

# CARBON AND NITROGEN LOSSES FROM SOIL DEPEND ON DEGRADATION OF TIBETAN *KOBRESIA* PASTURES

Shibin Liu<sup>1\*</sup>, Per-Marten Schleuss<sup>1</sup>, Yakov Kuzyakov<sup>1,2,3</sup>

<sup>1</sup>Department of Soil Science of Temperate Ecosystems, University of Göttingen, Büsgenweg 2 37077 Göttingen, Germany

<sup>2</sup>Department of Agricultural Soil Science, University of Göttingen, Büsgenweg 2 37077 Göttingen, Germany

<sup>3</sup>Institute of Environmental Sciences, Kazan Federal University, 420049 Kazan, Russia

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## ABSTRACT

Degradation of *Kobresia pygmaea* pastures has strongly increased on the Tibetan Plateau over the last few decades and contributed to a high loss of soil organic carbon and nutrients. The pathways of carbon (C) and nitrogen (N) losses from degraded *K. pygmaea* pastures are still unclear, but this is a prerequisite to assess the recovery of Tibetan grasslands. We investigated the response of day- and nighttime CO<sub>2</sub> efflux and leaching of dissolved organic C and N, NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> from *K. pygmaea* root mats in three degradation stages: living root mat, dying root mat and dead root mat. Dying root mat had the highest C loss as CO<sub>2</sub> and as leached dissolved organic carbon. This indicates *K. pygmaea* pastures shift from a C sink to a C source following plant death. In contrast, living root mat had the lowest daytime CO<sub>2</sub> efflux (0.38 ± 0.1 μg C g<sup>-1</sup> h<sup>-1</sup>) because CO<sub>2</sub> was assimilated via photosynthesis. Nighttime CO<sub>2</sub> efflux positively correlated with soil moisture for living and dead root mats. It indicates that increasing precipitation might accelerate C losses due to enhanced soil organic carbon decomposition. Furthermore, dead root mat had the highest average NO<sub>3</sub><sup>-</sup> loss (23 ± 2.6 mg N L<sup>-1</sup>) from leaching compared with other root mats. Consequently, leaching increases the negative impacts of pasture degradation on N availability in these often N limited ecosystems and thus impedes the recovery of *K.* pastures following degradation. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS: *Kobresia pygmaea* pasture; CO<sub>2</sub> efflux; NO<sub>3</sub><sup>-</sup> leaching; grassland degradation; dissolved organic carbon

## INTRODUCTION

Globally, grasslands occupy an area of about 24 million km<sup>2</sup> (Scurlock & Hall, 1998) and play an important role because they provide large grazing ground and store huge amounts of carbon (C) in soil (ca. 343 Gt C; FAO, 2010). However, about 20–35% of the world's grasslands are degraded with the consequence of declining vegetation cover, decreasing soil organic carbon (SOC) storage and soil fertility (FAO, 2010). The drivers for grassland degradation are numerous including biotic and abiotic impacts and are mostly amplified by human activities. For instance, overgrazing is expected to trigger grassland degradation by reducing the vegetation cover, changing vegetation composition and causing direct damages via trampling (Bilotta *et al.*, 2007; Yayneshet *et al.*, 2009; Schönbach *et al.*, 2011). Fire, permafrost and drought were also considered as factors that may influence soil structure and C storage (Liu & Diamond, 2005; Yang *et al.*, 2010; Novara *et al.*, 2013; Pereira *et al.*, 2014). A reversal of grassland degradation, however, can be induced by changing management options, that is, by planting legumes or shifting to organic farming (Hu *et al.*, 2016; Parras-Alcántara *et al.*, 2015).

The Tibetan Plateau (TP) covers up to 2.5 million km<sup>2</sup> and hosts the largest montane and alpine grasslands of the world. As the only dominant *Cyperaceae* mats in southeastern humid TP (450,000 km<sup>2</sup>), the pastures of *Kobresia pygmaea* C.B. Clarke (*K. pygmaea*) are often characterized by very dense root mats, which developed as a consequence of the long-term grazing history (Miehe *et al.*, 2008). This selected plants with very high belowground investments (Hafner *et al.*, 2012). Accordingly, *K. pygmaea* is very competitive compared with other plant species because its belowground reserves ensure a rapid regrowth following grazing and the recapture of nutrients such as nitrogen (N) is very efficient (Schleuss *et al.*, 2015).

Because of the high altitude of about 4500 m (Thompson *et al.*, 1997) and the harsh environment (i.e. strong solar radiation, high diurnal and annual temperature variations, low CO<sub>2</sub> partial pressure, strong temporal and spatial precipitation variations and steep slopes) (Ren *et al.*, 1997; Liu-Zeng *et al.*, 2008; Fan *et al.*, 2011; Zhang *et al.*, 2015), *K. pygmaea* pastures are considered to be very vulnerable ecosystems (Wang *et al.*, 2002; Schleuss *et al.*, 2015). The *Kobresia* pastures are intensively affected by grassland degradation (Wang *et al.*, 2015). Almost all *K. pygmaea* pastures are degraded in Nagqu, 90% of which is under medium degradation stage (Wei *et al.*, 2005). According to Babel *et al.* (2014), roughly 20% of the *Kobresia* root mats on the Kema study sites were dead, whereas still 65% were in intact conditions or showed only light degradation. For

\*Correspondence to: Shibin Liu, Department of Soil Science of Temperate Ecosystems, University of Göttingen, Büsgenweg 2, 37077 Göttingen, Germany.  
E-mail: sliu3@gwdg.de

the remaining part, the topsoil was removed (bare soil) by SOC decomposition or soil erosion.

Most researchers attribute the *Kobresia* pasture degradation to overgrazing (Shao & Cai, 2008; Lin *et al.*, 2015). Climate change, that is, increasing temperature or precipitation, can also stimulate SOC turnover and plant species richness and thus amplify degradation (Du *et al.*, 2004; Klein *et al.*, 2004). Soil pools of C and N and plant biomass decreased along grassland degradation from healthy to severe status (Wang *et al.*, 2015; Yao *et al.*, 2016). Seedling density in the soil seed bank also significantly decreased with grassland degradation (Kassahun *et al.*, 2009). Overall, it is of great importance to understand the effects of human activities on soil C and N cycles, especially their imbalance caused by changes in climate and management (Canadell *et al.*, 2010; Follet *et al.*, 2012; Yu & Jia, 2014; Peng *et al.*, 2015). However, knowledge about C and N losses via SOC decomposition and leaching is limited for *Kobresia* root mats in different degradation stages.

Therefore, root mats of different degradation stages were investigated in this study (Figure 1): (a) living root mat (Living), (b) dying root mat (Dying) and (c) dead root mat (Dead). The dying stage represents the transition between living and dead root mats. It was in living condition during sampling but died during transport, reflecting the initial stage of root mat degradation. We hypothesized that the dying root mat shows the highest C losses (mineralized as CO<sub>2</sub> and leached as dissolved organic matter (DOM)) and N losses (leached as organic and mineral N) because of rapid decomposition of SOC and fresh root litter (Hansson *et al.*, 2010). Considering the presence of living plants, we also hypothesized that living root mat assimilates CO<sub>2</sub> and counterbalances C losses (Ingrisch *et al.*, 2015). We also investigated the effect of soil moisture on nighttime CO<sub>2</sub> efflux and hypothesized that CO<sub>2</sub> efflux from living and dead *K. pygmaea* root mats will strongly increase with higher soil moisture because it stimulates SOC mineralization (Mukhopadhyay & Maiti, 2014).

## MATERIALS AND METHODS

### Site Description

Sampling was carried out on sites at the research station of the Tibet University and the Institute of Tibetan Plateau Research—“*Kobresia* Ecosystem Monitoring Area” (KEMA) (31°16′45″N 92°59′37″E, 4410 m) in Nagqu, Tibet. The station is located in the core area of the *K. pygmaea* distribution (Babel *et al.*, 2014) and lies in the ‘Plateau Frigid Monsoon Region with semi-moist climate’ (Leber *et al.*, 1995). Mean annual temperature and precipitation are −1.2°C and 430 mm, respectively. From June to September, the mean summer precipitation reaches 272 mm, whereas snowfall is low (climate station in Nagqu, Miede *et al.*, 2011). The growing season ranges from May to October and mainly depends on the on-set and off-set of the summer monsoon (Miede, 1988).

The soils are classified as *Stagnic Eutric Cambisol (Humic)* (WRB, 2014) with a texture of 50% sand, 33% silt and 17% clay. The mean pH value (H<sub>2</sub>O) is 6.9 ± 0.03, and the topsoil is free of carbonates. Large amounts of living and dead roots are present in the topsoil, developing very dense root mats (Schleuss *et al.*, 2015). The root mats are mainly covered by *K. pygmaea* and have an average shoot height of not more than 2 cm (Miede *et al.*, 2008).

*Kobresia pygmaea* is the dominant vegetation type across the whole catchment of the Nagqu River (He & Richards, 2015). Average shoot biomass was 0.3 ± 0.02 kg dry mass m<sup>-2</sup>. Besides *K. pygmaea* (covering up to 98%), other monocotyledons occur, such as *Carex spp.*, *Festuca spp.*, *K. humilis*, *Poa spp.*, *Stipa purpurea* and *Trisetum spp.* (Babel *et al.*, 2014).

Large areas on the study sites are affected by grassland degradation. The sites are grazed by livestock (yaks and sheep) from January to April and also by ground-dwelling Plateau pika (*Ochotona curzoniae*) (He & Richards, 2015).



Figure 1. Longitudinal section of chamber (left) and origin of three *Kobresia* root mat types (right). ‘Living’ = living root mat; ‘Dying’ = dying root mat; ‘Dead’ = dead root mat. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### Soil Sampling and Preparation

Samples were randomly selected within an area of about 25,000 m<sup>2</sup> to maintain equal environmental conditions. We used soil cores (diameter: 5 cm; height: 5 cm) to take undisturbed samples from living and dead root mats at a depth of 5 cm (Figure 1, right). Before transportation, the shoot biomass was removed and samples were put into PVC collars, which had the same size as the sampling cores. In the laboratory, samples were pre-incubated for 28 days but some samples of living stage did not recover. These recently died samples were used as an additional treatment (dying root mat). In total, we had three treatments: living root mat, dying root mat and dead root mat (Figure 1, middle). Because the dying stage was still living before sampling but died during transport or storage, they had the same initial soil characteristics compared with the intact stage, that is, C and N contents, microbial biomass and root biomass. The only difference between both root mats (Living vs Dying) is the presence of *Kobresia* shoots, which assimilate CO<sub>2</sub>-C. Consequently, the dying stage was disabled from C assimilation and began to degrade. In contrast, the soil characteristics of the dead root mat totally differed compared with the living and dying stages because of long-term degradation in the field: that is, lower C and N contents, microbial biomass and root biomass. Therefore, the three treatments reflect a gradual degradation sequence (Living < Dying < Dead).

Three samples were selected from living and dead root mats to determine water holding capacity (WHC). Another three samples were used to separate root from soil. Roots were washed carefully with distilled water to remove soil particles. Afterwards, roots were oven dried (60°C) and subsequently milled. Soil was oven dried under 105°C, sieved (2 mm) and grounded. Then soil and root were analyzed for total C and N using an elemental analyzer (Vario Max CN, Hanau, Germany). The dying root mat stage was considered to have the same initial C and N content and bulk density as living root mat.

### Experimental Set-Up

Six samples from each root mat were selected to conduct the experiment. These samples were put in incubation boxes (Figure 1, left) allowing simultaneous analyses of CO<sub>2</sub> efflux and leaching. According to Geng *et al.* (2012), diurnal soil temperature variation in Nagqu had no strong effect on soil respiration. Moreover, the average daily soil temperature during growing season was in the range of 9.3–21.3°C. Within the experiments, we used a constant temperature of 20°C during day and night. Samples were illuminated diurnally for 14 h with a photosynthetic photon flux density of 80 μmol m<sup>-2</sup> s<sup>-1</sup> and kept in the darkness for 10 h.

The first experiment was conducted to assess CO<sub>2</sub>-C loss and leaching of dissolved C and N. Living, dying and dead root mats were included. Daytime and nighttime CO<sub>2</sub> efflux was measured separately. To measure the CO<sub>2</sub> efflux, soil moisture was firstly adjusted to 70% of WHC (i.e. 59% of dry weight for living and dying root mats;

33% of dry weight for dead root mat) for all soil cores at the beginning of the photosynthetic period. Distilled water was added homogeneously on the surface using a syringe. Vials with 3 mL 1.0 M NaOH solution were placed into the incubation box to trap CO<sub>2</sub>. NaOH solution was exchanged before the start of the night period. Net ecosystem production (difference between gross primary production and ecosystem respiration) was measured with simulated solar radiation during daytime. Only ecosystem respiration was investigated during nighttime. The leaching was examined on the day following CO<sub>2</sub> measurement. Soil moisture of each sample was slowly adjusted to 100% of WHC (i.e. 84% of dry weight for living and dying root mats; 47% of dry weight for dead root mat). Distilled water (11 mL) was then added to each incubation box with a syringe to simulate increasing precipitation. The amount corresponded to 5 mm precipitation and reflected strong rainfall events, which occurred several times on the study sites (Ingrisch *et al.*, 2015). The leachates were collected at the outlet of the incubation box (Figure 1, left). After taking the leachate samples, the cover of the incubation box was opened again for ensuring photosynthesis. This 2-day collection of CO<sub>2</sub> efflux and leachate was repeated weekly and lasted in total 9 weeks.

The second experiment focused on the effect of soil moisture on nighttime CO<sub>2</sub> efflux. Soil moisture was regulated to two levels of WHC: 100% (at Day 11) and 70% of WHC (at Day 15 and 17) as above. Nighttime CO<sub>2</sub> efflux was measured every 2 days. Vials with 3 mL 1.0 M NaOH solution were placed into the incubation box to trap CO<sub>2</sub>. This second experiment included living and dead root mats and lasted for 17 days.

To measure CO<sub>2</sub> efflux, 1 mL of the NaOH trap solution was titrated against 0.1 M HCl solution. Leachate was passed through filter paper (0.45 μm) and analyzed for total carbon, total nitrogen and dissolved inorganic carbon using a multi N/C 2100s analyzer (Analytik Jena Inc, Germany). Dissolved inorganic nitrogen (NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>) was measured using Cenco (Dual Tubingpump, Instrumenten B.V., Breda, The Netherlands). Dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were calculated by subtracting dissolved inorganic carbon and dissolved inorganic nitrogen from total carbon and total nitrogen. Microbial biomass carbon (MBC) and nitrogen (MBN) were determined by the fumigation-extraction method (Brookes *et al.*, 1985; Vance *et al.*, 1987).

### Statistical Analyses

Soil and plant properties were analyzed and expressed as means with standard errors (mean ± SE). Normality (Shapiro-Wilk-test,  $p > 0.05$ ) and homogeneity of variance (Levene-test,  $p > 0.05$ ) were examined. The significance was tested at  $p < 0.05$  using one-way ANOVA following Tukey's HSD test for multiple comparisons. Relationship between soil moisture content and nighttime CO<sub>2</sub> efflux was analyzed using linear regression. The cumulative CO<sub>2</sub>-C for all replicates during this experiment was correlated

to their final SOC contents. All analyses were conducted using STATISTICA 10.0 (StatSoft Inc.).

## RESULTS

### Plant and Soil Characteristics

Carbon and N contents in soils of living and dying root mats were approximately 1.8 and 1.4 times higher than those of dead root mat, while the C and N contents of the root biomass did not differ significantly from each other (Table I). After the incubation, the MBC content of dying root mat was roughly twice that of dead root mat. MBC was positively correlated with nighttime CO<sub>2</sub> efflux and DOC concentration in the leachate (Figure 2). Living root mat had an average above-ground biomass of  $215 \pm 2.2 \text{ g m}^{-2}$ .

### CO<sub>2</sub> Efflux Related to Degradation Stages of *Kobresia* Pastures

The hypothesis of the highest C loss from dead root mats was confirmed considering the nighttime CO<sub>2</sub> efflux. It was roughly 1.2 and 3.1 times higher compared with living and dying root mats, respectively (Figure 3, top). Nighttime CO<sub>2</sub> efflux of dying root mat was stable over time, whereas it increased for living root mat until the fifth week and then remained stable. After the fifth week, the nighttime CO<sub>2</sub> efflux did not differ significantly from that of dying root mat. The cumulative CO<sub>2</sub>-C for all replicates during this experiment was positively related to their final SOC contents (Figure 4,  $p < 0.05$ ).

Daytime CO<sub>2</sub> efflux of living root mat was the lowest (Figure 3, bottom), confirming our second hypothesis about the strong CO<sub>2</sub> assimilation by living *Kobresia*. The average daytime CO<sub>2</sub> efflux of living root mat was even six and two times lower than dying and dead root mats, respectively. The trend of daytime CO<sub>2</sub> efflux for the three root mat types was stable during the 2 months.

Overall, the dying of *K. pygmaea* induced the significantly highest CO<sub>2</sub>-C losses, whereas the presence of living *K. pygmaea*, in reverse, showed a strong CO<sub>2</sub>-C uptake by photosynthesis.

### Effects of Soil Moisture on Nighttime CO<sub>2</sub> Efflux

A strong positive relation between nighttime CO<sub>2</sub> efflux and soil moisture was obtained for living and dead root mats considering the total duration of the second experiment

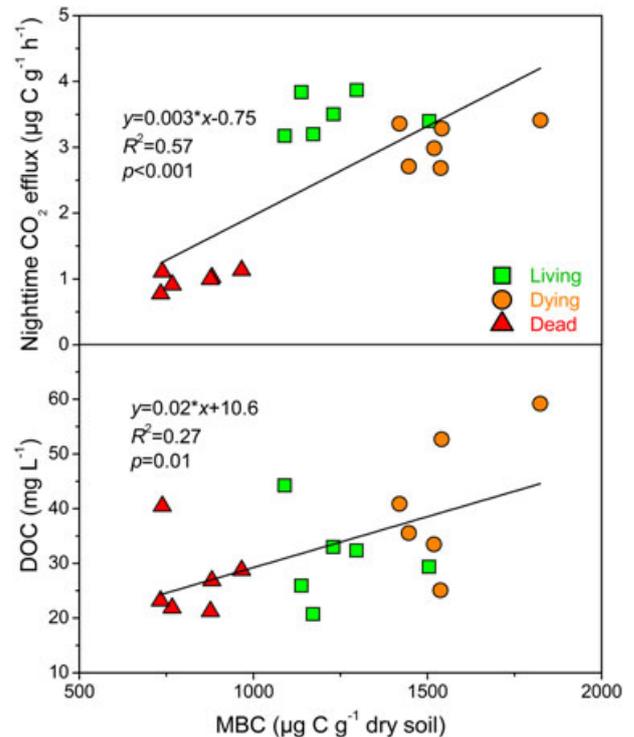


Figure 2. Relations between microbial biomass carbon (MBC) and nighttime CO<sub>2</sub> efflux (top) and dissolved organic carbon (DOC) concentration in the leachate (bottom) at Day 114. 'Living' = living root mat; 'Dying' = dying root mat; 'Dead' = dead root mat. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

(Figure 5,  $p = 0.001$ ). This confirmed our third hypothesis. Moreover, nighttime CO<sub>2</sub> efflux was the higher under the increased soil moisture level (70% vs 100% WHC) for living and dead root mats (Figure 6). Soil moisture of living root mat was also higher than dead root mat. After the first rewetting at Day 11, CO<sub>2</sub> efflux of living and dead root mats increased. The CO<sub>2</sub> efflux of living root mat continued to increase from Day 11 to Day 13 ( $p = 0.04$ ), although soil moisture decreased.

### Leaching of C and N Related to Degradation Stages of *Kobresia* Pastures

The dying root mat had the highest DOC and DON concentrations in leachates compared with living and dead root mats (Figure 7, top and middle). This was consistent with our first hypothesis. However, the NO<sub>3</sub>

Table I. Distribution of carbon and nitrogen in pools of soil, root and microbial biomass

Root mats	Soil			Root			MBC (mg C g <sup>-1</sup> dry soil)	MBN (mg N g <sup>-1</sup> dry soil)
	N (%)	C (%)	C/N Ratio	N (%)	C (%)	C/N Ratio		
Living	0.52 ± 0.01 a	6.2 ± 0.3 a	11 ± 0.3 a	0.74 ± 0.0 a	41 ± 6.3 a	55 ± 7.6 a	1.2 ± 0.1 b	0.12 ± 0.02 a
Dying	0.37 ± 0.03 b	3.4 ± 0.4 b	9.1 ± 0.1 b	0.83 ± 0.1 a	41 ± 2.3 a	51 ± 7.8 a	1.6 ± 0.1 a	0.23 ± 0.03 a
Dead	0.37 ± 0.03 b	3.4 ± 0.4 b	9.1 ± 0.1 b	0.83 ± 0.1 a	41 ± 2.3 a	51 ± 7.8 a	0.86 ± 0.1 b	0.18 ± 0.03 a

Values with the same letters among root mats are not significantly different at the  $p < 0.05$  level (determined by a Tukey's HSD test). 'Living', 'Dying' and 'Dead' represent living, dying and dead *Kobresia* root mats, respectively. As living and dying root mats were taken from the same plot, initial C and N composition was considered to be similar.

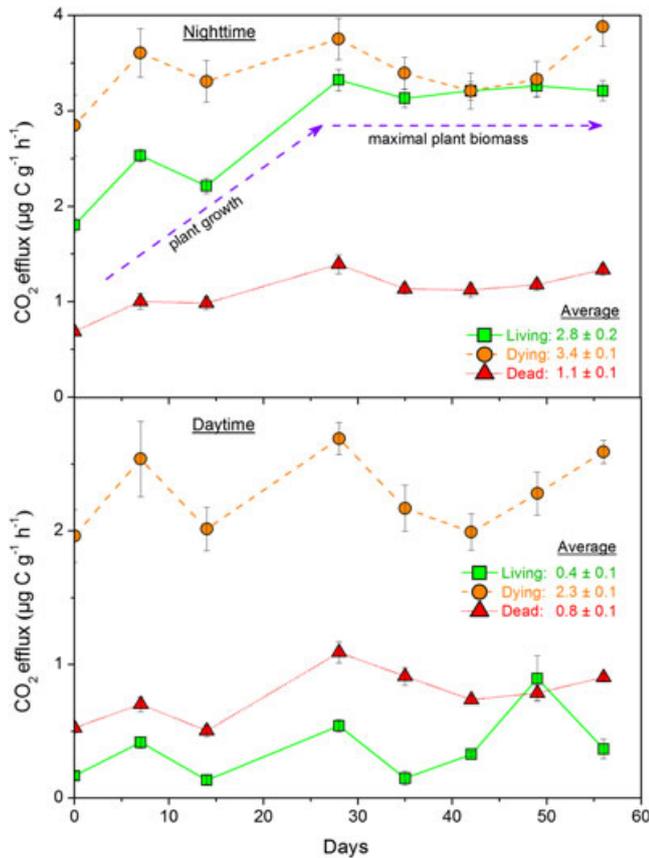


Figure 3. Nighttime (top) and daytime (bottom) CO<sub>2</sub> efflux of three *Kobresia* root mat types. 'Living' = living root mat; 'Dying' = dying root mat; 'Dead' = dead root mat. Error bars represent standard error ( $n=6$ ). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

concentration was highest from the dead root mat compared with the living and dying stages (Figure 7, bottom). It strongly decreased over time but was significantly higher throughout the experiment. The NO<sub>3</sub><sup>-</sup> concentration from the dying root mat was slightly higher than that of the living stage at the beginning and decreased to zero within the first 14 days. In contrast, no NO<sub>3</sub><sup>-</sup> was leached from the living stage (Figure 7, bottom). The NH<sub>4</sub><sup>+</sup> concentrations in leachates were very low (below the detection limit) for all three root mats. As we hypothesized, dying of *K. pygmaea* resulted in the highest DOM losses from the leaching; unexpectedly, dead root mat showed the highest NO<sub>3</sub><sup>-</sup> loss from leaching.

## DISCUSSION

### C Loss from Soil Respiration

The nighttime CO<sub>2</sub> efflux was highest from the dying, slightly lower from living and lowest from dead *Kobresia* root mat throughout the incubation period (Figure 8). In fact, the dead root mat had the lowest SOC content and consequently a lower C availability explaining the lower soil respiration rates. In contrast, the SOC contents were up to 1.8 times higher for living and dying root mats (Table I), indicating that the higher C-availability stimulated microbial

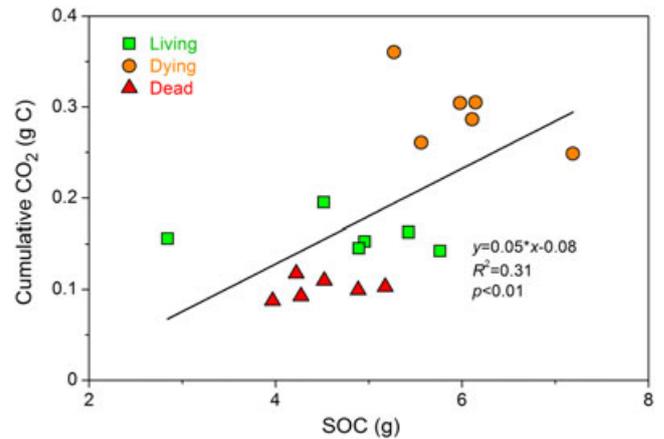


Figure 4. Correlation between cumulative CO<sub>2</sub>-C for all replicates and their final soil organic carbon (SOC) contents. 'Living' = living root mat; 'Dying' = dying root mat; 'Dead' = dead root mat. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

respiration (Cleveland *et al.*, 2007). This finding was supported by a positive correlation of cumulative CO<sub>2</sub>-C for all degradation stages and their SOC contents (Figure 4). The positive relation between MBC and nighttime CO<sub>2</sub> efflux also supported this finding (Figure 2, top).

The CO<sub>2</sub> efflux was slightly higher for the dying versus living root mat. This was especially pronounced in the first 4 weeks. We suggest that an additional supply of root litter following plant death was respired and slightly increased the CO<sub>2</sub> efflux to a constantly high level. However, the absence of living root biomass in the dying stage may have eliminated the competition between uptake by *K. pygmaea* and microbes for limited nutrients (i.e. nitrogen, Kuzyakov, 2002; Xu *et al.*, 2006). Therefore, the higher SOC and nutrient availability in dying root mat stimulated microbial growth and then increased heterotrophic respiration. In agreement with this, the highest microbial biomass C was detected for dying stage (Table I).

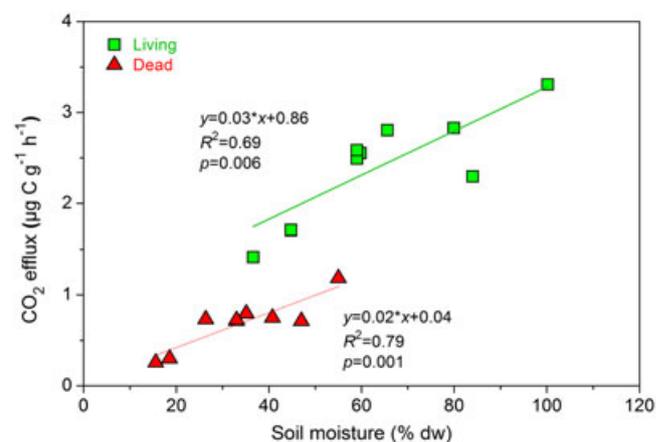


Figure 5. Correlation between soil moisture content (% dw) and nighttime CO<sub>2</sub> efflux during the second experiment. 'Living' = living root mat; 'Dead' = dead root mat. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

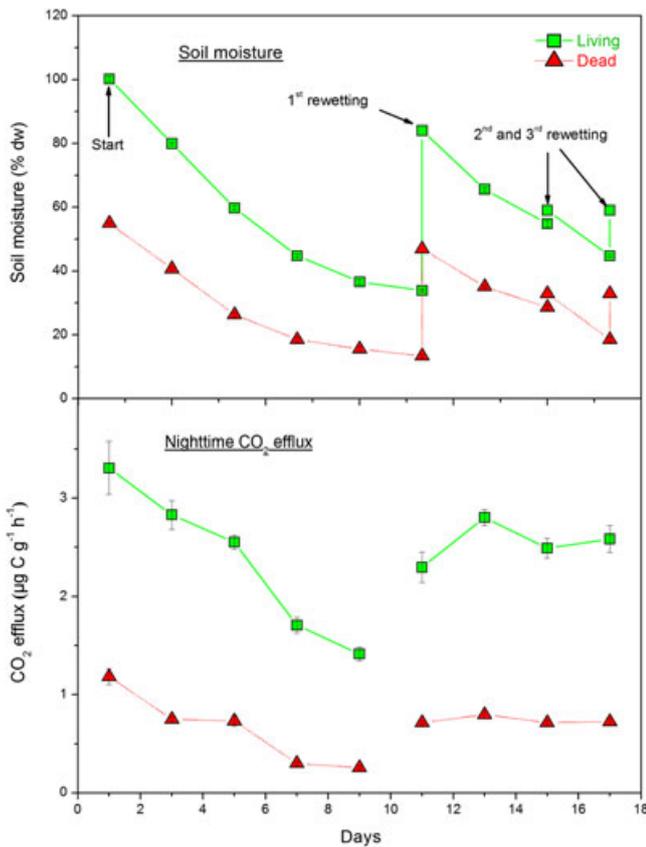


Figure 6. Change of soil moisture content (top) and response of nighttime CO<sub>2</sub> efflux (bottom) in living and dead root mats to increased moisture. 'Living' = living root mat; 'Dying' = dying root mat; 'Dead' = dead root mat. Soil moisture content is expressed as percent of dry weight (% dw). When the experiment started, samples were over-saturated. For the 1st rewetting, samples from living and dead root mats were rewetted to 84 and 47% dw, which correspond to 100% of WHC. For the 2nd and 3rd rewetting, their moisture were adjusted to 59 and 33% dw, which correspond to 70% of WHC. Error bars represent standard error ( $n=6$ ). [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

Nighttime CO<sub>2</sub> efflux from living root mat increased within the first 4 weeks because of the gradual growth of plant biomass. Respiration by living roots and shoots as well as microbial decomposition of root exudates contributed to a higher CO<sub>2</sub> efflux (Lehmeier *et al.*, 2008; Wild *et al.*, 2014). We argue that the release of exudates from living root biomass stimulated the microorganisms to decompose additional SOC ('priming effect', de Graaff *et al.*, 2014). However, after reaching the maximal shoot biomass the root respiration and the input of rhizodeposition remained stable (ca. 30 days, Peng *et al.*, 2010). This is because root exudation strongly depends on the photosynthetic assimilation during net primary production (Aulakh *et al.*, 2001). Thus, a constant input of root exudates explains the stable CO<sub>2</sub> efflux after Day 28.

#### Effects of Photosynthesis on CO<sub>2</sub> Losses

To consider for the photosynthetic C input with regard to SOC loss, we included daytime CO<sub>2</sub> efflux measurements and hypothesized that living root mat strongly mitigated C loss from *Kobresia* pastures. Daytime CO<sub>2</sub> efflux of living root mat was six times lower than that of dying stage

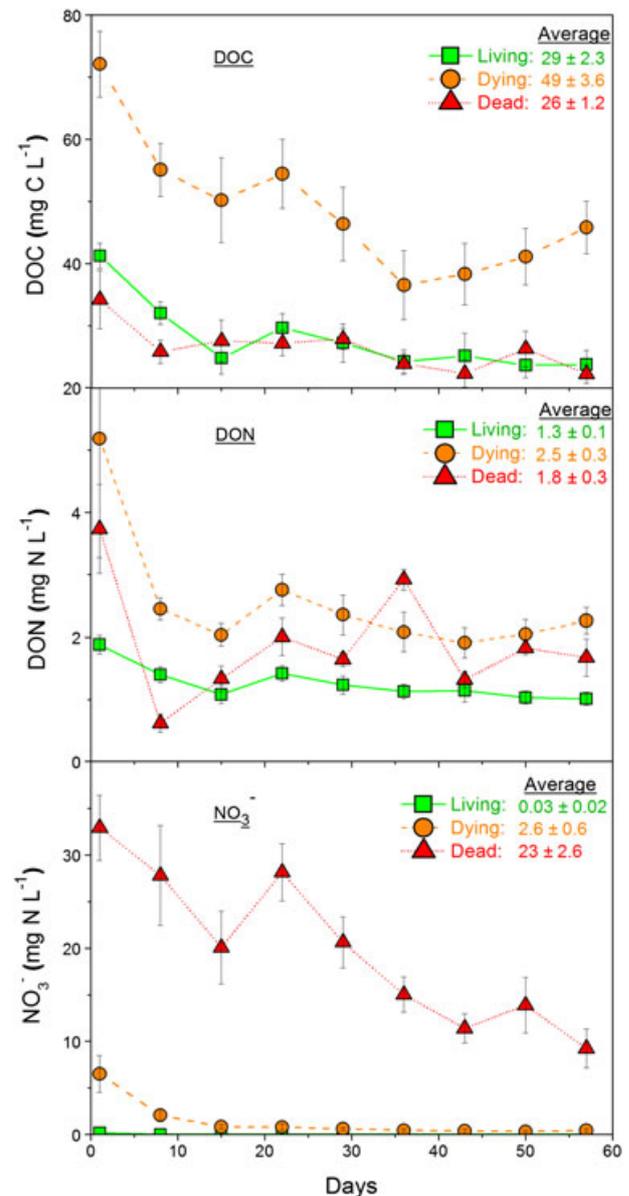


Figure 7. Concentrations of dissolved organic carbon (DOC) (top), dissolved organic nitrogen (DON) (middle) and NO<sub>3</sub><sup>-</sup>-N (bottom) in the leachate of three *Kobresia* root mat types during the leaching experiment. 'Living' = living root mat; 'Dying' = dying root mat; 'Dead' = dead root mat. Error bars represent standard error ( $n=6$ ). [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

because of CO<sub>2</sub> assimilation via photosynthesis. It mitigated the C loss from soil respiration compared with the dying and dead stages but did not totally prevent the switch from being a C sink to becoming C source. This is inconsistent with several other studies, demonstrating that alpine grasslands are considered to be C sinks due to the photosynthetic CO<sub>2</sub> fixation during the growing season (Peng *et al.*, 2014; Ingrisch *et al.*, 2015). We suggest that the increased soil moisture and the constant high temperature (20°C in this study) stimulated soil respiration. In fact we found that the nighttime CO<sub>2</sub> efflux increased during plant growth within the first 4 weeks, whereas the daytime CO<sub>2</sub> efflux remained on a constant low level for the living stage (Figure 3). It demonstrates that

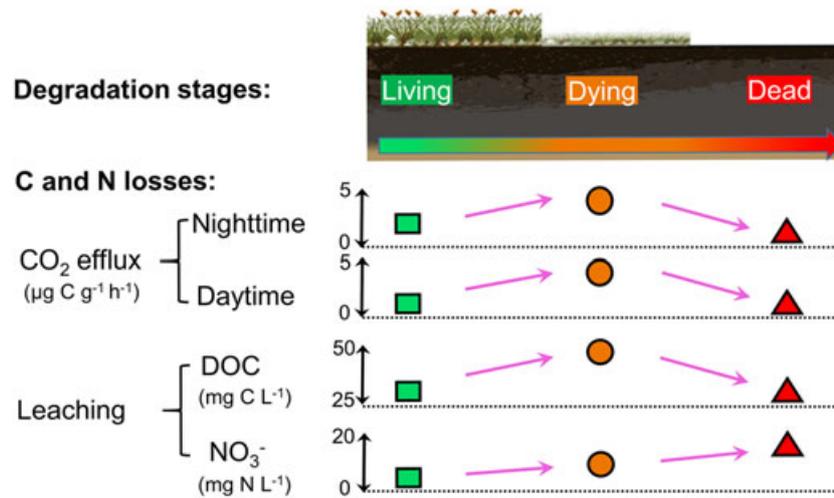


Figure 8. Conceptual diagram of C and N losses from *K. pygmaea* pastures depending on degradation stages. C loss as CO<sub>2</sub> emission and leaching was highest in dying root mat. This is mainly caused by the high initial root litter inputs after plant dying and the elimination of competition between plant and microbes for nutrient acquisition. N loss from the leaching of dead root mat was the highest compared with other root mats. We argued that NO<sub>3</sub><sup>-</sup> accumulated in the dead root mat during long-term decomposition in the field and later was leached by water amendments. 'Living' = living root mat; 'Dying' = dying root mat; 'Dead' = dead root mat. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

the increasing CO<sub>2</sub> uptake during plant growth was offset by a higher CO<sub>2</sub> release from soil respiration (Suter *et al.*, 2002).

#### Soil Respiration as Influenced by Soil Moisture

The effect of changing soil moisture on soil respiration (nighttime CO<sub>2</sub> efflux) for living and dead root mats was tested in the second experiment. Soil moisture was positively correlated with nighttime CO<sub>2</sub> efflux for living and dead root mats, indicating that increasing moisture enhanced SOC decomposition. Therefore, the expected increase of precipitation on the Tibetan Plateau (Xu *et al.*, 2008) is assumed to trigger additionally C and N losses from *Kobresia* pastures. This implies that the intact *Kobresia* pastures are at risk to become a C source by increasing precipitation rates, which accelerates the pasture degradation (Babel *et al.*, 2014).

Degradation from living to dead root mat is accompanied with a decrease of the plant biomass (especially the root biomass: 4.2 kg m<sup>-2</sup> for living and 2.5 g m<sup>-2</sup> for dead root mat). Consequently, it enhances the soil bulk density in this root-dominated soil after root turnover, which thereby decreased the WHC (Wang *et al.*, 2003). Therefore, lower soil moisture was observed for the dead root mat when we adjusted soil moisture to 100% of WHC (Figure 6, top).

Surprisingly, nighttime CO<sub>2</sub> efflux from living root mat continued to increase between Day 11 and Day 13, although soil moisture already decreased. This can be explained by the time lag for transporting photosynthetic assimilates from shoots to roots (Hill *et al.*, 2007). This time lag delayed the stimulation of root exudates to soil respiration and ultimately caused a delayed response of nighttime CO<sub>2</sub> efflux. This lag was longer than that for most other grassland ecosystems (Kuzuyakov & Gavrichkova, 2010).

When soil moisture was kept at around 100% dw on the first day, nighttime CO<sub>2</sub> efflux remained at a relatively high

level for living and dead root mats (Figure 6). This contrasted to some studies showing that SOC decomposition and CO<sub>2</sub> production decreased under a high soil moisture level because oxygen diffusion into the soil was inhibited (Tang *et al.*, 2006; Ganjurjav *et al.*, 2014). The *Kobresia* root mats, however, have very low bulk density (around 0.8 g cm<sup>-3</sup> for living and dead root mats, 1.1 g cm<sup>-3</sup> for dead root mat) and with a large pore system so that O<sub>2</sub> diffusion was not hindered in our study.

#### C and N Loss from Leaching

Dissolved organic matter (DOM) leaching was highest from dying root mats compared with living and dead root mats. This confirmed our hypothesis regarding highest C and N losses from dying root mat via leaching. We suggest that the strong decomposition of insoluble organic matter, especially of dying root mat, resulted in an enrichment of low-weight and high-weight molecular substances. Low molecular weight components of DOM will be very rapidly taken up or respired by microorganisms (Fischer *et al.*, 2010), whereas the high molecular weight pool with much lower turnover rates becomes the major source for DOM (Jones *et al.*, 2004). This explained why the dying stage showed far higher DOC losses (Figure 2, bottom).

The highest NO<sub>3</sub><sup>-</sup> losses were observed from dead root mat (Figure 8). This partly contradicted our first hypothesis about the highest N loss from dying root mat. We suggest that NO<sub>3</sub><sup>-</sup> accumulated in the dead root mat during long-term decomposition of organic matter in the field and later was leached by water amendments. To a minor contribution, it is also possible that N<sub>2</sub> fixation by lichen-dominated crusts increased the N transfer into soil (Neff *et al.*, 2005). In contrast, leaching of NO<sub>3</sub><sup>-</sup> from living root mat was always close to zero and only slightly higher for dying root mat in the first few days. We suggest that direct NO<sub>3</sub><sup>-</sup> uptake by living plants or immobilization by microorganisms significantly decreased the NO<sub>3</sub><sup>-</sup>

concentration in the soil during plant growth in the living stage (Von Wirén *et al.*, 1997; Xu *et al.*, 2011). Besides, mineralization of soil organic matter or organic N released by plant residues, which then was converted to  $\text{NH}_4^+$  (ammonification, Harmsen & Van Schreven, 1955). Then the released  $\text{NH}_4^+$  was rapidly taken up by plants and microbes preventing its transformation to  $\text{NO}_3^-$  (nitrification, Harmsen & Van Schreven, 1955). In fact, no  $\text{NH}_4^+$  was leached from the living stage confirming that  $\text{NH}_4^+$  uptake likewise lowered  $\text{NO}_3^-$  concentration in the living stage and consequently decreased N losses from leaching. The decreasing C/N ratio in the microbial biomass from the living ( $C/N_{\text{Living}}$ : 9.4), dying ( $C/N_{\text{Dying}}$ : 7.3) and dead stage ( $C/N_{\text{Dead}}$ : 4.9) also supported this finding. The C/N ratio of the microbial biomass in the living stage was 1.3 and 1.9 times higher than that of the dying and dead stage, respectively. It clearly demonstrates that N gets limited for microorganisms in the presence of living plants reflecting efficient plant uptake of  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . Although plant N uptake was not present in the dying and dead root mat (no living plants),  $\text{NH}_4^+$  leaching did not increase compared with the living stage (dying and dead stages:  $\text{NH}_4^+$  concentration close to zero). The *Kobresia* root mats are well aerated and nitrifying bacteria are abundant in the upper soil compared with that in subsoil (Guan *et al.*, 2013). Consequently,  $\text{NH}_4^+$  will be immediately converted to  $\text{NO}_3^-$ . Therefore  $\text{NO}_3^-$  accumulated in the dying and dead stage and consequently higher  $\text{NO}_3^-$  leaching was observed ( $\text{NO}_3^-$  leaching: dead > dying).

### CONCLUSIONS

The dying root mats showed the highest C losses from: decomposition of SOC and roots ( $\text{CO}_2$  efflux) and leaching of DOM. The dying of *K. pygmaea* provided more labile C to microorganisms because of the high initial root litter inputs after plant dying. It indicated that the initial dying of *K. pygmaea* will rapidly convert pastures to a C source. However, photosynthesis of *Kobresia* shoots in living root mat mitigated the respiratory C losses and consequently prevented *Kobresia* pastures from becoming a C source. Highest  $\text{NO}_3^-$  losses from dead root mat were mainly caused by long-term  $\text{NO}_3^-$  accumulation during SOC decomposition in the field and then flushed by leaching. Consequently, the increasing precipitation on the TP, as predicted with climate change, will enhance N losses. This induces a negative feedback, because N is often a limited nutrient in alpine grasslands and so, reduces the potential of *Kobresia* pastures to recover from degradation.

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