increase in soil temperature under crusted soil may increase mineralization of added low-molecular weight organic substances (LMWOS) and lead to more ¹³CO₂ emission from the crust soil. However, only a small difference in the ¹³CO₂ release from added LMWOS between crust and non-crusted soil were observed (Fig. 4). Three reasons may be responsible for the small differences despite the expected temperature differences. Firstly, the very dense *Kobresia* root mats have extremely well-insulating properties. Therefore, we assume that the temperature may be different between crusts and non-crusts on the surface, but is very similar in few mm of soil depths. Secondly, the intensive solar radiation, leading to high soil surface temperatures, is common at this site only for some days and only between 10 am and 2 pm. Nearly all afternoons are cloudy with frequent short thunderstorms. As the ¹³CO₂ release was measured continuously, the temperature increase for 3–4 h during some days has only a small contribution to the total decomposition of LMWOS. Thirdly, the small difference in ¹³CO₂ between the crust and non-crust might result from the fact that other factors such as low water content counteract the effect of soil temperature on mineralization of added LMWOS.

Significantly more ¹³C ($p < 0.01$) remained in the soil (0–5 cm) under crusts (Fig. 4). There are two possible explanations: (i) limitation by abiotic factors, mainly moisture (see above): the water content was considerably lower in the crust patches; (ii) lower microbial activity under crust with less living roots (Blagodatskaya et al. 2010), leading to slower decomposition of organic substances in the rhizosphere (Kuzyakov 2002; Cheng 2009). However, this needs further experimental confirmation.

An explanation to the lower ¹³C amount remaining in non-crust soil is the higher uptake of exudates and their metabolites by roots. Roots can take up dissolved low molecular weight organics passively or via a range of active proton cotransport systems mainly used for amino acid uptake (Jones 1999; Bardgett et al. 2003; Xu et al. 2004; Jones et al. 2005a). The relevance of this uptake, however, is low for most ecosystems, and the experimental approaches based on bulk ¹³C and ¹⁵N were questioned recently (Biernath et al. 2008; Sauehl et al. 2009; Rasmussen et al. 2010). In *Kobresia*

grassland, 16, 31 and 10% of the ^{13}C from glucose, glycine and acetic acid, respectively, were recovered in the roots (0–30 cm) and shoots 29 days after labeling. The higher uptake of glycine compared to glucose and acetic acid (Table 2) shows the importance of nitrogen (N) to plants in this N-limited ecosystem (Jones and Darrah 1994). However, only less than 6% of this amount was transferred in the shoots (except glucose without crust), with the minimal values under crusts. There are two possible explanations to this very low transport of ^{13}C substances and their metabolites from roots to shoots. First, the ^{13}C recovered in the roots was not really taken up by the roots, but was moved with water to the roots and remained at the pericycle without to enter in the symplast. Secondly, some ^{13}C allocated from roots to the shoots could be lost via shoot respiration. This has been observed by organic N uptake using ^{13}C -labeled amino acids (Näsholm and Persson 2001). The higher uptake of added substances compared to other studies (Boddy et al. 2007; Henry and Jefferies 2003) mainly reflects the first reason (passive movement and remaining at pericycle) by very dense roots of *Kobresia* mats. This is because the total uptake of substances strongly depends on root density (Xu et al. 2011) that was extremely high under *Kobresia* as compared to most other ecosystems. While other studies (Bardgett et al. 2003; Jones et al. 2005a) stated that roots are poor competitors for dissolved organics compared with microorganisms, we cannot support these findings. A significantly higher portion of organics entering the soil remains in soil under crust could be ascribed to lower uptake by living roots and longer period of this study than other studies. E.g., Jones et al. (2005a, b) showed no effects of agricultural management on amino acid mineralization and suggested that very fast processes do not reflect changes on medium- and long-term scales. In this study we observed that exudate decomposition did not differ significantly between crust and non-crust, confirming the conclusion of Jones et al. (2005a, b). Because the rate of $^{13}\text{CO}_2$ evolution was rapid, with half-lives ranging from 0.45 to 0.99 days (Table 3), we suggest that the initial mineralization of the added exudates is probably too fast to evaluate crust/non-crust differences under field conditions.

Glucose, glycine and acetic acid mineralization in soil is extremely rapid compared with more complex substrates, e.g., cellulose and proteins (Tate et al. 2000; Schneckenberger et al. 2008). Nevertheless, half-lives

are longer than those reported for low molecular weight solutes released from plant cells into the rhizosphere, e.g., glucose (Hill et al. 2008; Schneckenberger et al. 2008; Kuzyakov and Jones 2006), amino acids (Boddy et al. 2007) or carboxylic acids (Jones 1998; Fischer et al. 2010a, b). This indicates that microbial activity in both grassland soils in the Tibetan Plateau was lower than in soils of other ecosystems.

We hypothesized lower decomposition rates under crust because of lower microbial activity due to the two-times-lower living root biomass. However, the mineralization rates were similar in both vegetation patches. Thus, our study indicates that crust patches had no effect on fast processes of exudate turnover or these effects were not captured because of very fast mineralization and root uptake. However, we have to mention that only a very narrow range of fast decomposition processes were traced here based on ^{13}C labeled glucose, glycine and acetic acid. Therefore, the fate of substances with other biochemical properties as well as with slower decomposition rates should be compared in soils with and without crust.

Conclusions

The lichen-algae crusts on the *Kobresia* root mat resulting from heavy overgrazing mainly change the C stock in aboveground and living root biomass. Contrary to our hypothesis, we found no effects of crust on fast processes as reflected by mineralization of root exudates. Nonetheless, a significantly larger portion of organics entering the soil remains under crusts for a long period. Despite a smaller input, a larger portion of exudates is incorporated into SOM and microorganisms, while less is taken up by living roots and decomposed to CO_2 . The strongly decreased C input by living roots under crusts is therefore partly compensated by the slower medium-term processes and the higher portion of organics remaining in soil. It is partly confirmed by the decreased C content in the upper soil layer that the slower decomposition cannot compensate decreased C input in this fragile ecosystem, but longer studies are necessary to investigate the balance between the decreased C input and slower decomposition. Therefore, changing vegetation patterns and the increase in crust area need to be monitored to prevent far-reaching negative effects on the *Kobresia* pasture

ecosystems and to prevent a shift from a neutral C balance to a C source.

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