The Kobresia Pastures on the Tibetan Plateau:
Degradation Processes and Consequences for Carbon and Nutrient Stocks

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Summary

The *Kobresia* grasslands represent the world's largest pastoral ecosystem, covering about 450,000 km² on the eastern Tibetan Plateau. The vegetation is dominated by an endemic sedge (*Kobresia pygmaea*), forming a lawn with a very durable, felty root mat, which occurs from 3000 to nearly 6000 m a.s.l.. The *Kobresia* ecosystem supports the livelihood of the Tibetan herders, for whom it is an essential grazing ground. Furthermore, it hosts tremendous terrestrial biodiversity and stores large amounts of soil organic carbon (SOC) and nutrients. This unique ecosystem has, however, slightly been investigated in relation to the backdrop of natural and anthropogenic factors that affect it. As such, its origin, drivers, vulnerability or resilience, as well as its likely future development remain largely unknown.

This study focuses on the development and degradation of the *Kobresia* ecosystem. It is divided into four main parts, which correspond to the objectives (I. *Adaptation*, II. *Vulnerability*, III. *Degradation*, IV. *Consequences*). The first objective was to elucidate mechanisms making *K. pygmaea* highly competitive and the predominant plant species on the eastern Tibetan plateau. It was expected that species-specific plant traits enabled non-evolutionary adaptations to biotic and abiotic stresses such as long-term moderate grazing pressure and recurrent N and P limitation. Within the second objective it was expected that recent management intensification and a transition from a migratory to a sedentary grazing system have caused disadvantages to former adaptations and harmed this pastoral ecosystem. This mainly includes an (over)grazing-induced disturbance of the above and belowground plant trade-off in terms of photosynthetic CO_2 assimilation and belowground resource uptake (i.e. nutrients and water). The third objective was a mechanistic explanation of the recurrent degradation patterns that are common across the whole ecosystem. Degradation concepts were developed to explain the formation of polygonal cracks and bare soil patches as well for crust-covered dead root mats. Finally, the fourth objective was to quantify the consequences of degradation in terms of SOC and nutrient losses, assuming that these were mainly caused by soil erosion, organic matter mineralization and leaching.

This PhD thesis has identified certain mechanisms for efficient nutrient acquisition by *Kobresia pygmaea* that partly explain its dominance on the eastern Tibetan plateau. These include the development of a dense root network to take up nutrients very efficiently at the times and depths that they are available. Nutrients such as N and P often limit plant growth in the *Kobresia* ecosystem and therefore the high belowground investments are an important mechanism to overcome resource limitations. However, supporting the large root biomass (ca. 6 kg DM m^{-2}) involves high belowground C maintenance costs that must be covered by the comparatively low amount of photosynthetically active shoots (ca. 0.3 kg DM m^{-2}). The high root:shoot biomass ratio of 20 indicates that the efficient above- belowground trade-off might be vulnerable to increasing grazing intensities. Indeed, at the Kema research sites (alpine *Kobresia* pasture), (over)grazing decreased C allocation to belowground plant compartments compared to sites that had been ungrazed for three years. It means that a permanent removal of the shoot biomass leads death of the *Kobresia* turf, because the belowground C-costs cannot be maintained. Therefore, the large population that is dependent on livestock, the increasing stocking rates and the diminishing availability of quality grazing grounds due to degradation make it likely that degradation will be intensified in coming decades. It is estimated that about 30% of the *Kobresia* ecosystem has already suffered from degradation, mainly taking the form of (a) polygonal cracks and bare soil patches and (b) dead *Kobresia* root mats. However, the drivers and mechanisms of this degradation are not often considered. This thesis provides new mechanistic understanding of ecosystem degradation due to combined anthropogenic and natural impacts. Man-made changes (mainly via overgrazing) and their amplification by harsh environments (i.e. freeze-thaw, soil drought, and soil erosion) cause plant death, accelerate SOC mineralization, induce erosion, and increase element leaching. A literature review on degradation studies in this ecosystem revealed that these processes have caused high losses of C, N and P. For instance, on the Kema research site, up to 7.5 kg C m^{-2}, 0.63 kg N m^{-2} and 0.062 kg P m^{-2} had been lost from the most degraded stage compared with the intact stage.

In sum, it was concluded that high C and nutrient losses have far-reaching consequences for *Kobresia* pastures including several ecosystem functions and services from landscape to global scale. Degradation has decreased soil fertility and pasture quality on the landscape scale and therefore jeopardizes the livelihood of the Tibetan herders. The fates of lost elements remain unknown, but it is likely, that (a) very large amounts of C are released as CO_2 to the atmosphere and (b) that elements are deposited to subjacent landscape positions and rivers, polluting the Tibetan headwaters. Moreover, increased degradation affected carbon allocation and strongly reduced carbon uptake. Consequently, the best approach to maintain carbon storage, soil fertility and other important functions of this vulnerable *Kobresia* ecosystem is to lower livestock densities by limiting numbers, and perhaps more importantly improve mobility of livestock activities. This was the status quo for the traditional migratory rangeland management, which proved sustainable for millennia.

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Abbreviations

AGB	aboveground biomass
ANOVA	analysis of variance
a.s.l.	above sea level
BGB	belowground biomass
C	carbon
DM	dry matter
DOC	dissolved organic carbon
DOM	dissolved organic matter
DON	dissolved organic nitrogen
DRB	dead root biomass
KEMA	*Kobresia* ecosystem monitoring area
KP 2009	*Kobresia pygmaea* site fenced in 2009
KP 2010	*Kobresia pygmaea* site fenced in 2010
LRB	living root biomass
LRD	living root density
LSD	least significant differences
MLRA	multiple linear regression analysis
N	nitrogen
N_{inc}	nitrogen incorporation
N_{upt}	nitrogen uptake
P	phosphorus
R/S	root to shoot ratio
SOC	soil organic carbon
SOM	soil organic matter
SRA	specific root activity
TRB	total root biomass
TP	Tibetan Plateau
VSC	lignin monomers vanillyl, syringyl, and cinnamyl

1.Extended Summary

1.1 Introduction

1.1.1 Global change and grassland ecosystems

Human activities in the form of intensified fossil fuel burning and land-use change contribute greatly to the destabilization of several Earth systems, which especially matters in terms of biodiversity loss, ongoing climate change, and the interference with the global carbon (C) and nitrogen (N) cycles (Rockstrom *et al.* 2009). Grasslands play a key role in mitigating these changes, as they cover up to 30-40% of the world's terrestrial land surface (White *et al.* 2000; O'Mara 2012) and store large amounts of C and N (Scurlock *et al.* 2002). Furthermore, they harbor large parts of the terrestrial biodiversity (White *et al.* 2000) and provide the basis for livestock farming. It is estimated that about one billion people, mostly in the world's vulnerable regions, depend on livestock for their livelihood and food security (Neely *et al.* 2009; O'Mara 2012; White *et al.* 2000). However, grassland functions are increasingly impaired by human-induced impacts such as overgrazing, cultivation, climate change, fire, and species invasions (White *et al.* 2000). It is estimated that roughly 16% of the world´s rangelands are already affected by degradation (FAO 2010) and consequently several ecosystem services are jeopardized, endangering human well-being.

This study focuses on grassland degradation on the Tibetan Plateau. The Tibetan Plateau (TP) is the highest plateau on earth with an average altitude of 4,000 m a.s.l. (Lu *et al.* 2004), and comprises up to 3% of the world's grasslands, overall 1.5 million km² (Ma *et al.* 2016). The main ecosystems are the alpine steppe biome and the *Kobresia* ecosystem (Babel *et al.* 2014), which is the world's largest pastoral alpine ecosystem (ca. 450,000 km², Fig. ES-1, Miehe *et al.* 2008).

1.1.2 Development and relevance of the *Kobresia* pastures

The *Kobresia* ecosystem occurs across an area roughly 200 km in width and 2000 km in length, on the eastern Tibetan Plateau (Babel *et al.* 2014). A single plant species dominates in this ecosystem, *Kobresia pygmaea,* thus it is justified to simply speak of the *Kobresia* ecosystem. This ecosystem faces pressures from a set of abiotic factors that limit the net primary production (Berdanier & Klein 2011). In particular, these include the low mean annual temperature (~ -2°C – +3°C, Miehe *et al.* 2008) and precipitation (~ 300 mm – 500 mm, Miehe *et al.* 2008), the short vegetation period (~ 3 months), high solar radiation, and nutrient deficiency (Callaway *et al.* 2002; Körner 2003; Hermans *et al.* 2006)

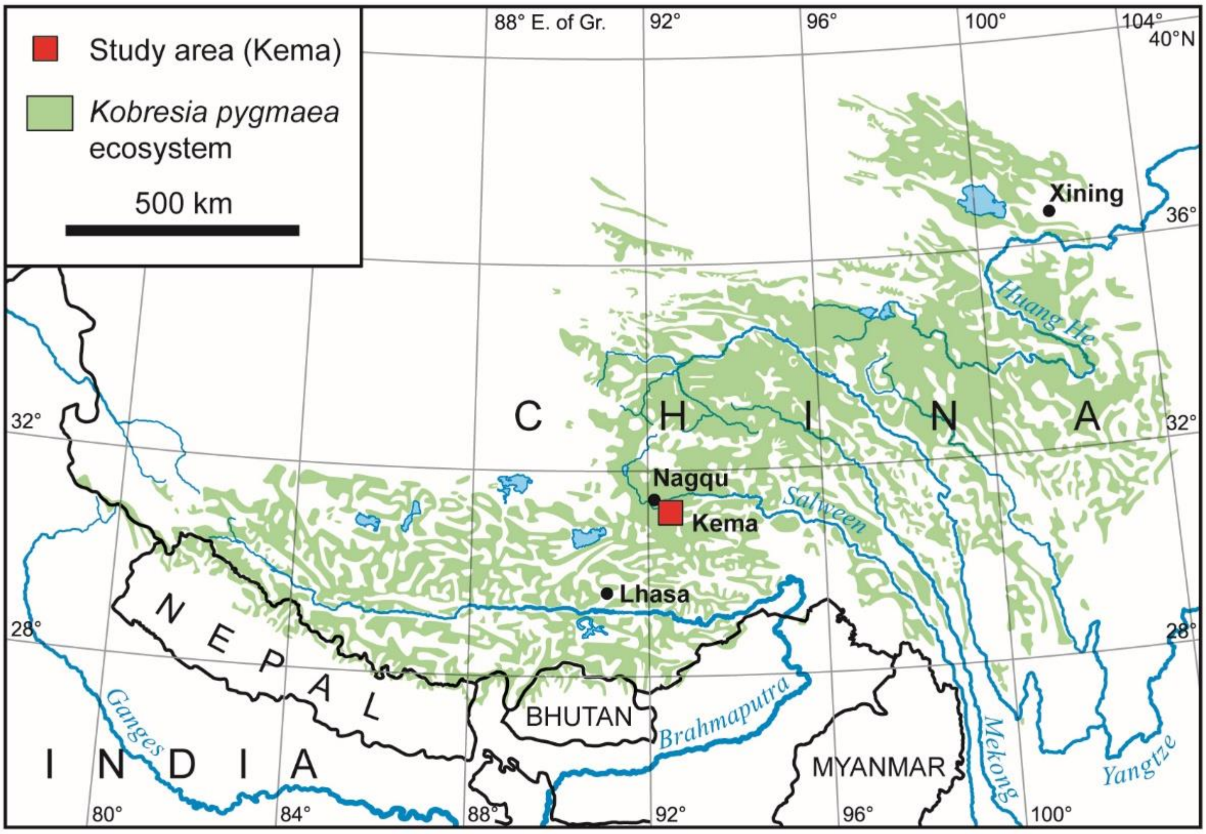

Figure ES-1: The distribution of the *Kobresia* ecosystem on the Tibetan Plateau. The red square indicates the location of the Kema study site, where field work was carried out. Cartography: C. Enderle, Data source: Miehe *et al.* 2008.

Nitrogen often limits net primary production in terrestrial ecosystems (Vitousek & Howarth 1991; LeBauer & Treseder 2008), and variations in N availability can therefore have large impacts on plant growth and ecosystem recovery, especially in ecosystems such as alpine grasslands (Xu *et al.* 2014). Nitrogen limitation is mainly due to low deposition rates, a high proportion of immobilized N in organic form, and a low N mineralization and N fixation rate caused by low temperature and a short vegetation period (Wang *et al.* 2005; Xu *et al.* 2006; Lü & Tian 2007; Liu *et al.* 2011; Zhang *et al.* 2012). Moreover, the dung of the main herbivore, the yak, is completely collected by nomads and serves as their only fuel source (Rhode *et al.* 2007). Alpine plants compete under these stressful conditions by developing specific strategies to ensure survival and reproduction (Choler 2005; Onipchenko *et al.* 2009).

Livestock grazing is an additional stress factor in many alpine ecosystems. Paleo records and pollen analysis indicate a grazing-induced origin for this ecosystem more than 8000 years ago, and at least since the domestication of the yak, 7500 years ago (Miehe *et al.* 2014; Qiu *et al.* 2015). This has favored plants that are highly adapted to livestock grazing. The specific growth form of *K. pygmaea*, near the ground level and the small height (~2 cm), often prevents complete removal of the shoot biomass during grazing. At the same time, it does not hinder fruiting, since *K. pygmaea* is able to fruit in dwarf heights of 1 to 2 cm (Miehe *et al.* 2008). As germination rates of *K. pygmaea* are generally low (i.e. Miao *et al.* 2008; Huang *et al.* 2009; Seeber *et al.* 2016), propagation occurs mainly vegetatively in the form of clonal growth (Deng *et al.* 2001; Seeber *et al.* 2016). The clones can extend over several square meters (probably more, Seeber *et al.* 2016), meaning that partial overgrazing does not ultimately lead to the death of a single individual. Overall, it is expected that the adaptation to recurrent abiotic and biotic stress factors over the past millennia has caused the development and wide distribution of the *Kobresia* ecosystem, which is of undisputed importance for several ecosystem services from local to global scale.

On the Tibetan plateau, roughly 5 million pastoralists rely on livestock products from 12 million yaks and 30 million goats and sheep (Suttie et al. 2005). The *Kobresia* pastures provide the main forage resources (Seeber 2015) and are consequently important as grazing grounds, ensuring the livelihood of the Tibetan herders. The *Kobresia* ecosystem partly controls the regional water cycle and thus the regional climate system (Boos & Kuang 2010).

It is the source of some of the largest rivers of South-East Asia, such as the Huang He, Yangtze, Salween and Mekong (Fig. ES-1). These rivers provide water security for one quarter of the world´s population living in the surrounding lowlands. Furthermore, this ecosystem provides a tremendous sink for carbon, nitrogen and biodiversity (Wang *et al.* 2008b). For instance, up to 10 kg C m^{-2} and 1 kg N m^{-2} are stored in the upper 30 cm of soil and are thus sequestered from the atmosphere (Gao *et al.* 2009; Ingrisch *et al.* 2015). This is roughly 2-3 times higher than the global average (Batjes 1996; Wang *et al.* 2002).

1.1.3 Degradation of the *Kobresia* pastures

The *Kobresia* pastures are intensively affected by grassland degradation (Harris 2010; Wang & Wesche 2016). For this study, grassland or pasture degradation is defined as a process of grassland deterioration and a decrease of forage production caused by disadvantageous natural factors and improper utilization (Liu *et al.* 2006). It is estimated that 30-60% of the *Kobresia* grasslands are moderately to severely degraded (Holzner and Krichenbaum 2001). For instance, most pastures are degraded in the Nagqu district (study region), where up to 90% under medium degradation stage (Wei *et al.* 2004). However, these numbers have to be treated with caution, as they often rely on inconsistent definitions, use different indicators for surveys, and include different temporal and spatial scales (Wang & Wesche 2016). Nevertheless, degradation patterns are diverse and widely distributed over the entire Tibetan Plateau, yet they are seldom mechanistically explained or even classified. Most researchers attribute the degradation of *Kobresia* pastures to overgrazing (Wei & Xiaobu 2008; Lin *et al.* 2015) because the grazing intensity has increased over the last fifty years (Zhou *et al.* 2005). This, on the one hand, has caused direct trampling damages and on the other hand has led to a permanent removal of the photosynthetically active biomass. Together with the harsh environmental conditions (i.e. low temperature, dry spells, heavy rain events, high wind speed, sloping landscape, snow cover, high radiation, low CO_2 partial pressure, nutrient and water limitation, (Callaway *et al.* 2002; Körner 2003) it places pressure on the ecosystem and reduces plant growth and productivity. In particular, the repeated drying/rewetting and freezing/thawing cycles lead to soil contraction and expansion, gradually cracking the *Kobresia* turf and amplifying pasture degradation. In addition, ongoing climate change is expected to exacerbate pasture degradation (Du *et al.* 2004). For instance, the annual mean temperature is predicted to increase by about 1.8°C in the next five decades and might stimulate the decomposition of already degraded *Kobresia* turf (Wang *et al.* 2008a). Precipitation predictions, however, do not show a clear trend, except for increasing variability (Zhai *et al.* 2005). This means a higher risk of extreme dry and wet years and thus amplifications of freeze and drought impacts.

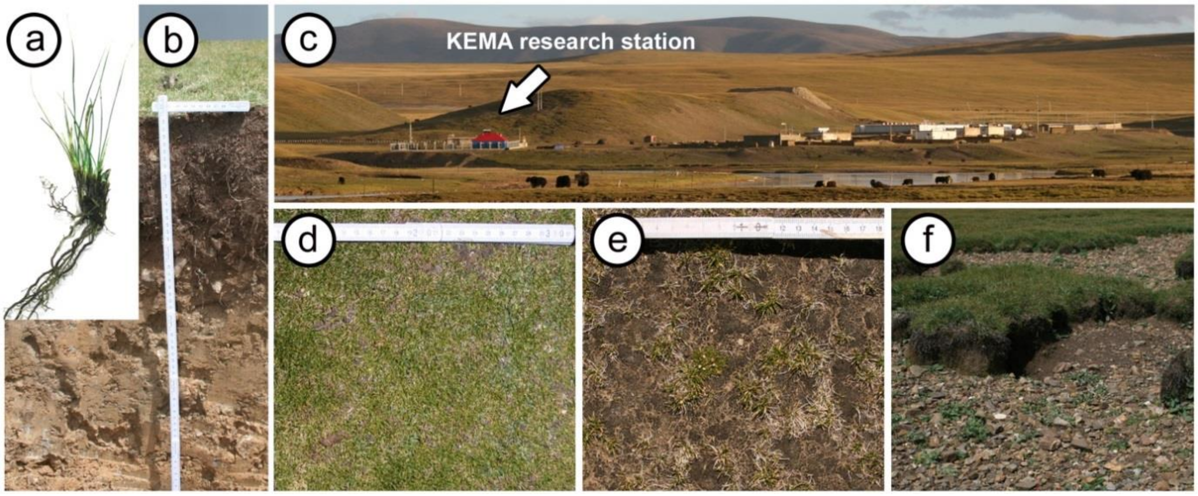

Figure ES-2: Overview of the *Kobresia* ecosystem and common degradation pattern. A single *Kobresia pygmaea* plant **(a)**, *Kobresia* develops dense root mats **(b)** and is the dominant species on the KEMA study sites **(c, d)**. The most common degradation patterns are crust-covered dead root mats (**e)** and polygonal cracks and bare soil patches **(f)**.

1.2 The Kobresia cluster

This work was part of the Priority Programme 1372 “Tibetan Plateau: Formation, Climate, Ecosystems (TiP)” and financed by the German Research Foundation (DFG). Within the subproject “The making of a Tibetan landscape” the focus was on the status and dynamics of the *Kobresia* ecosystem. This includes contributions from a multidisciplinary research group, termed the Joint *Kobresia*-Cluster (Fig. ES-3).

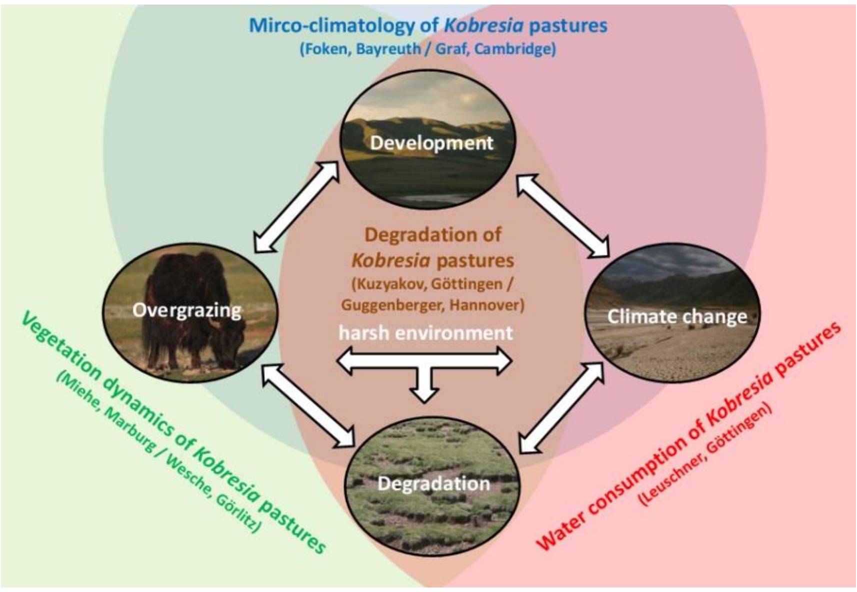

Figure ES-3: Overview of the working groups within the *Kobresia* research cluster and its main research tasks. This overview was implemented from the perspective of the soil science group, which is the reason why it is presented in the center.

It comprises scientific cooperations in China and Germany. Altogether this subproject covers a wide range of ecological issues such as plant biogeography, plant species genetics, plant physiology, life traits, grazing ecology as well as changes in biogeochemical cycles from local to landscape scale.

Botanical traits (i.e. plant morphology, reproduction, genetic diversity) as well as physiological traits (regulation of the water cycle, adaptation to a seasonally dry and cold environment, resistance to high solar radiation) were primary investigated by colleagues from related disciplines from the University of Marburg (research group focusing on plant biogeography, G. Miehe), Senckenberg Museum Görlitz (research group focusing on botany, K. Wesche), University of Göttingen (research group focusing on plant physiology, C.

Leuschner) and University of Bayreuth (research group focusing on micro-meteorology, T. Foken). This study mainly focuses on the degradation of the *Kobresia* pastures and its response in terms of SOC and nutrient stocks. The cooperation of several research disciplines helped to revise recent findings on the environmental history since the Late Quaternary, particular plant traits favoring the development of this specific ecosystem, as well as current impacts caused by climate and land-use changes.

1.3 Objectives

This PhD thesis was embedded in the DFG subproject "Degradation and Development of *Kobresia* root mats and their effects on C and N turnover and C sequestration". Evaluation of degradation mechanisms requires profound knowledge about the development of this pastoral ecosystem. Hence, this thesis is divided into four main parts, representing the main objectives (Fig. ES-4), which are outlined in detail below.

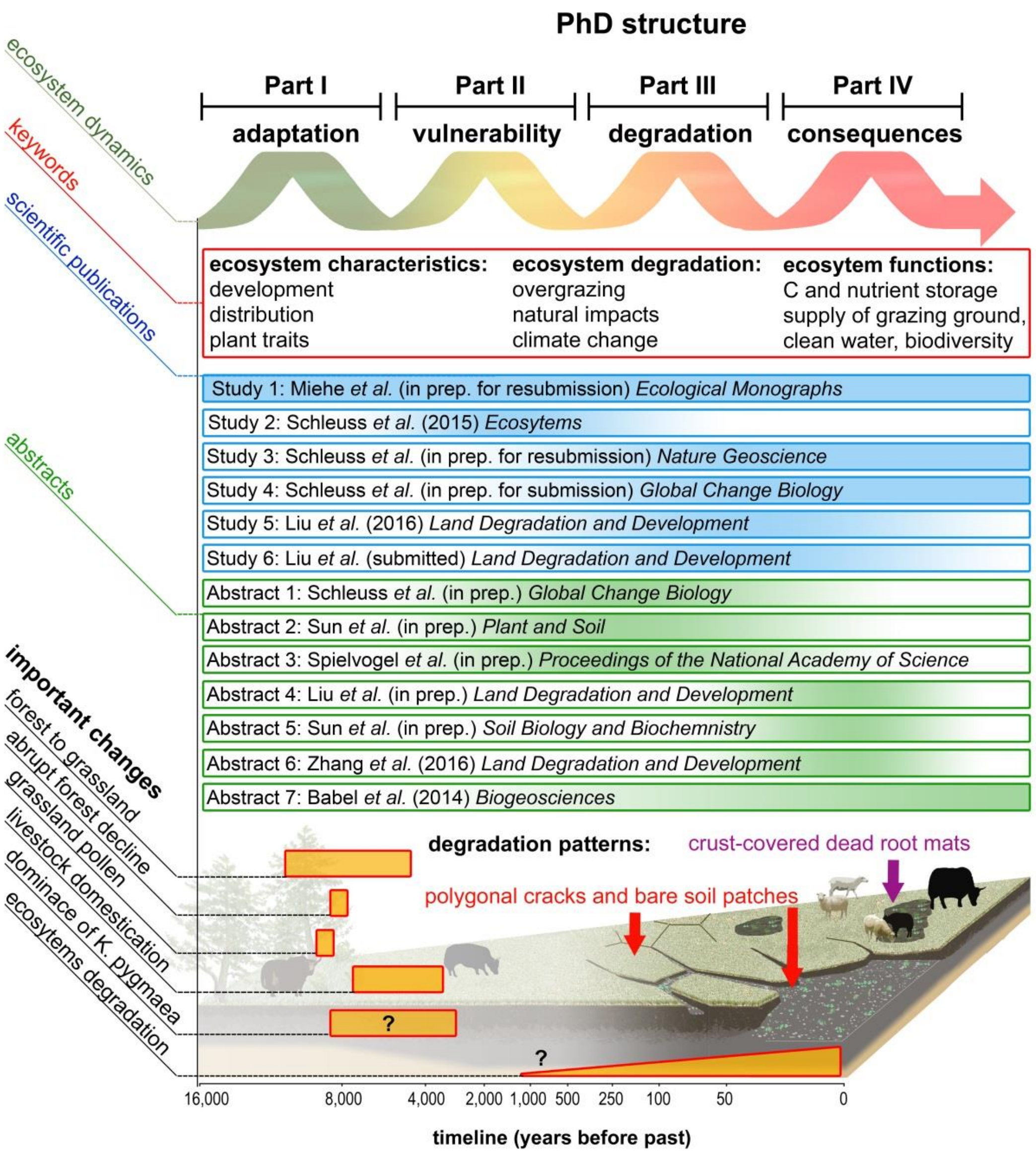

Figure ES-4: Schematic overview and structure of this PhD thesis. Publications and manuscripts (blue) as well as abstracts of ongoing research (green). The colored shadings illustrate the main focus of the studies. Orange bars show main historical changes important for the formation of the *Kobresia* ecosystem and its degradation. Main degradation patterns affecting the entire ecosystem are (a) polygonal cracks and bare soil patches and (b) crust-covered dead root mats

1.3.1 Objective I: Adaptation of *Kobresia pygmaea* to biotic and abiotic stress

Plant growth on the Tibetan Plateau must withstand harsh environmental conditions, long-term livestock grazing and limited nutrients such as N and P. One species (*Kobresia pygmaea*) prevails in this ecosystem over a broad altitudinal and climatic range. A central idea was that specific plant traits make *Kobresia pygmaea* highly competitive and therefore might explain its broad distribution over the eastern part of the Tibetan Plateau. Among other traits, it was expected that *Kobresia pygmaea* makes high belowground investments and therefore has developed very dense root mats. This stores resources (i.e. assimilates) belowground, protecting them from grazing removal and ensures fast regrowth following grazing events. Second, we expect that the dense root network guaranties efficient resource uptake, helping to overcome the prevailing N and P limitations.

1.3.2 Objective II: Vulnerability of the *Kobresia* pastures to land use changes

Nevertheless, it was hypothesized that increased grazing intensity in recent decades had upset the balance in shoot-root ratio, making this ecosystem particularly vulnerable to pasture degradation. It was expected that a permanent removal of the photosynthetic active shoot biomass due strong grazing events lowers the allocation of C assimilates to sustain the high belowground carbon costs of the densely rooted *Kobresia* turf. Consequently, it impairs the sensitive above-belowground trade-offs with negative consequences for resource uptake (i.e. nutrients and water) and over the long-term should result in a patch wise dying of the *Kobresia* pastures.

1.3.3 Objective III: Degradation mechanisms of the *Kobresia* pastures

The *Kobresia* pastures are extensively degraded. However, details regarding the extent of degradation, drivers and processes are still poorly understood. Thus a main objective was to present conceptual frameworks to explain interrelated degradation processes, incorporating anthropogenic impacts and natural amplifications. It was expected that this concerns mainly to overgrazing, trampling, and climatic changes (increasing temperature and precipitation variability) while the most important natural contributors to degradation were drought, frost and erosion by wind and water. The most widespread patterns of degradation are (a) polygonal cracking, leaving surviving sods separated by extensive bare soil patches and (b) patch-wise dieback of the *Kobresia* turf, with lichens and algae covering the surface (Fig. ES-2).

1.3.4 Objective IV: Consequences of degradation for carbon and nutrient storage

The fourth objective was to explain and estimate high carbon and nutrient losses arising from degradation and to indicate the mechanisms beyond and their consequences. It was hypothesized that degradation has induced high element losses (C, N, P) due to mineralization, leaching, soil erosion and an overall disruption of element cycles (unbalanced in- and output). This was tested for the dominant degradation patterns: (a) for polygonal cracks and bare soil patches and (b) for crust-covered dead *Kobresia* root mats. Within in the last step it was attended to show the impacts of degradation on several ecosystem functions from local to global scale

1.4 Material and Methods

1.4.1 Study sites

Most of the studies were conducted in the Nagqu Prefecture of the Tibetan Autonomous Region (TAR) on sites of the *Kobresia* Ecosystem Monitoring Area (KEMA) (Fig. ES-1). The KEMA research station was established in 2007 by the University of Marburg and the University of Lhasa with support from the Volkswagen foundation, and is currently managed by the Institute of Tibetan Plateau Research (ITP). The sites are located in the core area of the *Kobresia pygmaea* distribution at 4510 m a.s.l., close to the village Kema, on a gentle north-west exposed slope (92°05`39``E, 31°16´17´´N). The village was founded in the 1980´s resulting in a strong increase of the grazing intensity since then (He & Richards 2015). Grazing is mainly by Yak and sheep but, a large number of small mammals (Plateau pikas, *Ochotona curzoniae*) compete for with livestock forage. The soil is classified as a Stagnic Eutric Cambisol (Humic, IUSS Working Group WRB 2014) and developed from a Holocene loess layer. The mineral soil consists of loam (mainly fine sand and silt) and has neutral pH values (pH in H_2O: 6-7). The topsoil is strongly rooted and forms a dense mat roughly 15 cm thick (*Kobresia* turf). It protects the soil from mechanical degradation such as trampling and erosion.

According to the Nagqu meteorological station (4507 m a.sl.) the mean annual temperature (1971-2000) is -0.9°C with 15.6°C (monthly mean) in the warmest month (July). The mean annual precipitation is 430 mm but can range between 210 and 440 mm. The rainfall strongly depends on the onset and end of the summer monsoon (Miehe *et al.* 2008). Accordingly, most of the rainfall occurs in the summer months between May and August (Babel *et al.* 2014; Ingrisch *et al.* 2015). Together, the precipitation and the temperature control the length of the vegetation period, which normally lasts from mid-May to mid-September (Miehe *et al.* 2008).

1.4.2 Research approaches

Investigations were primary implemented on two sites of the *Kobresia* Ecosystem Monitoring Area KEMA (Fig. ES-1) between June and September in 2012 and 2013. Grazing exclosure plots were established in 2009 in a spring pasture and 2010 in a year-round pasture for yak, sheep and goats (sites are termed KP-2009 site and KP-2010 site). These sites were selected according to the following criteria: (a) a predominance of *Kobresia pygmaea,* (b) homogeneous root mat and soil characteristics, (c) appropriate relief position enabling footprinting for eddy-covariance measurements, (d) accessibility and (e) grazing regime. This chapter gives a general overview of the field sites, sampling design and experiments, with a more detailed description in each individual study.

Research sites

The KP-2009 site is mainly used as spring pasture from April to June, with exceptional winter grazing in years with heavy snowfall, and therefore has a low grazing intensity throughout the growing season. The site is characterized by very dense coverage of *Kobresia pygmaea* (average about 61%, maximum 81%), interspersed with perennial herbs such as *Lagotis brachystachya*, *Lamiophlomis rotata*, *Lancea tibetica, Potentilla bifurca*, *Potentilla plumosa*, *Potentilla saundersiana* and *Thalictrum alpinum* and monocotyledons such as *Carex ivanoviae*, *Carex* spp., *Festuca* spp., *Kobresia pusilla*, *Poa* spp., *Stipa purpurea*, *Trisetum* spp. (Seeber *et al.* 2016). The limited presence of other plant species enabled a species-specific investigation of *Kobresia pygmaea* nutrition and other plant traits (investigated by cooperation partners, see previous chapter 1.2). In contrast, the KP-2010 site is characterized by a shallow soil and less precipitation and is thus drier. Thus, although the total species set is comparable to KP-2009, the vegetation community contains a higher proportion of grasses such as *Stipa purpurea* and *Elymus* spec. (E. Seeber, pers. communication). The site has a high grazing intensity throughout the year and therefore was used to identify grazing effects on N and C dynamics using stable isotope approaches.

Isotope studies

Stable isotopes (in this study, ^{13}C and ^{15}N) provide a powerful tool in soil biogeochemistry. Methods can be classified as tracer or natural abundance approaches (Fry 2007). Both approaches were used in this PhD study. ^{13}C tracer studies were carried out using enriched $^{13}CO_2$ inside labeling chambers. The ^{13}C label was chased through several plant and soil compartments to identify how C allocations changed depending on grazing regime (chapter

3.1). ^{15}N tracer, in the form of ^{15}N enriched urea, nitrate, ammonia or ammonia-nitrate, was injected into the upper soil horizons to identify mechanisms of *Kobresia pygmaea* N nutrition (Chapters 2.2; 3.1; 3.2) as well as the fate of organic and inorganic N in various compartments for intact and degraded *Kobresia* root mats (Chapters 2.6 and 3.6). Isotope recoveries were calculated using mixing models (i.e. % of total input or % of recovered at initial stage).

Natural abundance approaches are based on altered isotope ratios ($^{14}N/^{15}N$ or $^{12}C/^{13}C$) mainly due to kinetic fractionations, preferential losses or changing C and N inputs (Högberg 1997; Fry 2007; Werth & Kuzyakov 2010). Thus the changing isotope ratio is a suitable proxy to reflect relevant biogeochemical processes (chapter 2.2; 2.3, 3.1) .

Degradation sequences

Based on theoretical concepts, experimental approaches and field surveys, various degradation sequences were selected on the Kema research sites (KP-2009 and KP-2010). Here, the soil- and root-mat characteristics (i.e. soil type, soil texture, root mat thickness, above- and belowground biomass, bulk density, SOC and nutrient contents) had relatively low variability and offered a good opportunity for investigating degradation-induced impacts on SOC and nutrient losses and its driving processes. Chapters 2.3 and 2.4 provide a comparison of intact *Kobresia* turf vs. *Kobresia* turf with extending polygonal cracks vs. bare soil patches (S0 to S5); in Chapters 2.5 and 2.6: intact *Kobresia* turf vs. dying *Kobresia* turf vs. crust-covered *Kobresia* turf (living, dying, dead); in Chapters 3.5 and 3.6: intact *Kobresia* turf vs. crust-covered *Kobresia* turf; and in Chapter 3.7 the most common surface patterns of the *Kobresia* pastures: intact *Kobresia* turf vs. crust-covered *Kobresia* turf vs. bare soil patches.

Laboratory incubation experiments

Research in the Autonomous Region of the Tibetan Plateau is challenged by unfavorable conditions: calculability, accessibility of research sites, physical demands at high altitude, intermittent supplies of clean water and electricity, and poorly equipped laboratory facilities. To overcome these restrictions, samples were taken *in situ* (mainly from the KP-2009 site), transported to Göttingen and investigated with incubation experiments (Chapters 4.5, 4.6 and 5.4). This allowed the investigation of more sensitive and dynamic parameters such as microbial characteristics or quantities of organic and mineral N forms (i.e. DON, NO_3^-, NH_4^+).

1.5 General discussion and conclusions

1.5.1 Adaptations of Kobresia pygmaea to grazing pressure and N and P limitations

A central issue of the *Kobresia* research cluster was to explain the dominance and wide distribution of *K. pygmaea* on the Tibetan Plateau (Fig. ES-1). It was hypothesized that *K. pygmaea* has specific plant traits for coping with the moderate grazing pressure, nutrient limitations and other stress factors such as water stress and high radiation (not discussed here, see chapter 2.1.3.3). Co-limitations of N and P were confirmed by a meta-analysis of fertilization experiments (additions of +N, +P, +NP). It showed that aboveground biomass increased by ~ 30% following single additions of N and P, whereas combined N and P additions increased the aboveground biomass by ~50 to 100%, (chapter 2.1.6).

This study demonstrates that *K. pygmaea* has optimized C allocation in order to minimise resource limitation. Results of Ingrisch *et al.* (2014) showed that 70% of recently assimilated ^{13}C was allocated to roots 15 days after $^{13}CO_2$ pulse labelling. Of the belowground C allocation, about two-thirds and one-third were recovered in the soil horizons of 0-5 cm and 5-15 cm depth, respectively (Babel *et al.* 2014). This agreed well with results from the ^{15}N pulse labeling, where a high belowground investment and high ^{15}N recovery in the upper layer was observed (0–5 cm, chapter 2.2.4.1). Consequently, most recently assimilated C and N are incorporated into the root biomass and are therefore protected from grazing. This enables fast regrowth following grazing events. Overall, the high belowground investments cause the development of a dense root-mat (chapter 2.2.5.1). This protects the soil from trampling and erosion, lowering the potential for grassland degradation. The formation of dense root networks also ensures an efficient uptake of resources: up to 60-70% of ^{15}N was recovered in plant biomass after 45 days (chapter 2.2.4.1). The efficient recapture of N at times and depths when it is available is crucial in this partly N-limited ecosystem, because other plant species and microbes compete for the same resources. Kuzyakov & Xu (2013) demonstrated that once the root biomass exceeds 4 kg m^{-2}, plants can outcompete microbes for nitrogen uptake. The root biomass of *Kobresia* pastures ranges between 3-6 kg m^{-2}, indicating very efficient N uptake and a competitive advantage for plants over microorganisms. In summary, the formation of a dense root network (a) protects against physical impacts, (b) stores resources beyond the reach of grazers, (c) provides a fast regrowth following grazing events, (d) ensures an efficient N uptake (shown for ^{15}N) and (e) provides a competitive advantage for nutrient uptake over other plants and microbes.

1.5.2 Vulnerability of Kobresia grasslands to land use change

The enormous root biomass of 3 to 6 kg m^{-2} carries high C maintenance costs, which must be covered by comparatively small amounts of photosynthetically active aboveground plant parts (0.1 to 0.3 kg m^{-2}). The very high R/S ratio therefore indicates that the C balance of *Kobresia* pastures might be critical and vulnerable to overgrazing (chapter 2.2.5.2). A ^{13}C pulse labeling experiment indicated that strong grazing decreased belowground input of recently assimilated C compared to ungrazed sites (three years after grazing exclosure, chapter 3.1). Thus continuous removal of the shoot biomass under high grazing pressure reduces the supply of assimilates to sustain the root biomass. If this happens too frequently, the large belowground carbon costs cannot be covered, leading to death of the root biomass (Trlica & Rittenhouse 1993; McSherry & Ritchie 2013). In turn, this is likely to reduce uptake of nutrients and water, causing a feedback effect that further impacts the aboveground photosynthetic biomass. This agreed with a lower ^{15}N recovery in the shoot biomass in grazed versus ungrazed sites. In contrast, there were no differences in ^{15}N recovery for the root biomass (chapter 3.1). This presumably indicates that this particular site could still recover, if grazing intensity were to be reduced. However, a fourfold increase in livestock numbers in recent decades (Zhou *et al.* 2005) make decreased grazing intensities unlikely. It was concluded that the increasing grazing pressure is an important driver leading to plant death, the disappearance of *Kobresia* cover and its turf-forming root mats. In combination with naturally occurring forces (dry spells, extended frost periods) it puts this ecosystem under immense pressure and contributes to large-scale grassland degradation (chapter 2.1.7; 2.2.5.3; 3.1).

1.5.3 Degradation concepts and driving forces

A central objective of this study was to develop conceptual frameworks combining anthropogenic and/or natural amplifications to explain interrelated degradation processes. However, degradation rates are slow (ranging from years to decades, perhaps centuries), which makes it difficult to measure processes *in situ* during short-term field trips. To overcome this problem, degradation sequences were selected and investigated. The main drivers and their impacts were explained by means of biogeochemical proxies, geomorphological features and literature knowledge.

Two main degradation patterns are common for the *Kobresia* ecosystems, namely polygonal cracks together with bare soil patches as well as crust-covered dead root mats. These patterns are present from the Qilian Shan in the North to the Himalayas in the South. Degradation surveys on the Kema research sites revealed that about 15% of the total surface was classified as bare soil patches and about 19% as crust-covered dead root mats (Babel *et al* 2014, chapter 3.7).

1.5.3.1 Formation of polygonal cracks and bare soil patches

Within the pasture degradation concept (chapter 2.1.7; 2.3.3; 2.4.5.1) it was postulated that soil drought and frost lead to polygonal cracking of the *Kobresia* turf already weakened by overgrazing. This can occur during times of drought, when the summer monsoon is delayed, and in winter with very low temperatures (cold dry winters, Miehe *et al.* 2008). Repeated drying/rewetting leads to contraction/expansion of the soil and causes a gradual cracking of the *Kobresia* turf (Walker *et al.* 2008; Lehmkuhl 2016). Once the *Kobresia* turf cracks, it forms a micro-relief. The micro-relief increases water infiltration at the cracks via preferential and surface flow and enhances soil moisture content. Moist soil at the beginning of the frost season in combination with strong diurnal frost events then leads to expansion during freezing, extending the surface cracks. The risk of repeated drying and frost cracks might be accelerated by climate change due to increasing temperatures and precipitation variability on the Tibetan Plateau (Zhai *et al.* 2005; Wang *et al.* 2008a)

The gradual degradation of the *Kobresia* turf initiates a die-off of the above- and belowground plant compartments and the decay of the root litter expands the surface cracks. Overall this favors soil erosion, which is promoted by the sloped landscape and the soil texture, comprising mainly easily erodible particles such as fine sand and coarse silt (chapter 2.4.4.1). Erosion results in an accumulation of coarser material, as indicated by the high stone cover on the strongly degraded stages. As an additional degradation driver, small mammals (i.e. the Plateau Pika *Ochotona curzoniae*) accelerate soil degradation. Pika densities are highest at sites where the root mat is completely removed (Pech *et al.* 2007). The pikas use existing surface cracks for easy access to construct burrows below the root mats. Further, pikas often graze the remaining plant biomass, exacerbating the loss of vegetation and promoting further erosion.

1.5.3.2 Formation of crust-covered dead root mats

Patches of dead root mats covered by crustose lichens are scattered across the pastures without any apparent abiotically- or biologically-controlled pattern (chapter 2.1.7). The patches are rarely re-colonized by *K. pygmaea* and rosettes of *Lancea tibetica* or *Kobresia macrantha* are more common. The most plausible explanation is dieback as an effect of overgrazing (chapter 2.1.7; 3.1). Constant removal of the photosynthetically active shoot biomass by grazing decreases the belowground C allocation. If this happens too frequently it causes the death of the root biomass, because the high belowground C demands can no longer be met. It consequently lowers the uptake of limited resources such as N, P and water, and leads to a positive feedback with negative consequences on aboveground biomass maintenance (chapter 2.2.5.3). In the long-term, it initiates a patch-wise dying of the *Kobresia* turf. This encourages the formation of crusts with lichens and algae (chapter 3.1). A alternative explanation for the formation of dead root mats is the natural process of ageing of a *Kobresia* clone or due to death during extreme years with low precipitation or low temperatures (chapter 2.1.7).

1.5.4 Biogeochemical consequences of degradation

Accounting for the main degradation patterns (1. polygonal cracks and bare soil patches, 2. crust-covered dead root mats, Fig. ES-2) on landscape scale revealed that increasing degradation of the *Kobresia* turf (in % of total surface) affects carbon allocation and strongly reduces carbon uptake (chapter 2.5.4.2; 3.7). It therefore compromises the function of *Kobresia* pastures as a carbon sink. From this it was concluded that the changes in surface properties due to pasture degradation have a significant influence at larger scales. In the following studies the two main degradation patterns and their effects on SOC and nutrients were elaborated separately.

1.5.4.1 C, N and P losses from polygonal cracks and bare soil patches

To elucidate the consequences of polygonal cracks and bare soil patches on SOC and soil nutrient storage, a sequence of six degradation stages was selected (S0-S5, chapter 2.3.6.2). It was proposed that this degradation sequence was initiated by repeated drying-rewetting and freeze-thaw cycles. The cracking of the topsoil triggered the death of the above- and belowground plant compartments, caused an imbalance of C in- and output and promoted the decay of the *Kobresia* turf. Together with the decreasing vegetation cover and ground-dwelling pikas, this promoted soil erosion. Erosion gradually extended the surface cracks (S2-S5) and caused a high SOC loss from the upper soil horizons (chapter 2.3.3). For the bare soil patches (S5), soil erosion had removed up to 5 kg C m^{-2} (SOC loss: 48% compared to intact stage). In contrast, the SOC loss below the surface cracks was caused by both decreasing C input and SOC mineralization (~2.5 kg C m^{-2} reflecting a loss of 23% of the total SOC of the intact stage). The decreasing root biomass with increasing degradation stage indicated lower C input, which agreed with the lower contribution of plant-derived neutral sugars with intensified degradation. Mineralization was reflected by decreasing SOC contents and decreasing δ^{13}C values with degradation. The negative δ^{13}C shift corresponded to an enrichment of more complex organics such as ^{13}C-depleted lignin and hydrolysable lipid components. These compounds accumulated in the soil organic C pool due to preferential mineralization of more labile components (chapter 2.3.4). The microbial community composition in the deeper soil horizons changed progressively with degradation intensity. It showed pronounced changes in the fungal community as revealed by t-RFLP analysis, 16S rDNA and IST sequencing. These findings were confirmed by the activities of enzymes involved in the decomposition of more complex OC compounds (e.g. fungal phenoloxidases), which were highest in S3 and S4. In contrast, the reference soil (S0) and the initial degradation stages (S1-S2) showed lowest phenoloxidase activities relative to soil OC (chapter 3.3).

Since soil fertility in Tibetan soils strongly depends on SOC storage, a marked decrease of nutrients (N and P) was observed following intensified degradation. Erosion led to an export of soil (ca. 85 kg m^{-2}) and consequently of its contained nutrients. Losses were about 45% and 35% from erosion and about 20% and 15% from leaching on the strongest degraded site (S5), respectively (chapter 2.5.4.2). Degradation induced a decoupling between the losses of N and P due to erosion and mineralization followed by leaching. That is, erosion removed relatively more N than P from the soil profile due to a decreasing N/P ratio with depth, and because leaching induced N and P losses to different extents (N > P) in the erosion-unaffected horizons. In particular, N was leached after it was released by organic matter mineralization (chapter 2.5.4.3).

1.5.4.2 C and N losses from crust-covered dead root mats

Patches covered by blue-green algae and crustose-lichen crusts that are induced by overgrazing or natural aging of *Kobresia* clones are often observed on the eastern part of the Tibetan Plateau (Fig. ES-2). Such crusts have changed the C and N cycling due to an imbalance of in- and outputs. Over the long term this has induced high C and N losses, mainly due to organic matter mineralization, leaching and decreasing inputs following plant death (chapter 2.5.5.1; 2.6.5.4; 3.6). For instance, the SOC content decreased by 46% and N by 28% in the upper 5 cm as compared to the intact *Kobresia* root mats. A transect study across the Tibetan Plateau from Xining in the north to Nagarze in the south revealed average losses of about 35% for C and 25% for N (chapter 3.1), indicating that C losses were in the upper range at the Kema research sites. To identify the dominant processes causing high C and N losses, root mats of different degradation stages were investigated using laboratory incubation experiments for (a) living root mat (Living), (b) dying root mat (Dying) and (c) dead root mat (Dead).

C losses: The dying root mats showed the highest C losses from decomposition of SOM and root litter (measured as CO_2 efflux) and from leaching of DOM (chapter 2.5.4). This was attributed to the high initial root litter inputs after plant death, which stimulated microbial respiration. Overall, it was revealed that the dying of *K. pygmaea* will rapidly convert pastures to a C source. The C loss from soil respiration in the living stage, however, was 6 times lower than that of the dying stage. This was attributed to ongoing photosynthesis by *Kobresia*, which mitigated the respiratory C losses and consequently prevented *Kobresia* pastures from becoming C sources (2.5.5.2). The dead root mat had the lowest SOC content compared to the living and dying stages because mineralization had already led to high SOC losses before sampling (probably over years to decades). Consequently, the lower C availability reduced fluxes of CO_2 and DOM in the dead root mats. Additionally, it was expected that the SOC composition had changed in the dead root mats, with more recalcitrant compounds than labile organics. Based on this, it was hypothesized that an activation of the microbial community by labile C input and increasing temperature would stimulate the microbial decay of the more passive SOC pool (known as priming effects). Therefore, non-degraded and degraded stages were labeled with ^{14}C-glucose with high or low additions (x and y, respectively) and incubated at 0 °C, 10 °C and 20 °C for 80 days (chapter 3.5). Priming effects responded positively to increasing temperature, with about 80 % increment in degraded soil and about 15 % in non-degraded soil. At 20 °C, priming was higher in degraded than non-degraded soil. At 0 and 10°C, low glucose input caused an activation of the microorganisms, leading to positive priming effects, meaning that the microbial activation induced the mineralization of the stable SOC pool. In contrast, high glucose additions caused significantly lower priming effects (even negative priming effects for 0°C and 10°C), presumably because microbes preferred to utilize the added glucose rather than the more stable and energy-intensive passive SOC pool (chapter 3.5).

N losses: In further experiments it was tested how N cycling changed with intensified degradation and with increasing N deposition. Nitrogen (^{15}N enriched) was added at different rates (fertilized and unfertilized) to account for increasing N deposition (chapter 2.6). After 7-8 weeks, plant growth and ^{15}N uptake slowed down in the intact stage, because most of the added N was already consumed by plant uptake or lost via leaching (chapter 2.6.5.1). After this period, NO_3^- losses were close to zero. In contrast, NO_3^- leaching substantially increased in dying and dead root mats (especially for N-fertilized root mats) and accounted for most of the N loss ($NO_3^- > DON > NH_4^+$). Dead root mats had the highest average NO_3^- losses from leaching compared to other root mats. Leaching N losses from dying and dead root mats were 2.2 and 6.3 times higher than from living root mats. The high NO_3^- losses from dead root mats were mainly caused by long-term NO_3^- accumulation during SOC decomposition in the field and then flushed by leaching. No losses, however, were found for NH_4^+, independent of degradation stage, presumably due to high nitrification rates in dying and dead stages and rapid ammonium uptake in the living stage. Overall, N losses from leaching were up to 32 and 330 times higher than those from N_2O emissions in the dying and dead root mats, respectively (chapter 2.5.5.4; 2.6.5.4). In summary, it was demonstrated that increased atmospheric N deposition can facilitate plant growth in intact *K. pygmaea* pastures, whereas in the degraded pastures N deposition directly increased N leaching. Consequently, leaching exacerbates the negative impacts of pasture degradation on N availability in these often N-limited ecosystems, and thus impedes the recovery of *Kobresia* pastures following degradation.

1.5.5 Consequences of degradation on ecosystem functions

Degradation has far-reaching consequences for various ecosystem functions. Large amounts of soil, SOC and nutrients are lost on-site via mineralization, leaching and water and wind erosion. This locally compromises soil fertility, reduces pasture quality and ultimately threatens the livelihood of the Tibetan herders. Moreover, the unbalanced losses of N and P (N > P) alter prevailing N and P limitations for growth and could impede natural or managed grassland restorations. The exact fates of the lost materials are unknown, but they have likely been deposited in rivers and water basins, polluting the Tibetan headwaters. Since the *Kobresia* ecosystem is the source of some major rivers, erosion jeopardizes the clean water supply for large populations in SE Asia. Further, wind erosion is the origin of dust pollution, a growing problem in densely populated Asian cities.

On a landscape scale, it was shown that increasing degradation of the *Kobresia* turf affected carbon allocation and strongly reduced carbon uptake. Together with intensive SOC losses from mineralization (investigated on plot scale), which has released CO_2 back to the atmosphere, degradation may have contributed to climate change globally. Furthermore, pasture degradation led to a shift from transpiration to evaporation, resulting in an earlier onset of convection and cloud generation. Consequently, precipitation started earlier and clouds decreased the incoming solar radiation.

To conclude, degradation has far-reaching consequences from local to global scale, because it threatens several ecosystem functions: soil organic carbon (SOC) and nutrient storage, floral and faunal biodiversity, erosion control, clean water provision, livestock forage production, and regional climate control. Since the traditional migratory rangeland management with moderate grazing intensity was sustainable over millennia, it was concluded that the best way to conserve and possibly increase the carbon and nutrient stocks in the turf and its functions is an extensive grazing regime.

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2 Publications and Manuscripts

2.1 Study I: The *Kobresia pygmaea* ecosystem of the Tibetan highlands – origin, functioning and degradation of the world's largest pastoral alpine ecosystem

In preparation for resubmission to *Ecological Monographs*

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2.1.1 Abstract

Kobresia pastures in the eastern Tibetan highlands occupy an area of 450000 km² and form the world's largest pastoral alpine ecosystem. The main constituent is an endemic dwarf sedge, Kobresia pygmaea, which forms a lawn with a very durable turf cover anchored by a felty root mat, and occurs from 3000 m to nearly 6000 m a.s.l. The existence and functioning of this unique ecosystem and its turf cover have not yet been explained against a backdrop of natural and anthropogenic factors, and thus its origin, drivers, vulnerability or resilience as well as its future development remain largely unknown. Here we present a summary of our own studies and literature data on ecosystem diversity, pasture health, cycles of carbon (C), water and nutrients, and on the palaeo-environment, as well as results from studies on the reproduction and ecology of the key species K. pygmaea. The methods employed include molecular analysis, grazing exclusion, measurements with micro-lysimeters and gas exchange chambers, 13C and 15N labelling, eddy-covariance flux measurements, remote sensing and atmospheric modelling.

The following combination of traits makes Kobresia pygmaea resilient against disturbance and highly competitive under grazing: dwarf habit, predominantly below-ground allocation of photoassimilates, mixed reproduction strategy with both seed production and clonal growth, and high genetic diversity. For an unknown period Kobresia pastures have been co-limited by low rainfall during the short growing season and livestock-mediated nutrient withdrawal. Changing rangeland policies during the last 50 years, together with overstocking, have caused pasture degradation, yet the overall extent of this remains a matter of debate. In addition to the grazing-driven changes, we newly describe natural autocyclic processes of turf erosion initiated through polygonal cracking of the turf cover, and increased by soil-dwelling endemic small mammals. The major consequences of the deterioration of the vegetation cover and its turf include: (1) the release of large amounts of C and nutrients to the atmosphere, rivers and surrounding terrestrial ecosystems; (2) earlier diurnal formation of clouds resulting in decreased surface temperatures with likely consequences for atmospheric circulation on large regional and, possibly global, scales.

Palaeo-environmental reconstruction, in conjunction with grazing experiments, suggests that much of the present grazing lawns of Kobresia pygmaea are a synanthropic ecosystem that has developed over millennia, since the onset of pastoralism. The traditional migratory rangeland management was largely sustainable and possibly still offers the best strategy to conserve, and possibly increase, the C stocks in the Kobresia turf, as well as its importance for climate regulation.

2.1.2 Introduction

The Tibetan highlands encompass 90% of the Earth's terrain above 4000 m and host the world's largest pastoral alpine ecosystem: the Kobresia pastures of the south-eastern highlands, with an area of 450000 km² (Fig. SI-1). This ecosystem is globally unique as it is: (1) dominated by a single endemic sedge species of 1 to 4 cm in height; (2) forms a golf-course like lawn, with a very durable turf cover anchored by a felty root mat; (3) occurs over an elevational extent of 3000 m, stretching between 3000 m (in the north-eastern highlands) to nearly 6000 m a.s.l. (on the north slope of Mt. Everest; Miehe 1989, Miehe et al. 2008b).

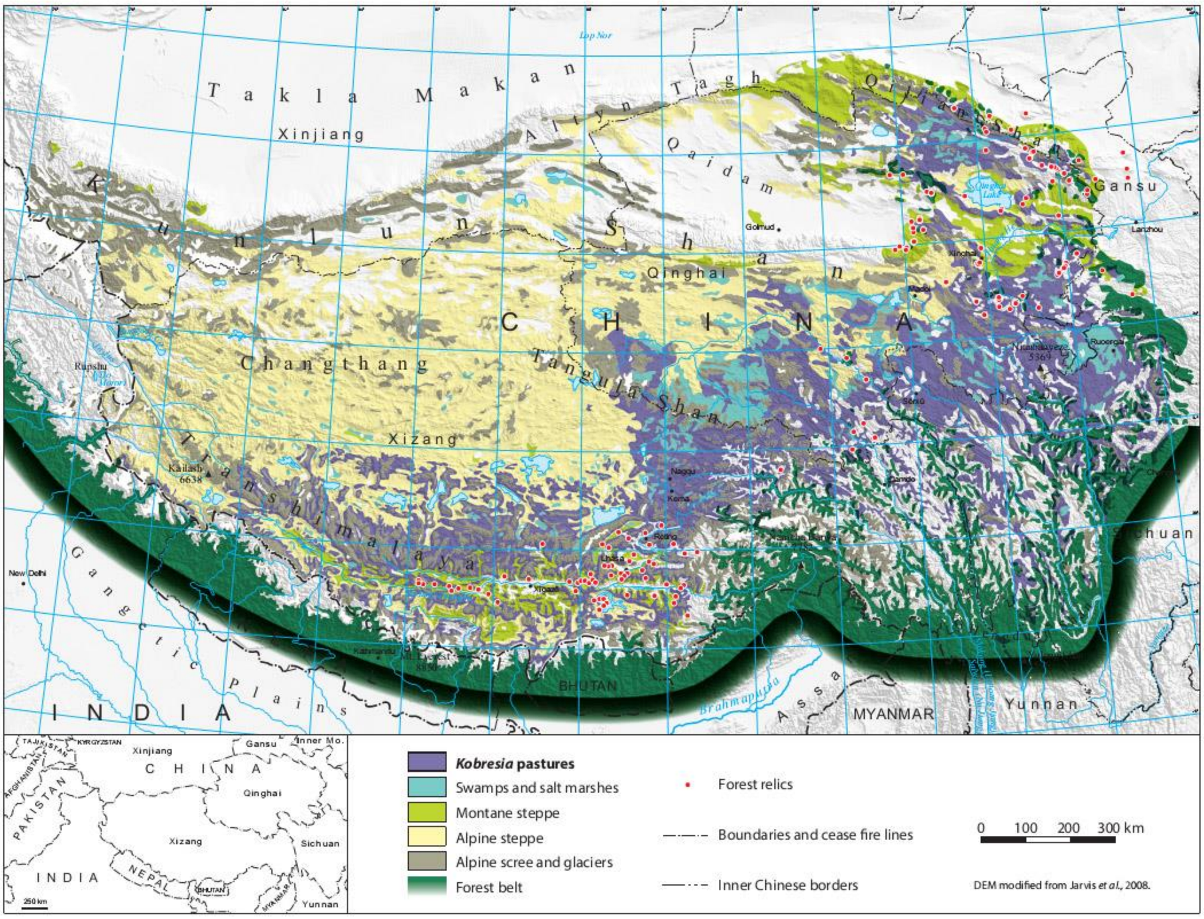

Figure SI-1: Kobresia pygmaea pastures of the Tibetan highlands and forest relics. After Atlas Tibet Plateau 1990, Miehe et al. 2008b, 2014, Babel et al. 2014.

The evolution and recent changes of the Kobresia ecosystem, as well as its future development, are of great importance because surface properties of the highlands have an undisputed effect on the global climate (Cui and Graf 2009, Babel et al. 2014, Yang et al. 2014). The whole Tibetan plateau is significant in terms of C turnover and CO_2 fluxes from regional to global scales (Zhao et al. 2005, Zhang et al. 2007). Its soil stores huge amounts of carbon

(C), mounting to up to 2.5% to the global C pool (Ni 2002, Wang et al. 2002, Hafner et al. 2012). The Kobresia ecosystem in particular contributes about 1% (Batjes 1996, Wang et al. 2002), though covering only about 0.3% of the global land surface (equivalent to one-third of the whole Tibetan plateau). The livelihoods of 5 million pastoralists depend on forage resources from the rangelands, which sustain about 13 million yak, and 30 million goats and sheep (Wiener et al. 2003, Suttie et al. 2005). One quarter of the world's population living in the surrounding lowlands ultimately depend on ecosystem functions of the Kobresia mats, which represent the upper catchment areas of the Huang He, Yangtze, Salween, Mekong, and partly of the Brahmaputra, rivers.

The aim of this review is therefore to summarize recent findings relating to: (1) the diversity and the distribution of plant species of the ecosystem and its palaeo-ecological background; (2) the ecology and reproduction of the dominant species, Kobresia pygmaea (C.B.Clarke) C.B.Clarke; (3) the ecosystem's water budget and hydrological fluxes; (4) fluxes in the carbon cycle; (5) soil properties and functions, including productivity and nutrients stocks; (6) the current extent of rangeland degradation and its causes; (7) the human impact shaping this ecosystem; (8) the current understanding of the age of this human impact. In addition, a new concept of natural autocyclic processes of turf erosion, initiated through polygonal cracking of the turf cover increased by overgrazing and facilitated by soil-dwelling endemic small mammals, will be presented.

Building on available literature, this review integrates field observations from surveys in the highlands undertaken by the first author between 1984 and 2015, and related studies on the status and dynamics of the ecosystem from grazing exclusion-experiments, obtained mainly in the northeastern montane Kobresia rangelands near Xinghai (Qinghai Province, 3440 m, 35°32'N / 99°51'E), and in the core area of alpine Kobresia pygmaea pastures next to the 'Kobresia pygmaea Research Station' (Kema), now managed by the Institute of Tibetan Plateau Research, Chinese Academy of Science, southeast of Nagqu (Xizang Autonomous Region, 4450 m, 31°16'N / 92°06'E).

2.1.3 Diversity, distribution and the palaeo-ecological background

2.1.3.1 Species diversity and distribution

The Tibetan highlands are a centre of Cyperaceae diversity (Global Carex Group 2015), with more than 30 Kobresia species (Zhang and Noltie 2010). Recent studies have shown that the genus Kobresia should be included within Carex and that K. pygmaea should be called Carex parvula O. Yano (Global Carex Group 2015). However, given that these new proposals have not yet been implemented either in any of the locally relevant floras, or in the ecological literature, the traditional nomenclature is retained here.

At altitudes between 3000 and 4000 m a.s.l. in the eastern highland forest-grassland ecotone, pastures of Kobresia species have developed: the height of the plants is between 10 and 20 cm, but the species vary, with K. capillifolia (Decne.) C.B.Clarke and K. pusilla N.A.Ivanova dominant in the north; and K. nepalensis (Nees) Kük. in the south (Fig. SI-1). Sedge swamps along streams or in waterlogged areas over permafrost in the catchments of the Huang He, Yangtze, Mekong and Salween rivers are characterized by K. tibetica Maxim.; those along the Yarlung Zhangbo and Indus are composed of K. schoenoides Boeckeler –both species are between 15 and 60 cm high. Two species, K. pygmaea and K. yadongensis Y.C.Yang reach hardly 4 cm in height. The latter has been described recently and its distribution is poorly known (Zhang and Noltie 2010, Miehe et al. 2011a). By far the most important species of the Tibetan rangelands is K. pygmaea. It was first collected in 1847 by Thomas Thomson in Rupshu (NW India), and is endemic to Tibet and the Inner Himalayas, ranging from the Deosai Plains of northern Pakistan to the Yulong Shan in northern Yunnan (Dickore 1995, Zhang and Noltie 2010). The interspecific relationships between species as currently delimited remain unknown, because standard DNA for phylogenetic analysis (nuclear ITS and chloroplast DNA regions, including matk, trnl-F and trnC-D) show low mutation rates and little divergence within Kobresia (J. Liu [unpublished data]). The weak genetic differentiation suggests that these morphologically defined species may have evolved rapidly within the recent past. Further calibration, based on genomic data and fossils (where available) are needed to clarify evolutionary relationships among the Kobresia species as currently defined.

Vascular plant α-diversity of alpine Kobresia pastures (measured in plots of 100 m2) varies between 10 species in closed lawns with a Kobresia pygmaea cover of 98% (Miehe et al. 2008b, E. Seeber [unpublished data]), and, in the eastern part of the plateau, more than 40 species in communities with mosaics of Kobresia patches and grasses, other sedges and perennial forbs growing as rosettes and cushions (Wang et al. [in revision]). Similar levels of richness were recorded in montane grazing lawns hosting a set of weeds of grazing (Miehe et al. 2011c). The inter-annual variability of species richness is high, accounted for the variability of annual herbs depending on annual precipitation (E. Seeber [unpublished data]).

In general, the Tibetan highlands, and specifically the eastern plateau, are poor in endemic plant genera and rich in endemic plant species (Wu et al. 1981). In contrast, and peculiar to the alpine Kobresia mosaics, is the high number of endemic monotypic genera of rosette plants, which colonize open soils around small mammal burrows (e.g., Microcaryum pygmaeum I.M.Johnst., Przewalskia tangutica Maxim., Pomatosace filicula Maxim.; Miehe and Miehe 2000)

Similarly, the faunistic diversity is heterogeneous among taxonomic and ecological groups. For example, while most predators are not endemic, a number of herbivores are, including wild yak, chiru and kiang, but also small mammals such as the plateau pika (Schaller 1998). In contrast, the beetle soil-fauna, which generally has a very high diversity in the Tibetan highlands (for example along wet gullies), is very poor and endemics are absent from the grazing lawns. Apparently the poor aeration of the turf, and the soil compaction due to trampling effects, are not suitable for the strictly edaphic ground beetle larvae (J. Schmidt [unpublished data]). Important insects of the Kobresia pastures are Lepidoptera caterpillars of the genus Gynaephora (Erebidae, Lymantriinae; e.g., Yuan et al. 2015) which are known to cause severe damage (http://www.fao.org/ag/agp/agpc/doc/counprof/china/china2.htm, Yan et al. 1995, Xi et al. 2013, Zhang and Yuan 2013, Yuan et al. 2015). How regularly outbreaks occur, and how grazing intensity of Kobresia systems, or climatic effects, affect population dynamics of Gynaephora species are unknown. It appears that strongly grazed Kobresia ecosystems maintain only few phytophagous insects in terms of abundance and species richness – presumably because of the dominance of a single plant species, the high grazing intensity and the unfavorable environment. This coincides with the common finding that strong grazing by livestock decreases abundance and diversity of insects as caused by resource limitation, unfavorable microclimatic conditions and the lack of shelter due to reduced habitat heterogeneity (e.g., Littlewood 2008). Detailed studies across elevational gradients and across sites differing in grazing intensity are, however, needed to gain deeper insights as to how interactions with phytophagous insects affect the Kobresia pygmaea ecosystem in the long term.

2.1.3.2 The palaeo-ecological background

The development of biodiversity and endemism in relation to the highlands' uplift and climate history has not yet been fully understood, hampering our understanding of the present diversity patterns. It is likely, however, that today's biodiversity has been shaped by varying evolutionary histories depending on respective life-history traits with respect to climatic niches and dispersal ability. Depending on those two traits, the likelihood of extinction due to Pleistocene climatic changes has necessarily varied. In this context it is useful to review the independent climate proxies of the Last Glacial Maximum (LGM; see Table SI-1). Most probably the world's most elevated highlands were even more hostile for life during the cold periods of the Quaternary than today. While the former idea of a complete ice cover across the highlands (Kuhle 2001) has been soundly rejected on the basis of biotic and abiotic proxies, replaced with a concept of fragmented but locally extensive mountain glaciations, at least in the more humid eastern highlands (Shi 2006, Heyman et al. 2009), palaeo-scenarios for humidity and temperature still offer a wide range of possibilities, depending on the proxies on which they rely. The two most divergent palaeo-scenarios – ecological stability or complete extinction and Holocene re-migration – can be assessed against the presence or absence of local endemics or populations with private haplotypes, because 10000 years is too short a period for in-situ speciation. In the case of the Tibetan highlands summer temperatures are particularly important. If these drop below minimum requirements for a given species, then local and endemic populations are lost – a phenomenon most important in closed-basin systems.

The huge number of tiny, wingless, locally endemic ground beetles in the southern highlands is important in this respect, because it testifies to a persistence of alpine habitats and the absence of a glacial 'tabula rasa' (Schmidt 2011). The mean altitudinal lapse rate for summer temperatures across 85 climate stations (records between 1950 and 1980) in the highlands is 0.57 K per 100 m (Schmidt et al. 2011). Biogeographical data of the current distribution of endemic, tiny, wingless ground beetles in the mountainous topography of southern Tibet point to a decline in LGM summer temperature of only 3–4 K as compared with present conditions (Schmidt et al. 2011), which is much lower than earlier estimates (Table SI-1). This is supported by estimates based on the presence of private haplotypes of juniper trees and endemic flowering plants in interior basins of the central Tibetan highlands ('Changthang') (Miehe et al. 2011b, Schmidt et al. 2011), while records of terrestrial molluscs in loess deposited during the LGM on the Loess Plateau revealed annual temperatures 3–5 K lower than today (Wu et al. 2002). Biomarkers in the southern slope of the Himalaya (Lake Rukche, 3500 m; Glaser and Zech 2005) indicate a downward shift of the upper treeline of 500 m, similar to shifts of distribution boundaries of two Pinus species in the Kathmandu basin of Nepal (Paudayal and Ferguson 2004). These also lead to an estimation of LGM temperature drop by only 3–4 K (Miehe et al. 2015).

Table SI-1: Estimates of temperature depression during the Last Glacial Maximum (maxDT) for the Tibetan highlands and the Central Himalaya.

Location	Method	maxDT [K]	Time [ka BP]	Reference
Tibet Plateau	$\delta^{18}O$ value in ice core, ice wedges	7 (annual)	16-32	Shi et al. 1997
Guliya Ice cap, West Kunlun	$\delta^{18}O$ value in ice core	9 (annual)	23	Yao et al. 1997
Dunde Ice cap, Qilian Mountain	$\delta^{18}O$ value in ice core	6 (annual)	30	Thompson 1989
Qarhan Salt Lake, Qaidam Basin	$\delta^{18}O$ and δD of intercrystalline brine	8 (annual)	16–19.5	Zhang et al. 1993
Eastern Qilian Mountain	Paleo-peat in frost heave	7 (annual)	31+/– 1.5	Xu et al. 1984
Gonghe Basin, Qinghai Province	Paleo-sand wedge	7 (annual)	17 +/– 0.25	Xu et al. 1984
Zoige Basin, East Tibet	Pollen analysis	6 (annual)	18	Shen et al. 1996
Zhabuye lake, southwest Tibet	Pollen analysis	6 (annual)	18	Xiao et al. 1996
Hidden Lake & Ren Co, Southeast Tibet	Pollen analysis	7–10 (January)/ 0–1.5 (July)	18–14	Tang et al. 1999
South and central Tibet	Atmospheric model	3–5 (winter)/ 2–4 (summer)	21	Liu et al. 2002
High Asia	Estimate	<5 (mean summer)	LGM	Shi 2002
Tibetan Plateau	Atmospheric model	0.8–1.9 (annual)	21	Zheng et al. 2004
High Asia	Atmospheric model	6.3–6.4 (annual)/ 5.6–6.1 (July)	21	Böhner and Lehmkuhl 2005
Nyenquentangula Shan	Present elevational range of endemic beetles	3–4 (summer temperature)	LGM	Schmidt et al. 2011
Southern Tibet	Private juniper haplotypes	3–4 (summer temperature)	LGM	Schmidt et al. 2011
Changthang	Present elevational range of endemic plants	3–4 (summer temperature)	LGM	Miehe et al. 2011
Loess Plateau	Terrestrial mollusk	3–5 (annual)	LGM	Wu et al. 2002
Lake Rukche, Nepal	Forest/grassland biomarker	3 (annual)	LGM	Glaser and Zech, 2005
Kathmandu, Nepal	*Pinus*-Pollen	3 (annual)	LGM	Paudayal and Ferguson 2004

The development of humidity scenarios for the LGM may also benefit from applying ecological indicator values of endemic plants or palaeo-pollen records. For example, the persistence of juniper trees in Tibet (Opgenoorth et al. 2010) throughout the LGM imply that rainfall was never lower than 200 mm/yr, because the present drought line of junipers correlates with 200–250 mm/yr. Grass pollen records in the north-eastern highlands (Lake Luanhaizi; Herzschuh et al. 2006) and in southern Tibet (Nangla Lu; Miehe et al. [unpublished data]), reveal the presence of steppe vegetation and thus an annual rainfall of more than 100 to 150 mm. However, the true figures may be somewhat lower as colder climates would result in less evapotranspiration. The LGM–loess records in Tibet (Kaiser et al. 2009) also testify to the presence of grass cover as a precondition for loess accumulation. Thus, both temperature and humidity during the LGM allowed the persistence of plants, herbivores and hunters in the Tibetan highlands.

2.1.3.3 Life history traits and reproduction of Kobresia pygmaea

Kobresia pygmaea is one of the smallest alpine sedges, but dominates the largest alpine pastoral ecosystem, stretching over an altitudinal range of 3000 m. Its lawns have an estimated Leaf Area Index (LAI) of only ~1 (Hu et al. 2009) and a roughness length of only about 3 mm. They represent a vegetation cover with a small transpiring surface and low aerodynamic coupling to the atmosphere (Babel et al. 2014).

Due to high solar radiation input and night-time long-wave radiation, Kobresia pygmaea has to cope with steep soil-to-air temperature gradients and high leaf over-temperatures on sunny days. However, the species shows low sensitivity to low soil temperatures, as leaf gas exchange was found to be negatively affected only by soil temperatures below freezing point, i.e., when soil-water availability approaches zero (Coners et al. 2016).

In fully sun-exposed sites, Kobresia pygmaea grows mostly in lawns of 2 cm in height, yet lawns of only 1 cm or up to 4 cm can occur locally, regardless of being grazed or ungrazed, and whether growing in water-surplus sites such as swamps or on steep, dry slopes. The phenotypic similarity across the whole range of environmental conditions in the Tibetan highlands shows the species' adaptation to the cold and seasonally dry environment, and is probably one of the factors explaining its wide distribution in the highlands. Grazing exclusion experiments, however, have revealed that K. pygmaea can attain 20 cm when overgrown and shaded by taller grasses or under tree crowns (S. Miehe and Y. Wang [unpublished data]). The same effect was observed in a plant growth chamber with climatic parameters closely simulating the conditions of a typical summer day at the Kema site (H. Coners [unpublished data]). Although the lamps used were chosen for their spectral similarity to sunlight, after some weeks Kobresia pygmaea plants reached up to 20 cm in height. Artificial lighting cannot reach the intensities pertaining on the plateau, (especially in the UV-B part of the spectrum), which have among the highest peaks in radiation intensities occurring on earth (Beckmann et al. 2014). Whether permanently high radiation loads represent an inhibitor, with a photo-toxic growth effect that reduces the growth of Kobresia, remains unclear. No doubt, the dwarf habit could also have been evolved as an effective strategy to avoid plant biomass loss and damage by grazing.

A microsatellite-based survey of alpine Kobresia pygmaea populations revealed the presence of large (>2 m^2) clones, and an overall high genetic diversity (with more than 10 genets/m^2). This probably results from consecutive events of sexual recruitment under favourable conditions, coupled with extensive periods of vegetative persistence (Seeber et al. 2016). Thus, in contrast to many alpine species that largely abandon sexual reproduction (Steinger et al. 1996, Bauert et al. 1998), K. pygmaea benefits from a mixed reproduction strategy, with clonal growth ensuring long-term persistence and competitiveness, while intermittent reseeding facilitates colonization and genetic recombination. A diaspore bank supports short-term persistence. According to microsatellite studies, populations are hardly separated between montane and alpine altitudes, indicating high gene flow within the species’ distribution range (Seeber 2015). The genetic diversity in the species is also promoted by polyploidy; K. pygmaea mostly has 2n = 4x = 64 chromosomes and is tetraploid. Ploidy of congeners ranged from di- to hexa- or even heptaploidy (Seeber et al. 2014). An assessment of ploidy levels along an elevational gradient in Qinghai also revealed one diploid, one triploid, two octoploid and one dodecaploid individual, indicating ongoing cytological evolution in K. pygmaea (E. Seeber [unpublished data]).

Kobresia pygmaea plants are mostly monoecious, with androgynous spikes (upper flowers male, lower female; Zhang and Noltie 2010), yet dioecious forms do occur (own observations at 4200 m, 33°12’N/97°25’E, plants with entirely male spikes). High numbers of inflorescences are produced (~100 to 5000 inflorescences/m^2; Seeber et al. 2016), depending on the weather conditions in the respective year, but not on the grazing regimes. Diaspores are highly viable and adapted to (endo)-zoochorous dispersal. Germination rates differ greatly between seeds from alpine and montane environments (e.g., Li et al. 1996, Deng et al. 2002, Miao et al. 2008, Huang et al. 2009, Seeber et al. 2016) but are in general low, both in laboratory experiments as well as in situ. Huang et al. (2009) reported 13% germination of untreated diaspores, while most studies obtained no seedlings at all (Li et al. 1996, Miao et al. 2008, Seeber et al. 2016). The water-impermeable pericarp hinders germination and its removal, by chemical or mechanical interventions, increases germination rates. Under natural conditions, microbial activity or digestion by herbivores may have the same effect and, consequently, increase germination. Nonetheless, the variability in germination was high between different studies, which may reflect population responses to different abiotic conditions, such as nutrient availability or elevation (Amen 1966, Seeber 2015).

2.1.4 Water budget and hydrological fluxes of ecosystems

Kobresia pastures exist over a wide range of precipitation, from 300 to 1000 mm/yr (Miehe et al. 2008b), which falls nearly exclusively during summer. Apart from nutrient limitation (see below), the growth of Kobresia pygmaea is co-limited by low summer rainfall, at least under the conditions of the ecosystem's alpine core range (Kema; Coners et al. 2016) with 430 mm/yr and mean maximum temperature of the warmest month of 9.0 °C (1971 – 2000; Babel et al. 2014). Onset of the growing season is controlled by rainfall amount in early summer and under low-temperature control in autumn (September and October, depending on latitude and altitude). The leaf growth of K. pygmaea is not temperature-driven (unlike that of Androsace tapete Maxim., a cushion plant of the alpine steppe), but depends strictly on water availability (Li et al. 2016). Greening of the Kobresia pastures after the onset of the summer rains is well known and usually occurs between mid-May and mid-June (Fig. SI-2).

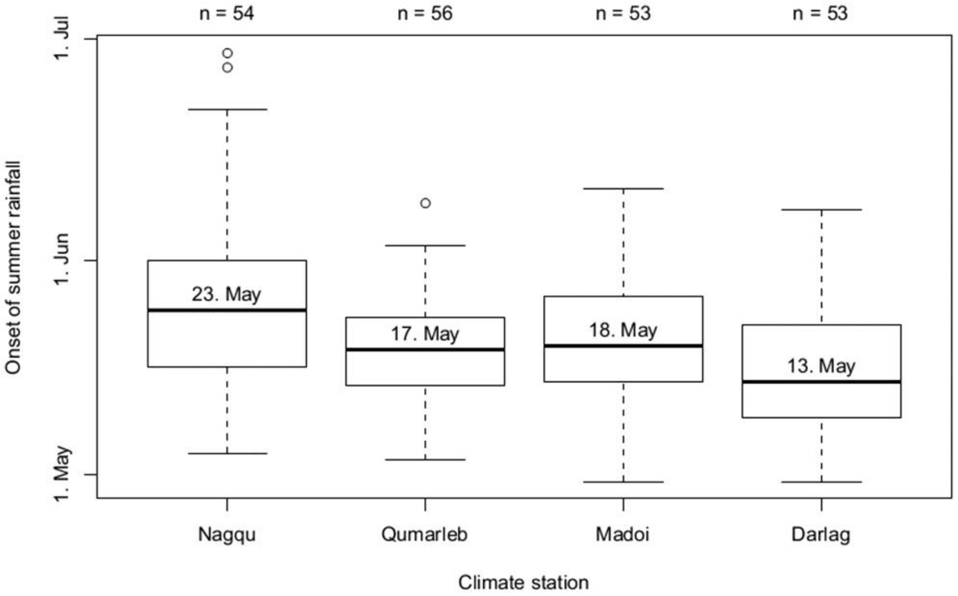

Figure SI-2: Date of the onset of the summer precipitation observed at selected climate stations. In the box-plots, lines and boxes correspond to extreme values, the first quartile and the third quartile. The written date is the median (black solid line in the boxplots) of the onset for the respective station (n is the number of years with sufficient observations). For the calculation of the onset, the first derivation of a 6th order polynomial fitted between daily precipitation sums and the day of the year is derived for each year. The date of the onset is defined as the date when the maximum of the first derivation occurred. Precipitation data is from the Global Historical Climatology Network (GHCN-d; Menne et al. 2012).

However, onset of the summer monsoon can be delayed by up to six weeks, sometimes starting as late as early August, with critical effects for livestock (Miehe and Miehe 2000). Despite its low leaf area index, alpine Kobresia pastures can reach high transpiration rates (up to 5 mm/day) in moist summer periods even at elevations >4000 m a.s.l.: a consequence of specific microclimatic conditions on the plateau, which enhance evaporation (Coners et al. 2016). While dry periods, due to delayed onset of the summer rains, visibly hamper K. pygmaea growth (browning of the pastures), a constant daily irrigation with 2.5 mm/day or even 5 mm /day did not increase the total above-ground biomass production after 40–70 days (corresponding to 100–350 mm of added water; Coners et al. [unpublished data]). This matches observations of constant biomass production despite large variation in precipitation (Climatic station of Naqu 2011: 574 mm, 2012: 437 mm, 1971–2000: 430 mm; Seeber 2015, http://www.geodata.us/weather/index.html, accessed January 2015). Lysimeter experiments show that the evapotranspiration closely depends on precipitation. Most of the atmospheric water input, except for heavy rainfall, is lost immediately by evapotranspiration (Coners et al. 2016).

Due to the highlands' relevance for global circulation changes, the surface properties have impacts on a large, possibly global, scale. In terms of landscape-level moisture cycles, pasture degradation leads to a shift from transpiration to evaporation because of reduced biomass, although the evapotranspiration changes are not significant over a longer period (Babel et al. 2014). Modelling indicates an earlier onset of convection and cloud generation, probably triggered by a shift in evapotranspiration timing when dominated by evaporation. Consequently precipitation starts earlier, and clouds decrease the incoming solar radiation. Thus the changes in surface properties by pasture degradation have a significant influence on larger scales with respect to the starting time of convection and cloud- and precipitation-generation: convection above a degraded surface occurs before, instead of after, noon. Due to the dominant direct solar radiation on the Tibetan highlands, the early-generated cloud cover reduces the energy input and therefore the surface temperature (Babel et al. 2014). This can have negative effects on the intensity of plant photosynthesis, and thereby reduces the ecosystem's ability to recover from degradation. The changes in the water cycle are, furthermore, influenced by global warming and an extended growing season (Fig. SI-3; Che et al. 2014, Shen et al. 2014, Yang et al. 2014). In many years, however, effects are overtaken by the water availability of the delayed onset of the summer rains.

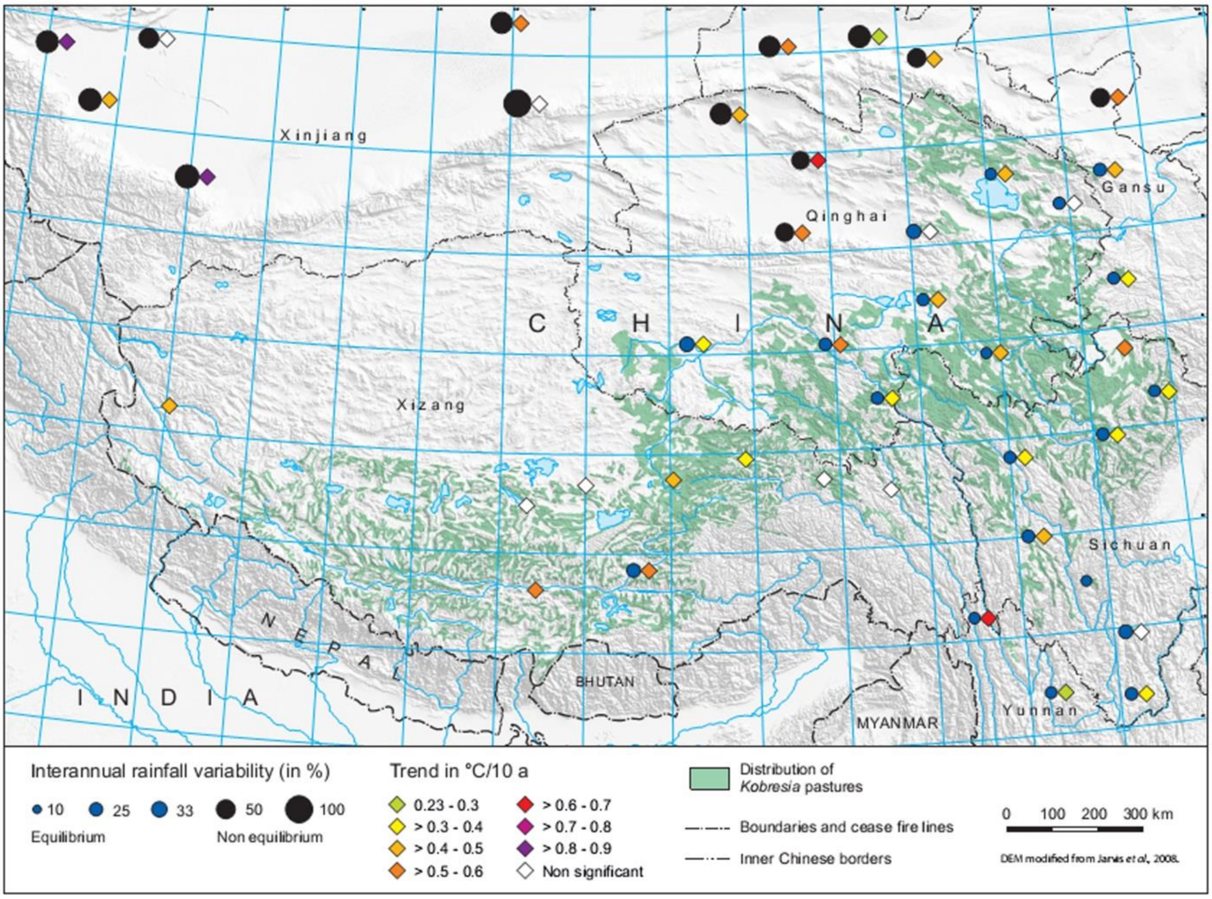

Figure SI-3: Inter-annual variability of summer rainfall sums defined as the standard deviation of summer rainfall sums divided by the mean summer rainfall sum across the Tibetan Plateau (June, July, August) between 1986 and 2015, and trends in summer mean temperatures (June, July, August) between 1985 and 2015 based on daily stations' observations from the Global Historical Climatology Network (GHCN-d; Menne et al. 2012). The trend is calculated from linear models and significance is derived using Mann-Kendall correlation techniques.

The status of the Kobresia cover and its root mat is nowhere of greater importance than in the permafrost areas of the Salween, Yangtze and Huang He headwaters, covering an area of approximately 180000 km². Their insulating effect buffers the melting of the permafrost; soil temperatures under a patchy vegetation cover of 30% were found to be 2.5 K higher than under a closed mat of 93% (Wang et al. 2008). The recent (1980–2005) increase in surface soil temperatures in the Huang He headwaters of 0.6 K per decade has led to a drastic increase of the depth of the thawing layer (Xue et al. 2009), and to a deterioration of Kobresia tibetica swamps. In summary, overgrazing induces degradation of root mats and leads to changes in water cycle and balance at both local and regional levels; this may decrease the recovery of damaged Kobresia pastures.

2.1.5 The carbon cycle

Kobresia turf is a key component of the C stocks and cycle in these pastures. The root : shoot ratio ranges from 20 (Li et al. 2008, Unteregelsbacher et al. 2012, Schleuss et al. 2015) up to 90 (Ingrisch et al. 2015), depending on season and grazing intensity. SOC storage within the root mat reaches up to 10 kg C/m^2 (Li et al. 2008, Unteregelsbacher et al. 2012, Schleuss et al. 2015), making up roughly 50% of the overall C stocks. Representing a highly significant C stock, the turf is also a highly active component of the C cycle, which receives the largest fraction of the photoassimilated C. For alpine Kobresia pastures at 4450 m, Ingrisch et al. (2015) showed that a large fraction of the assimilates is used for the build-up of new fine roots with a high turnover rate. The measured fluxes into below-ground pools, mainly associated with the root and released later as soil CO^2 efflux, were roughly twice as high as reported for pastures of K. humilis (C.A.Mey. ex Trautv.) Serg. (Wu et al. 2010) and montane K. pygmaea pastures at lower elevation (3440 m; Hafner et al. 2012). This emphasizes the importance of below-ground C allocation and cycling in alpine K. pygmaea pastures.

Net ecosystem exchange (NEE) measurements, derived by the eddy-covariance method, identified the alpine pastures at Kema as a weak C sink during the summer of 2010 with an ecosystem assimilation of 1.3 g $C\cdot m^{-1}\cdot day^{-1}$ (Ingrisch et al. 2015), which is roughly 50% smaller than recorded in pastures at lower altitudes (e.g., Kato et al. 2004, 2006, Zhao et al. 2006, Hirota et al. 2009), but agrees well with the results of a study by Fu et al. (2009) at a similar altitude. By combining the net ecosystem exchange measurements with pulse labelling, Ingrisch et al. (2015) were able to estimate absolute fluxes into the different ecosystem compartments during the main growing season. With a magnitude of 1 g C/m*day, the flux into below-ground pools was twice as high as the CO_2 efflux from soil, and 10 times larger than the flux into the above-ground biomass.

The key role of grazing for C sequestration and C cycling was demonstrated in two grazing exclusion experiments combined with $^{13}CO_2$ pulse labelling studies. The effect of grazing on the C cycle, specifically on differences in below-ground C stocks and C allocation, was shown for: (1) a montane Kobresia winter pasture of yaks, with moderate grazing regime, compared to a 7-year-old grazing exclosure plot, both at 3440 m (Xinghai; Hafner et al. 2012); (2) an alpine Kobresia pasture compared to a 1-year-old grazing exclosure, both at 4450 m (Kema; Ingrisch et al. 2015).

Short-term grazing exclusion in the alpine pasture affected only the phytomass of above-ground shoots, while neither C stocks nor assimilate allocation were altered (Ingrisch et al. 2015). In this system, roots and soil were of equal importance to C storage and cycling. By contrast, 7 years of grazing exclosure revealed that grazing is a major driver for below-ground C allocation and C sequestration in soils of montane Kobresia pastures (Hafner et al. 2012). Under a grazing regime, a higher fraction of assimilated C was allocated to below-ground pools; moreover, a larger amount was incorporated into roots and SOC. Fencing, in contrast, led to a significant reduction of C sequestration in the soil and fostered turf degradation, emphasizing the key role of grazing for the biogeochemistry of these ecosystems.

Based on the long-term grazing exclosure experiments in montane pastures, we conclude that the larger below-ground C allocation of plants, the larger amount of recently assimilated C remaining in the soil, and the lower soil organic-matter derived CO_2 efflux create a positive effect of moderate grazing on soil C input and C sequestration in the whole ecosystem. Due to the large size of the below-ground C stocks and the low productivity of the ecosystem, changes in the C stocks after cessation of grazing can be expected to take at least several years to become apparent. However, the roots in the turf mat are a highly dynamic component of the C cycle, which might have implications for the interannual variability of the C budget even on the landscape scale. The C cycle appears largely to be driven by grazing, supporting the hypothesis of the pastoral origin of the Kobresia ecosystem.

At Kema research station, synchronous measurements with micro-lysimeters, gas exchange chambers, ^{13}C labelling, and eddy-covariance towers were combined with land-surface and atmospheric models, adapted to the highland conditions. This allowed analysis of how surface properties, notably the disintegration of the Kobresia sward (i.e., degradation stages), affect the water and C cycle of pastures on the landscape scale within this core region. The removal of the Kobresia turf fundamentally alters the C cycling in this alpine ecosystem and its capacity of acting as a C sink (Babel et al. 2014).

2.1.6 Soils, productivity and plant nutrition

Kobresia lawns typically produce a felty root mat (Afe, ‘rhizomull’; Kaiser et al. 2008) up to 30 cm thick, which is situated on top of the predominant soils of Tibet’s pasture ecosystems – Leptosols, Kastanozems, Regosols, Cambisols and Calcisols (Fig. SI-4; Kaiser 2008, Kaiser et al. 2008, Baumann et al. 2009). The root mat consists of mineral particles, humified organic matter and large amounts of dead and living roots and rhizomes (Schleuss et al. 2015), and is formed in a loess layer of Holocene age (Lehmkuhl et al. 2000). The question still remains as to whether the Kobresia lawns and their root mat sealed a pre-existing Ah-horizon of a tall grassland, or if the lawns have grown up with the loess that they have accumulated (Fig. SI-4; Kaiser et al. 2008).

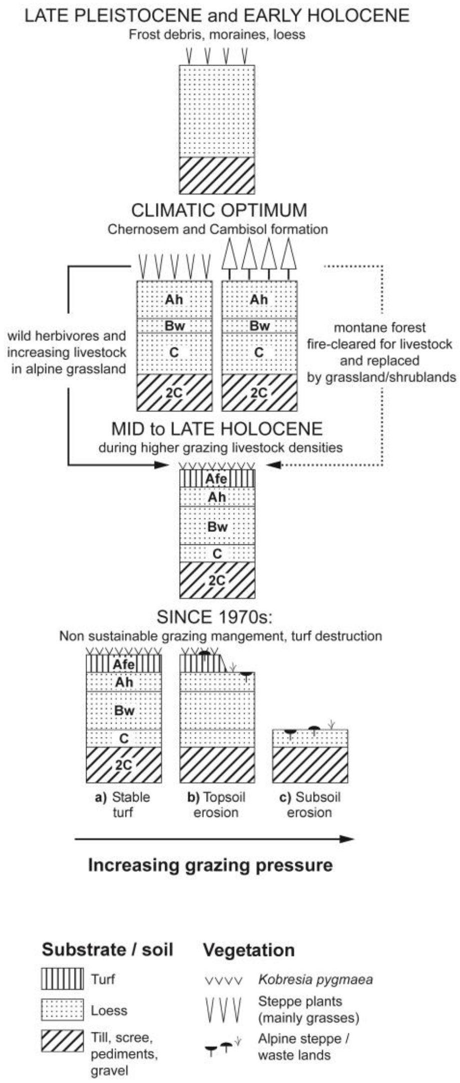

Figure SI-4: Hypothetical dynamics of soils in alpine grasslands of the southeastern Tibetan highlands. After Kaiser et al. 2008, Miehe et al. 2011*c*.

At the core alpine Kema study site, the root-mat is characterized by low bulk densities, moderate pH values, high SOC contents and a high effective cation exchange capacity (CEC), of which calcium (Ca_2^+) is the most abundant base cation (up to 80% of the effective CEC; Fig. SI-5). The root mat stores about 1 kg N/m and 0.15 kg P/m (0–30 cm; Fig. SI-5), but most nutrients are stored in SOM and dead roots and are not plant-available. Prevailing low temperatures and moisture hamper the mineralization of root residues and slow down nutrient release to plant-available forms (Hobbie et al. 2002, Luo et al. 2004, Vitousek et al. 2010). From this perspective, the relatively close soil C/N and C/P ratios (Fig. SI-5) do not necessarily indicate an adequate N and P supply. Further, P can be precipitated in the form of calcium-phosphates due to the high abundance of exchangeable Ca.

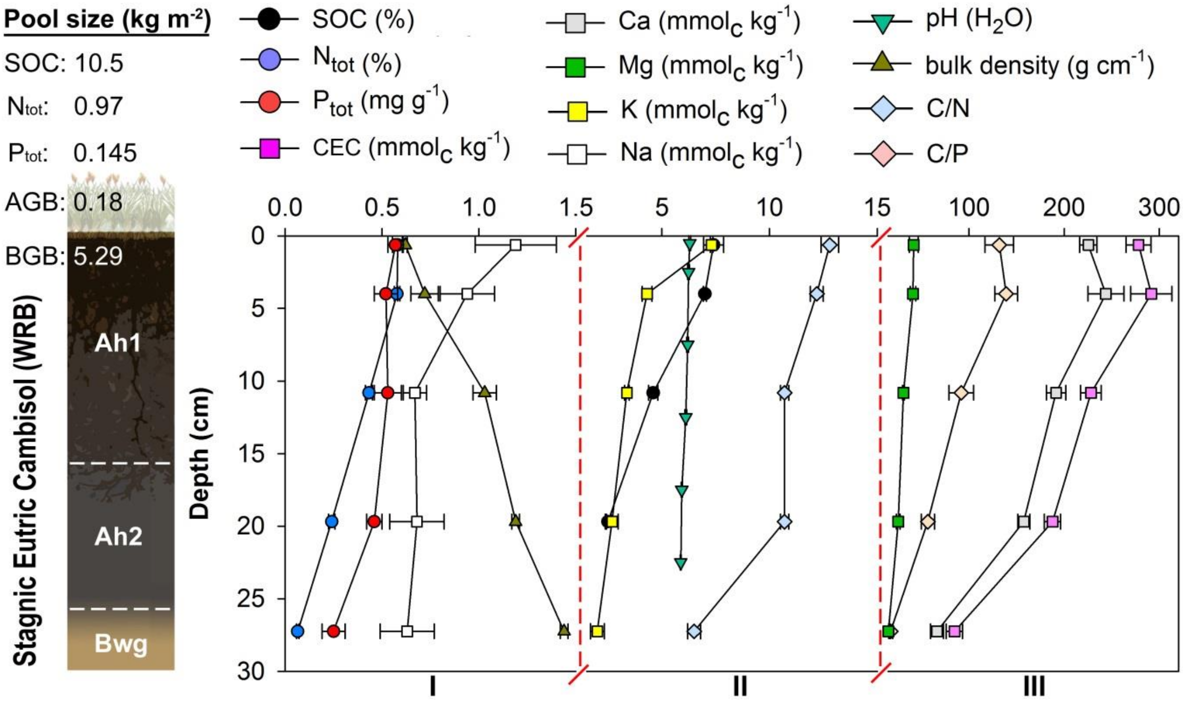

Figure SI-5: Basic characteristics of root mats at the Kema research sites in the *Kobresia pygmaea* core area. Pool sizes include below-ground-biomass (BGB), stocks of soil organic carbon (SOC), total nitrogen (N_{tot}) and total phosphorus (P_{tot}) down to 30 cm, and aboveground biomass (AGB). Note that the soil physical and chemical properties are plotted on three different scales (I: 0–1.5, II: 1.5–16, III 16–300). Data are represented as means (n = 4) and error bars indicate standard errors.

Indeed multiple limitations of N and P control pasture productivity, which is shown by increased Kobresia growth following single and combined applications of N and P fertilizers. Even though single applications of either N or P favor above-ground biomass on most sites throughout the Kobresia ecosystem, the productivity strongly increases after combined N and P application (Fig. SI-6). This finding was also supported by three years of single and combined application of potassium (K), N and P in alpine Kobresia pastures at the Kema station. Nitrogen fertilization increased above-ground productivity about 1.2–1.6 times, while NP addition resulted in 1.5–2.4 times higher values, whereas no effect was found for the below-ground biomass (Seeber 2015). Furthermore, fertilization increased the tissue concentrations of N, P and K in K. pygmaea and in accompanying herbs. Overall, fertilization experiments clearly indicate that co-limitations of N and P prevail in the Kobresia ecosystem.

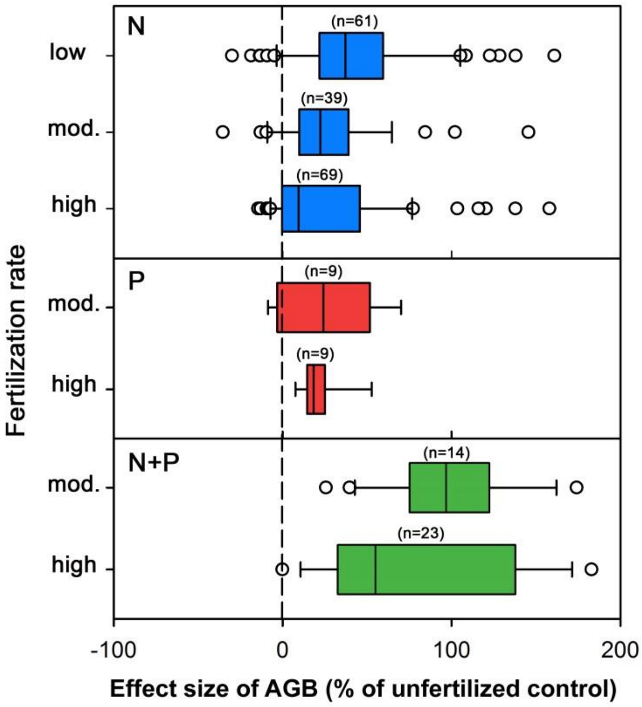

Figure SI-6: Effects of single and combined fertilization with N and P at varying rates on above-ground biomass (AGB) extracted from 35 studies from all over the *Kobresia* ecosystem. Shown are Whisker-Box-Plots with outliers (white circles) and median (black line in the box) for low, moderate and high application rates (for N: low = 0–25 kg/ha*yr, moderate = 25–50 kg/ha*yr, high >50 kg/ha*yr; for P: moderate = 0–50 kg/ha*yr, high >50 kg/ha*yr; for N+P: moderate = 0–50 + 0–50 kg/ha*yr, high >50+50 kg/ha*yr). The dashed line indicates no effects, with negative effects on the left and positive effects following fertilization on the right.

To mitigate nutrient limitations, and to enable productivity and competitive ability, Kobresia pygmea develops a dense network of roots and rhizomes. The high below-ground biomass (a) ensures an efficient uptake of nutrients (shown for ^{15}N; Schleuss et al. 2015) at depths and times when nutrients are released via decomposition; (b) makes K. pygmaea highly competitive for mineral N acquisition in comparison with other plant species (Song et al. 2007) and microbes (Xu et al. 2011, Kuzyakov and Xu 2013); (c) stores nutrients belowground, protecting them from removal via grazing, which ensures fast regrowth following grazing events to cover the high below-ground C costs. That considerable amounts of resources were allocated and stored below-ground was confirmed by labelling studies showing that about 45% of 13C (after 48 days) and 50% of 15N (after 45 days) were transferred into root biomass (0–15 cm) (Ingrisch et al. 2015, Schleuss et al. 2015).

In alpine Kobresia pastures around Kema the annual above-ground biomass productivity is low (~132 g/m2, S. Träger and E. Seeber [unpublished manuscript]) compared to below-ground plant biomass (0–15 cm horizon about 5–6 kg/m2; Seeber 2015). This corresponds well with other sedge-dominated montane and alpine Tibetan grasslands (134 g/m2) but is more than double that of the above-ground productivity of alpine steppes in the arid north-western highlands (56 g/m2; Ma et al. 2010).

Comparing montane (Xinghai) with alpine pastures (Kema) also revealed clear differences in above-ground productivity with altitude (montane: 185 g/m2, alpine: 132 g/m2; S. Träger and E. Seeber [unpublished manuscript]). Presumably the higher temperatures in Xinghai (Babel et al. 2014), together with a longer vegetation period and higher nutrient availability (N, P) due to enhanced mineralization rates in warmer sites, resulted in increased biomass production in montane as compared with alpine sites.

The above results refer to the scale of soil profiles and individual plots, and neither consider the redistribution of nutrients within the very heterogeneous landscape, nor account for the reallocation of nutrients by intensive grazing and animal movement. On a landscape scale the striking contrast between the widespread, chlorotic, yellowish Kobresia mats and the localised, bright-green, cattle resting places around settlements, points to the livestock-mediated nutrient translocation that has been described in Chinese and Mongolian steppes (Stumpp et al. 2005, Holst et al. 2007, Wesche and Ronnenberg 2010). Yak dung is the exclusive and indispensable fuel for highland nomads (Rhode et al. 2007). Dung collection has resulted in nutrient export since the onset of pastoralism, i.e., since the mid-Holocene up to 8000 year BP (Miehe et al. 2014, see below). Increased stocking rates and reduced migration distances since the late 1970s (Zhou et al. 2005) have certainly aggravated naturally existing gradients in nutrient availability with very high concentrations around villages.

2.1.7 Pasture health and degradation

The term ‘degradation’ can refer not only to widespread negative effects of rangeland management, but also to natural processes of ecosystem disturbance that are often poorly understood. On the Tibetan highlands, degradation is by no means equally distributed; it is more severe (1) in the vicinity of settlements, (2) on the lower slopes of southern exposures and (3) in the ecotone areas between steppes and alpine meadows with moderate rainfall (Miehe and Miehe 2000, Wang 2016).

The Kobresia ecosystem is an equilibrium grazing system with less than 33% interannual rainfall variability (Fig. SI-3; Ellis and Swift 1988, Ellis 1995, von Wehrden et al. 2012). In contrast to more variable (semi-)arid, non-equilibrium systems, grazing impact is not regularly set back by largescale loss of livestock caused by shortage of rainfall and thus forage. With their relatively stable forage resources, equilibrium systems may degrade if livestock numbers increase until the carrying capacity is exceeded. The impact of severe snowstorms that occur irregularly and regionally on the plateau, and lead to losses of livestock (Yeh et al. 2014), has not, however, yet been analysed with respect to forage availability. Snowstorms introduce another form of climate variability and may prevent livestock from increasing beyond the carrying capacity. The question, therefore, is whether the alpine grazing lawns are as vulnerable as other equilibrium pasture systems. With respect to the specific traits of the prevailing species, degradation threat may also be limited from a population-ecology perspective.

Estimates of grazing-induced degradation vary: the most frequently quoted value for the Tibetan highlands is that 30% of the grasslands are degraded (Harris 2010, Wang and Wesche 2016). It has been estimated that this degradation has led to a loss of approximately 2.95 Pg C in the highlands (Wang et al. 2002). The loss in ecosystem services caused by the C emission and N export associated with pasture degradation has been calculated to amount to $13315/ha (Wen et al. 2013) in the Dawu area; in the Ruoergai Plateau, also known as Zoige Plateau, the ecosystem services value expressed as a multiple of the gross domestic product (GDP) has decreased by about 84% between 1990 and 2005 (Li et al. 2010). Inconsistent definitions, unclear baselines, varying standards and indicator systems, as well as the merging of different spatial scales, result in uncertainties in these calculations. Desertification is often not differentiated from degradation (Wang et al. 2008, Cui and Graf 2009) and, in general, climate change and human impact are rarely separated (Chen et al. 2014, Zhou et al. 2014, Fassnacht et al. 2015, cf. He et al. 2015).

Remote sensing may offer an option for large-scale assessments of degradation, yet suffers from drawbacks. Degradation itself cannot be detected directly, and remote sensing requires extensive ground-truthing to calibrate and validate the results. Thus remote sensing can detect changes in degradation only over time, as it has been proposed by Lehnert et al. (2016) based on an area-wide plant cover dataset (Lehnert et al. 2015). The results show that degradation since the year 2000 is proceeding only in the less productive Kobresia pastures in the western part of the highlands, where it is driven mostly by a slight decrease in precipitation, in combination with rising temperatures. In contradiction to the widely assumed high importance of human influence on the degradation process, stocking numbers had a low effect on large-scale plant cover changes (Lehnert et al. 2016).

The value of large-scale remote-sensing-based assessments and models as tools are sometimes questionable, due to difficulties in properly selecting and interpreting spectral data (Yang et al. 2005). Fine-scale changes in vegetation and soils represent appropriate indicators for local, site-based assessments, but they are not easily detected by spectral data, and are not representative for the entire highland region. Thus pasture degradation is clearly a phenomenon with diverging regional gradients, depending on climate, soils and the regionally different impacts of rangeland management change.

Traditional nomadic systems cope with environmental heterogeneity, and variability in resource availability, by conducting seasonal migratory and other movements. Since the 1960s, government interventions have changed rangeland policies and led to an increase of sheep and goats by 100% in the early 1980s, causing severe damage to rangelands regionally (Zhou et al. 2005). State regulations nowadays focus on destocking, sedentarization, privatization and the fencing of pastures, thereby reducing the mobility and flexibility of the herders, with potentially severe consequences for the development of pastures and an increased threat of degradation (Qiu 2016). To maintain the ecosystem’s services the development and implementation of scientifically proven, and regionally sustainable, modern rangeland management systems are necessary.

Under optimum conditions Kobresia pygmaea builds almost closed, mono-specific, golf-course like lawns in high altitudes above 4600–4900 m (Fig. SI-7A and B). More common, however, are patterns showing degradation phenomena of uncertain origin and dynamics. The most widespread are (1) polygonal crack patterns (Fig. SI-7C) and the drifting apart of polygonal sods (Fig. SI-7D), (2) sods resting like stepping-stones on a deflation-pavement, otherwise covered with alpine steppe plants (Fig. SI-7E, F), and (3) patchwise dieback of the lawn in front of the burrows of soil-dwelling small mammals (e.g., Ochotona curzoniae

Hodgson, pika; Fig. SI-7H, J). All three patterns can be observed across the entire range of the ecosystem, but have been best documented in an ecotone stretching 200 km in width over 2000 km across the whole highlands between the Qilian Shan in the north and the Himalayas in the south (Miehe et al. 2011c).

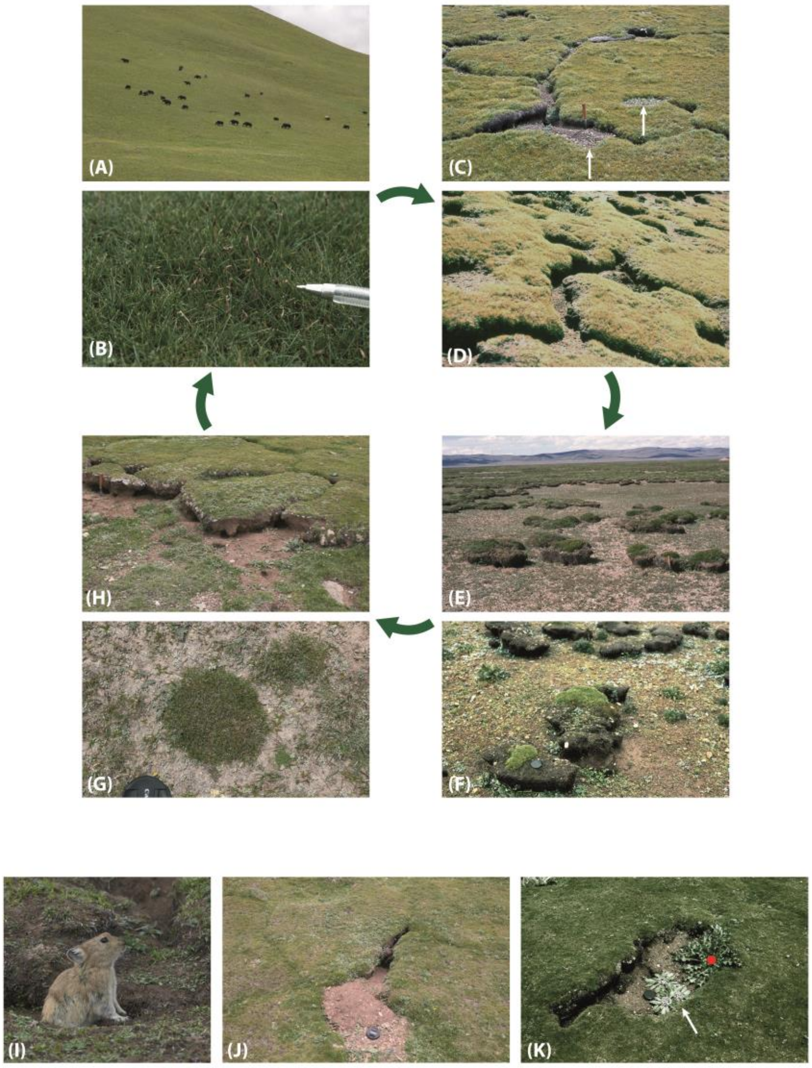

Figure SI-7: Autocyclic model of turf degradation in *Kobresia pygmaea* pastures. (AB) Closed grazing lawns are the best yak pastures. (C) Polygonal separation of the felty root mat, and D) downslope drift of the sods. (EF) The former turf cover is destroyed into stepping-stone like relics. The turf cliffs of 25 cm in height are corroded by needle-ice, wind and undercut by pika excavations. The surrounding open soil and gravel carry alpine steppe species. (GH) Recolonization of pancake-like *Kobresia pygmaea* mats in the open soil in front of the turf-cliff. (IJK) Pikas increase habitat diversity mainly through their digging; the excavated soil covers the lawns and root mats (J) A patchwise dieback of lawns and erosion of the felty root mat follows (*cf*. arrows in Fig. C). (K) The open soil is colonized by endemic annuals *Microula tibetica* (arrow) and *Przewalskia tangutica* (red dot). Photos G. Miehe 1994–2015.

Polygonal cracks are found all over the range of Kobresia lawns, but they occur only in root mats of more than 5 cm thickness. Interviews with herders confirm that low winter temperatures cause the cracking, but there also is evidence of desiccation effects (Miehe and Miehe 2000, Schleuss et al. [unpublished data]). Both extreme events cause changes in the volume of the sods. As soon as the root mat has reached a certain thickness, with a large portion of dead roots, tensions resulting from the volume changes lead to the formation of polygonal cracks. Overgrazing and trampling may play an additional role in weakening the stability of the root mat. On prevailing, inclined sites, polygons are separated while drifting downhill with gravity, frequently above a wet and frozen soil layer (Fig. SI-7D). The widening of the cracks is accompanied by high SOC losses (~5 kg C/m^2). Moreover, SOC loss was aggravated by decreasing root C input following root decay and SOC mineralization indicated by decreasing SOC contents with intensified degradation. A negative δ13C shift of SOC caused by the relative enrichment of ^{13}C-depleted lignin confirmed this mineralization-derived SOC loss (~2.5 kg C/m^2). Overall up to 70% of the SOC stock (0 cm to 30 cm) was lost in comparison with intact swards of alpine Kobresia pastures in the Kema region. Here, a degradation survey revealed that about 20% of the surface area has lost its Kobresia turf with bare soil patches remaining (Babel et al. 2014). Assuming that the whole Kobresia ecosystem has suffered from this type of degradation to a similar extent, and that the soil conditions in Kema are representative across the highlands, this would imply a total SOC loss of 0.6 Pg C for the whole ecosystem. Consequently a high amount of C is released back to the atmosphere as CO_2, or is deposited in depressions and rivers – leading to a decline of water quality at both landscape and regional levels (Schleuss et al. [unpublished data]).

The widening space between the crack margins is frequently, but not exclusively, used by pikas to dig their burrows, and they also undermine the ‘cliffs’ for deposition of their faeces. Excavated soil covers the lawns in front of their burrows (white arrows in Figs. SI-7C, J), which leads to dieback and decomposition of the felty root mat. Throw-off is also subject to erosion by wind and water. Through their burrowing activity, pikas may increase the ecosystem’s net emission of C (Qin et al. 2015), although Peng et al. (2015) could not find a direct effect of rodent activity on NEE in a Kobresia pasture. Bare soil patches are then colonized by endemic and often monotypic rosette plants (Fig. SI-7K). In the long run, the windward cliffs are eroded and the open soil patches slowly develop into a gravel surface, depending on the duration and intensity of deflation (west-winds during winter, foehn from the Himalayas during the monsoon in southern Tibet; Miehe 1988). The re-establishment of Kobresia pygmaea in those open soils with pancake-like mats (Fig. SI-7G, H) is less common than the destruction of the turf, and is restricted to the eastern part of its distribution range with >300 mm/yr precipitation (Miehe and Miehe 2000).

Another common pattern is found, mostly on south-facing slopes, where the lower parts lack any root mat, whereas the upper slope and the ridges are covered with lawns and their root mat. The mats form a steep cliff towards the slope with sods drifting downhill, probably along with gelifluction processes. The pattern suggests that the lower slopes had been derived from the lawns by erosion, and the opening of the root mat may have been initiated by yak when chafing and wallowing.

Patches of dead roots covered by crustose lichens or algae (Fig. SI-8) are scattered across the pastures without any apparent relation to abiotic or biotic factors. The patches are rarely recolonized by Kobresia pygmaea; rosettes of Lancea tibetica or Kobresia macrantha Boeckeler are more common.

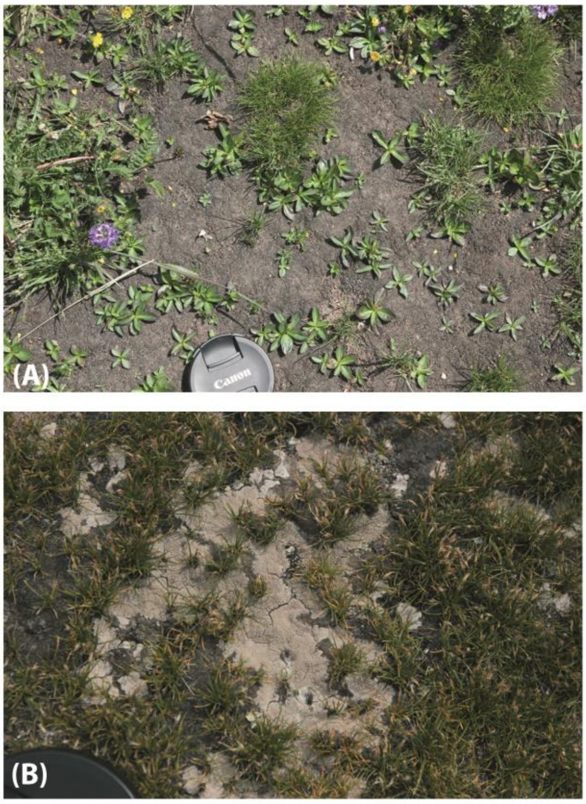

Figure SI-8: (A) Lichens and (B) Algae seal the felty *Kobresia* root mat. Photos G. Miehe 2009, 2015.

The most plausible explanation is dieback as a natural process with the ageing of a Kobresia clone, but this remains to be confirmed. Comparing the C cycle of closed lawns and crust-covered root mats by ^{13}C-labeled amino acids revealed that more ^{13}C remained in soil under crusts, reflecting less complete decomposition of exudates and lower root uptake (Unteregelsbacher et al. 2012). The crust patches decrease the rates of medium-term C turnover in response to the much lower C input. Very high ^{13}C amounts recovered in plants from non-crust areas, and a two-times lower uptake by roots under crusts, indicate that very dense root mats are efficient competitors with microorganisms for soluble organics. In conclusion, the altered C cycle of the crust-covered root layer is associated with strongly decreased C input and reduced medium-term C turnover.

In most parts of Tibet, severe changes in plant species composition and soil fertility are spatially restricted around camps where livestock rest during night and trample frequently (i.e., piospheres; Wang 2016). Heavy mechanical disturbance, in combination with excessive nutrient input (dung, urine), results in strongly altered vegetation and dieback of Kobresia pygmaea. The most extreme stage of degradation is a complete removal of mats (Ma et al. 1999), which can be found on landscape-scale on silty and sandy soils of the north-eastern highlands (e.g., Madoi 4300 m, 34°55’N/98°13’E; Ruoergai Plateau 3450 m, 33°35’N/102°58’E). The formation of this so-called “black soil” is widely attributed to unsustainable rangeland policies of overstocking in the late 1970 to 1980s. The bare soils are colonized by poisonous plants (Aconitum luteum H.Lév. and Vaniot) or by tiny, biennial, aromatic plants (e.g., Artemisia spp., Smelowskia tibetica Lipsky). It is here that pika densities are highest (Miehe et al. 2011c). In the Serxu County of the eastern highlands, 30% of the pastures have up to 4500 pika burrows/ha with 450 individuals, and an estimated harvest loss of 50% of the annual forage production (Zhou et al. 2005). Grazing exclosure experiments at Kema showed that pikas take the opportunity to avoid forage competition with livestock by excavating their dwelling burrows at a perennial grazing site or inside an undisturbed fence. Not only was the density of pikas higher inside the exclosure plots, but it was shown (by using colour marking) that a large number of pikas (with burrows outside the fence used its interior for foraging (at least 15%; M. Holzapfel [unpublished data]).

Sun et al. (2015) studied the impact of pikas around Dawu (3700 m, 34°37’N/100°28’E): at highest densities of 200–300 animal/ha, these caused a decrease in species richness, vegetation cover, plant height and seasonal biomass. This pattern seems not to be the rule in the highlands generally, because the most common disturbance indicators are forbs, and it is generally stated that pikas’ presence increases habitat diversity and plant species richness (Smith and Foggin 1999, Smith et al. 2006). Herders explain high pika densities as a consequence of overstocking, and not as the cause of pasture degradation (Pech et al. 2007). Pikas have been regarded as “pests” and poisoned; meanwhile the negative and long-lasting negative effects of poisoning on natural predators have been recognized and eradication programmes stopped (Pech et al. 2007).

2.1.8 Have grazing lawns formed as a consequence of pastoralism?

The ecosystem’s high proportion of endemics (Wu et al. 1994–2011, Miehe et al. 2011c) may indicate naturalness, and indeed Kobresia mats have been described as natural (e.g., Ni 2000, Song et al. 2004, Herzschuh and Birks 2010). With their tiny leaves, a root : shoot ratio >20, very low shoot biomass but a very large root system (Kaiser et al. 2008) and associated large C-storage, the Kobresia pygmaea lawns are one the world’s most extensive ecosystems with a very high below-ground share of biomass. Similar root : shoot ratios are known from other cold-adapted ecosystems including arctic tundra (Bazilevich and Tishkov 1997) and high alpine communities (Körner 2003), or from vegetation types exposed to extreme nutrient shortage like the Kwongan of western Australia (Lambers et al. 2010). Climatic parameters (Lehnert et al. 2015, 2016), including soil temperatures (Miehe et al. 2015) and the nutrient status (see section VI), cannot, however, explain the prevailing structures, at least for the montane pastures. The most likely explanation of the allocation patterns found in Kobresia lawns is nutrient shortage in combination with intensive grazing.

The Kobresia-dominated pastures are commonly known as ‘alpine meadows’, which is misleading in two ways. ‘Meadow’ in a European sense is an agriculturally managed grassland regularly mown for livestock forage (UNESCO classification; Ellenberg and Mueller-Dombois 1965–1966). The term meadow steppe is widely used in, for example, Mongolia (Hilbig 1995) and also refers to rangelands, yet of very different structure. In the Tibetan case the designation ‘pasture’ would be in most areas be correct (even where animal husbandry has no major impact). Whereas ‘alpine’ is defined strictly as a mountain climate not warm enough to allow for tree growth (Körner 2012), many ‘alpine meadows’ occur on the same slope as isolated tree-groves (Miehe et al. 2008c; Fig. SI-9) under a climate suitable for tree growth. Thus pastures within the drought-line of tree growth (200–250 mm annual rainfall; Miehe et al. 2008a), and at altitudes below the upper treeline (3600–4800 m across the eastern highlands between the Qilian Shan and southern Tibet), have presumably replaced forests (see Fig. SI-1: ‘forest relics’).

Figure SI-9: *Juniperus przewalskii* groves surrounded by *Kobresia* pastures (‘alpine meadow’, Qinghai Province, 3800 m, 35°45’N/100°14’E). Photo G. Miehe 1998.

If all pastures were climax vegetation, exclusion of livestock would have no effect. Plots of Kobresia grazing lawns being 2–5 cm in height were fenced in 1997 in southern Tibet (Reting; Fig. SI-10A), and in 2002 in the northeastern rangelands (Xinghai; Fig. SI-10B), both 300–400 m below the upper treeline. In the course of one year the lawns changed to tall Poaceae-dominated grassland 30–50 cm in height, and poisonous herbs decreased in cover (Miehe et al. 2014).

Figure SI-10: After exclusion of grazing, tall grassland overgrows lawns of *Kobresia pygmaea* giving evidence of its livestock-grazing-dependent status. (A) In Reting Forest (4250 m, 30°18’N/91°31’E) grazing lawns in a *Juniperus tibetica* woodland were fenced in 1997 and developed into a tall grassland in the first season after exclosure. Photo G. Miehe 2010. (B) In montane *Kobresia* pastures (Xinghai, 3440 m, 35°32’N/99°51’E) with a high abundance of poisonous grazing weeds (in flower: *Stellera chamaejasme*), tall *Stipa-Leymus* grasslands replaced the grazing lawns after fencing (2002) in the first season, and the grazing weeds disappeared. Photo G. Miehe 2015.

The degree of coverage of Kobresia also decreased, but the sedge still survived under the taller grasses. Thus grazing exclusion triggered a change from a sedge mat, with dwarf dicot rosettes, to a richly structured grassland, with elongated dwarf sedges and rosettes in its undergrowth. In truly alpine environments (Kema), effects of fencing (erected between 2009 and 2013) were small, with grasses increasing in cover from ~4% to 14% and reaching 15 cm in height, though this is still equivalent to a 7-fold increase of vegetation height. By contrast, Kobresia pygmaea leaf size increased only from ~1.8 cm to 2.4 cm (E. Seeber [unpublished data]). Shorter exclusion experiments in various locations in the southern highlands (Yan and Lu 2015) revealed an increase in vegetation cover, plant height and above-ground biomass, but, surprisingly, no change in species composition. Grazing exclusion experiments thus proved that a large share of the present 'alpine meadows' depend for their existence on grazing.

Changes from forest to grassland during the Holocene are well-documented (e.g., Herzschuh et al. 2006, Ren 2007, Miehe et al. 2014), yet the explanations are divergent. As the forest decline in various areas of the highlands took place during the mid-Holocene climatic optimum (Zhang et al. 2011), a climatic driver is not plausible. Given the huge climatic niche covered by current Kobresia pastures, grazing offers a more parsimonious explanation. With a total height of 2–4 cm and hardly any biomass within reach of grazers (Miehe et al. 2008b), grazing-adapted matted plants like Kobresia pygmaea and affiliated species will spread at the cost of taller plants. The high root : shoot ratios and the formation of a felty turf can also be viewed in this context. Grazing selection may also have promoted the expansion of grazing weeds. Phylogeographic studies on Stellera chamaejasme L. (Zhang et al. 2010), the prevalent grazing weed of Kobresia pastures (Fig. SI-10B), revealed a single haplotype over the whole of the highlands. Its presumably rapid expansion should also be explained in the context of livestock expansion.

Indeed, the Tibetan highlands have been grazed over evolutionary timescales by large herbivores (as testified by their richness, including endemic taxa; Schaller 1998). Former distribution, and natural densities, of these herbivores are largely unknown in Tibet, as they are in any other rangelands of the world; and shortcomings over the identification of pollen types (Miehe et al. 2009) render mapping of the historical extent of natural rangeland systems impossible. In any case animal husbandry has progressively replaced wild grazing, and there is anthracological and palynological evidence that herders extended the rangelands well into the montane forest belt (Kaiser et al. 2007, Miehe et al. 2008a, 2008c). Similar patterns have been described for the European Alps (Kral 1979) and the Himalayas (Miehe et al. 2015). This would explain why forests disappeared in spite of relatively favorable conditions, and also why montane pastures of Kobresia pygmaea change quickly after grazing exclusion. With increasing grazing pressure, biomass is increasingly allocated below-ground. Most probably the grazing lawns, and the felty root layer, can be interpreted as an adaptation to high grazing pressure. It remains unknown if the absence of a specific endemic fauna of soil beetles can be seen as an effect of an ecosystem under stress. Due to the specific traits of the prevailing species (especially growth habit), this equilibrium system is less threatened by overstocking than is the case in other equilibrium grasslands.

2.1.9 The Tibetan Anthropocene: For how long have humans shaped this environment?

The age and intensity of the human impact on Tibetan ecosystems is debated, and estimates based on evidence from various disciplines diverge by more than 20000 years. The earliest migrations and adaptation of Tibetans to high altitude hypoxia was dated to 30 ka BP with a second migration between 10 and 7 ka BP (Qi et al. 2013), to pre-LGM and 15 ka BP (Qin et al. 2010), or to 25 ka BP (Zhao et al. 2009), yet it remains uncertain where this mutation occurred (Madsen [submitted]). Human population genomic data suggest that the most critical EPAS1 genetic variant for hypoxia adaptation of Tibetans derived from extinct Denisovan people who hybridized with Tibetans and Han Chinese (Huerta-Sánchez et al. 2014). Whereas the Tibetan population retained this genetic variant, and its frequency increased due to the strong natural selection, it was lost in the Han Chinese and other groups. The widespread occurrence of artefacts, including stone tools, provide archaeological evidence for human presence on the plateau (Brantingham and Gao 2006, Bellezza 2008, Chen et al. 2015), but the dating of scattered surface remains difficult. While archaeology-based estimates of the time for the first intrusion of hunters range between 30 and 8 ka BP (Aldenderfer 2006, Brantingham et al. 2007), 14C- and OSL-dated remains suggest a more recent date, and that hunting parties first travelled in the region between 16 and 8 ka BP. Obsidian tools dated between 9.9 and 6.4 ka BP) have been shown to have been transported over more than 900 km (Perreault et al. 2016). In any case, humans have most probably travelled within the region during the Last Glacial Maximum (LGM). Long-term residential groups of hunters, or perhaps early pastoralists, may have settled in the area between 8 and 5 ka BP (Madsen et al. 2016), a date supported by independent evidence from the genomic signature of yak domestication (Qiu et al. 2015).

So far no direct proof has been forthcoming for early human impact on vegetation structures. The presence of humans is commonly associated with the use of fire, if fuel loads in the dry season are high enough (Bond and Keeley 2005); fire traces observed in Tibetan sediments may relate to human action (see Fig. SI-11). As highland plants lack obvious adaptations to fire (e.g., pyrophytes as present in the Boreal Forest, the South African Fynbos, or the Australian Kwongan) it seems unlikely that fire had been present over evolutionary timescales prior to human arrival. Lightning occurs nearly exclusively during the rainy season, followed by torrential rains. Between 2002 and 2005, 96% of lightning records of 36 climate stations in Qinghai Province occurred during the rainy season (Meteorological Service Qinghai [unpublished data]); lightning imaging sensors gave similar results for the central and eastern highlands (Qie et al. 2003).

The seasonality of the highland climate favors the use of fire as a tool to modify vegetation structures. This is especially true for the mid-Holocene climatic optimum between 10 and 5 ka BP, when summer growing conditions were wetter and warmer than present (Zhang et al. 2011), resulting in a high fuel load available for burning during the dry cold winter. Fires lit by hunters were most probably the first impact, as they are associated with the first intrusion of humans in other parts of the world (e.g., Ogden et al. 1998). Landscape-scale management by burning has probably intensified with the introduction of livestock grazing: forests were burnt to provide better pastures, and to destroy places of concealment for predators. Charcoal of Picea (P. crassifolia Komarov) and Juniperus (J. przewalskii Komarov) has been found in the north-eastern highland pastures, where current precipitation is double the minimum amount of rainfall necessary for tree growth. Moreover, these sites are situated at altitudes 200–400 m below the upper treeline (Miehe et al. 2008c). Dating of the charcoal implies ages between 10 and 7.4 ka BP (Kaiser et al. 2007). On the south-eastern slope (Hengduan Shan, 4200 m, 31°06’N/99°45’E), fire has been recorded since 13 ka BP, and a decline of Betula pollen between 8.1 and 7.2 ka BP occurs synchronously with charcoal peaks (Kramer et al. 2010). Other charcoal records of burned shrubs date back to 48.6 ka BP (Kaiser et al. 2009). Phylogeographic analyses of now disjunct forest relicts (Picea crassifolia, Juniperus przewalskii) with shared haplotypes across the northeastern pastures suggests that post-glacial recolonization resulted in continuous forests (Zhang et al. 2005, Meng et al. 2007), that have been opened up and fragmented more recently by pasturing.

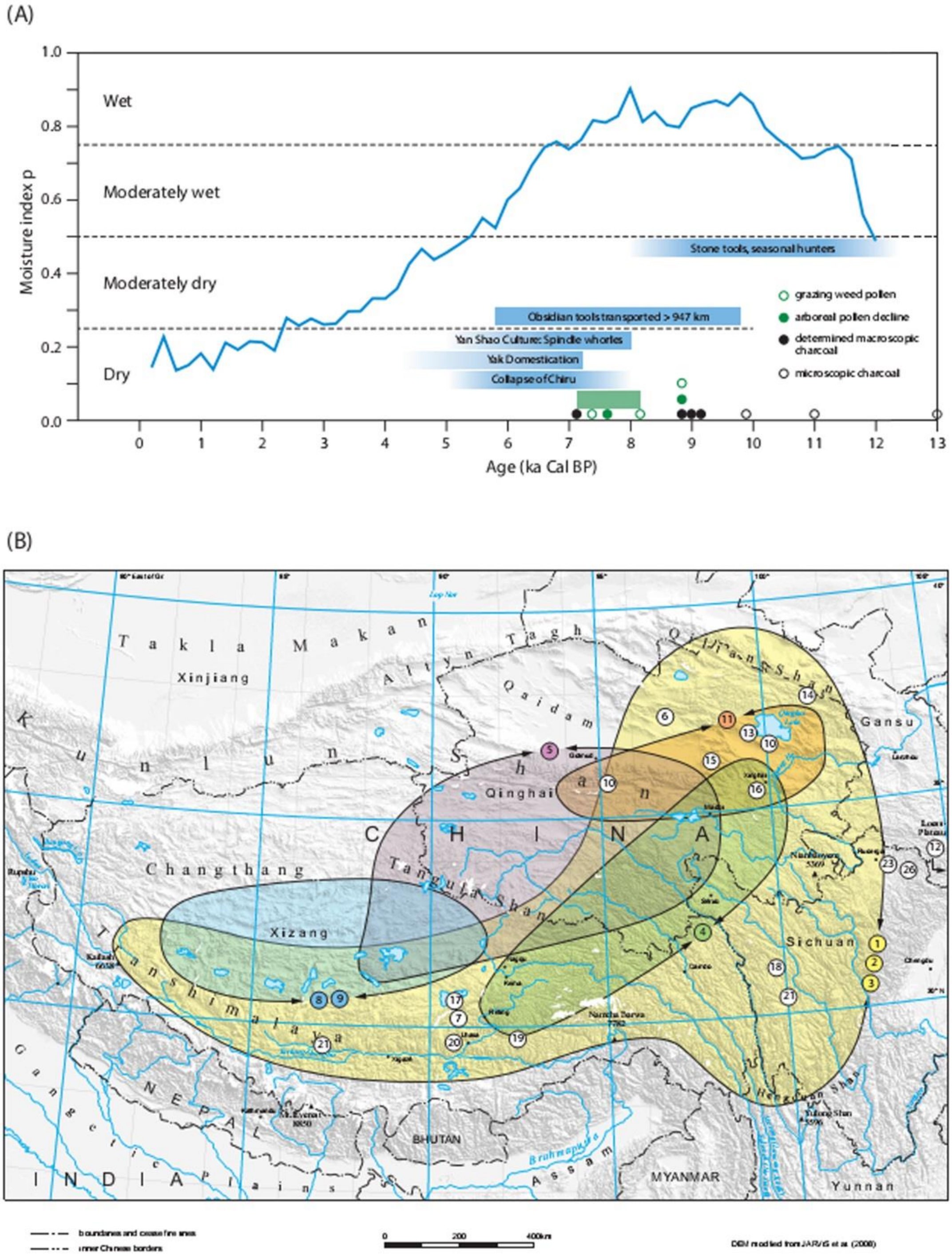

Figure SI-11: Summary diagram of moisture conditions and evidence of human impact during the early Anthropocene in the Tibetan highlands: The use of fire by early hunters changed vegetation structures from forest to grassland from the time of the mid Holocene climatic optimum. The present grazing lawns have developed with increasing grazing pressure since the onset of pastoralism. After data of Zhang et al. 2011, and the sources mentioned in the table (all ages in ka cal. BP). References are given in the Supplementary Material Table SI-2.

Table SI-2: Evidences of human impact on the Tibetan Plateau according to different authors.

	Area	Method	Evidence	Time (cal. ka BP)	Source
1	Southern Tibet, Hengduan Shan	Mitochondrial human DNA	High altitude adaptation	>21	Zhao et al. 2009
2	Tibetan highlands	Mitochondrial human DNA	Phylogeographic evidence of plateau-specific sublineages	30 and 10-7	Qi et al. 2013
3	Tibetan highland, Gansu	Phylogeography	Yak-domestication	7.7	Qiu et al. 2015
4	Eastern highlands	Phylogeography	Rapid expansion of grazing weed haplotype	Holocene	Zhang et al. 2010
5	Northern highlands	Phylogeography	Population collapse Chiru	8–5	Du et al. 2010
6	Xiao Qaidam	Archaeology, OSL	Stone tools	35–33/3–11	Huang 1994, Sun et al. 2010
7	Southern Tibet	OSL	Hand- and footprints	26–21	Zhang and Li 2002
8	Changthang	Archaeology	Stone tools	‘Palaeolithic’	Aldenderfer and Zhang 2004
9	Changthang	Archaeology	Microlithic stone tools	25–15	Brantingham et al. 2001
10	Changthang + Qinghai Lake (Jiangxigou2, Xidatan2)	Christallography, Archaeology, ^{14}C	Obsidian tools transported over 947 km	9.14–5.58 9.9–5.4	Perreault et al. 2016
11	Northeastern highlands	Archaeology, ^{14}C	Stone tools in hearth middens of seasonal hunters	16–8	Madsen et al. 2016
12	Loess Plateau	Archaeology	Spindle whorles Yan Shao Culture	8–5	Parzinger 2014
13	Qinghai Lake	Palaeopedology	Picea charcoal	9.2	Kaiser et al. 2006
14	Lake Luanhaizi	Palaeopedology	*Picea* charcoal	8.9	Kaiser et al. 2006
15	Dulan	Palaeopedology	*Juniperus* charcoal	7.2	Kaiser et al. 2006
16	Xinghai	Palaeopedology	*Juniperus* charcoal	9.0	Miehe et al. 2008
17	Damxung	Sedimentology	Microscopic charcoal	<13	Miehe et al. 2009
18	Hengduan Shan	Sedimentology	Microscopic charcoal	>13	Kramer et al. 2010
19	Rutok	Sedimentology	Microscopic charcoal	11	La Duo 2008
20	Nienang	Sedimentology	Microscopic charcoal	>9.8	La Duo 2008
21	Nangla Lu	Sedimentology	Microscopic charcoal	>9.8	Miehe et al. (*unpublished data*)
22	Lake Luanhaizi	Palynology	Arboreal pollen decline	7.8	Herzschuh et al. 2006
23	Ruoergaoi Plateau	Palynology	Arboreal pollen decline	8.8	Yan et al. 1999
24	Hengduan Shan	Palynology	Arboreal pollen decline	8.1–7.2	Kramer et al. 2010
25	Damxung	Palynology	Grazing weeds	8.8	Miehe et al. 2014
26	Nianbaoyeze	Palynology	Grazing + ruderal weeds	7.3	Schlütz and Lehmkuhl 2009
27	Nangla Lu	Palynology	Grass-pollen decline, grazing weeds appear	8.2	Miehe et al. (*unpublished data*)

Charcoal and pollen records point to a forest decline (Picea, Betula) after between 8 and 6 ka BP (Shen et al. 2005, Herzschuh et al. 2006, Cheng et al. 2010, Miehe et al. 2014), at a period that, according to the human impact-independent proxy of Ostracod assemblages (Mischke et al. 2005), was the most favorable climatic period of the Holocene. As the pollen record does not show the usual post-fire succession (Epilobium>Populus>Betula), it is plausible that humans suppressed forest recovery because they preferred grassland for their livestock instead of forest. In the forest ecotone of the eastern highland slope (Nianbaoyeze, 33°22’N/101°02’E), the fire record covers the whole of the Holocene, while pollen of ruderals (Tribulus) and grazing weeds (Stellera chamaejasme) start to appear around 7.3 ka BP (Schlütz and Lehmkuhl 2009, Miehe et al. 2014). Pollen-diagrams from Kobresia-swamps of the Ruoergai Plateau (650 to 780 mm/yr; Yan et al. 1999) show an abrupt forest pollen decline around 8.8 ka BP, followed by increased values of Poaceae and Chenopodiaceae, similar to a pollen-sequence typical for the ‘landnam’ in Europe (Frenzel 1994).

In southern Tibet (Damxung 4250 m, 30°22’N/90°54’E; Miehe et al. 2009), the charcoal record since the Late Glacial is uninterrupted; and the most common human-indicator pollen types (Stellera chamaejasme, Pterocephalus, Cyananthus, Plantago) first appear around 8.5 ka BP. As the endemic large herbivores in Tibet have similarly selective grazing habits to those of livestock (Miller and Schaller 1996), the increase of grazing weeds could well be a result of increased numbers of wild herbivores. Phylogeographical analysis of Panthelops hodgsonii Abel (chiru, Tibet antelope), however, shows a clear decrease in herd-size during this period (Du et al. 2010), probably synchronous with the domestication of the yak (7.3 ka BP; Qiu et al. 2015). Spores of dung fungi (Sporormiella), indicate pasture degradation in Damxung over the last 1200 years, and Glomus spores show that roots had been exposed through erosion. Other sites in southern Tibet (Rutok, 29°41’N/92°16’E, Nienang, 29°43’N/90°42’E; van Leeuwen in La Duo 2008) show charcoal peaks between 11.3 and 6 ka BP.

The archaeo-zoological record of early animal husbandry and agriculture is still very limited; earliest fossil records of domestic yak reveal ages of only 3.8 ka BP (Flad et al. 2007), which are similar to the oldest records of cereals (barley in the northeastern highlands: 4 ka BP, in the Yarlung Zhangbo valley: 3.4 ka BP; Setaria italica (L.) P.Beauv. on the eastern slope of the highlands: 4.6 ka BP; Chen et al. 2015, d’Alpoim Guedes 2015). The permanent human occupation of the highlands is thought to have depended on mutual exchange between cereal farmers (trading barley as the key staple food of Tibetans) and pastoralists (giving animal products and salt), and has thus been dated as younger than 3.6 ka BP (Chen et al. 2015). Recent genomic evidence, however, implies a much older date for the domestication of the yak (7.3 ka BP; Qiu et al. 2015).

One of the most important prehistoric excavations in China, near Xian on the Loess Plateau, is possibly also relevant for the question of the onset of pastoralism in the Tibetan highlands: In settlements of the Yangshao Culture (7–5 ka BP; Parzinger 2014), spindle whorls, found in large quantities, most probably testify to the weaving of sheep wool. Whether similarly aged bones of Caprini found at those sites are of domestic origin or not, is unclear (Flad et al. 2007). Given that sheep must have been introduced from their centre of domestication in the mountains of the Middle East (Zeder and Hesse 2000), and that Tibet is 1600 km closer to this centre of origin than is Xian, pastoralism may have onset earlier in the former than the latter. If we hypothetically apply the same rate of diffusion of the Neolithic Package from the centre of domestication towards Europe (3 km/yr from the Zagros Mountains in western Iran to the south-east European Vojvodina; Roberts 1998), then domestic sheep and goats may have reached the Tibetan highlands around 8.6 ka BP. The question of when increased livestock numbers first had an impact on plant cover, and the below-ground C allocation that forms the felty root mats, is still, however, unanswered.

2.1.10 Conclusions

The Kobresia pastures of the Tibetan highlands are a nutrient- and water-limited high-altitude ecosystem. They form equilibrium rangeland systems, yet their vulnerability to grazing degradation is limited due to the prevalence of a dwarf sedge with its main above-ground phytomass below the grazing reach of livestock.

Mats are characterized by a felty root layer that represents a larger carbon (C) store. Natural degradation phenomena with polygonal crack patterns and the drifting apart of polygonal sods are widespread. The widening of the cracks is accompanied by high SOC losses (~5 kg C/m^2). Overall up to 70% of the SOC stock was lost in comparison with intact swards of alpine Kobresia pastures. Assuming that the whole Kobresia ecosystem has suffered to a similar extent, this would imply a total SOC loss of 0.6 Pg C for the whole southeastern highlands. Consequently a high amount of C is released back to the atmosphere as CO2, or is deposited in depressions and rivers.

Pastoralism may have promoted Kobresia pygmaea and is a major driver for below-ground C allocation and C sequestration, stabilizing these mats with their distinctive C allocation patterns. Grazing exclosure experiments show that the larger below-ground C allocation of plants, the larger amount of recently assimilated C remaining in the soil, and the lower soil organic-matter derived CO2 efflux create a positive effect of moderate grazing on soil C input and C sequestration in the whole ecosystem.

Due to the highlands' relevance for atmospheric circulation patterns, surface properties of these pastures have an impact on large, possibly global, spatial scales. The removal of the lawns, caused by climatic stress as well as excessive human impact leads to a shift from transpiration to evaporation in the water budget, followed by an earlier onset of precipitation and decreasing incoming solar radiation, resulting in changes in surface temperature, which feedback on changes in atmospheric circulations on a local to regional scale.

The age of the world's largest alpine ecosystem, and its set of endemic plants and animals, remains a matter of considerable dispute, though the degree of this uncertainty is rarely admitted (reviews in Liu et al. 2014, Favre et al. 2015, Schmidt et al. 2015, Renner 2016). Further calibrations based on genomic data and fossils (where available) are needed to clarify evolutionary relationships and divergences between the currently recognised species of Kobresia.

The palaeo-environmental evidence, as well as simulations, suggest that the present grazing lawns of Kobresia pygmaea are a synanthropic ecosystem that developed through selective free-range grazing of livestock. The age of the present grazing lawns, however, is not yet known. The presence of humans using fire and replacing forests by grassland may date back as far as the LGM, while archaeological evidence for the onset of pastoralism is missing. A multi-proxy approach, however, suggests a mid-Holocene climatic optimum age.

The traditional migratory, and obviously sustainable, rangeland management system conserved and increased the C stocks in the turf and its functioning in the regional and global C cycles. However, rangeland management decisions within the past 50 years have caused widespread overgrazing leading to erosion and reducing the C sink strength. Considering the large area of the grasslands, even small reductions in carbon sequestration rate would affect the regional carbon balance, with possible impacts on the future climate of China and beyond.

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2.1.12 References

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2.2 Study II: Nitrogen uptake in an alpine Kobresia pasture on the Tibetan Plateau: localization by ^{15}N labelling and implications for a vulnerable ecosystem

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2.2.1 Abstract:

Grasslands are very important regionally and globally because they store large amounts of carbon (C) and nitrogen (N) and provide food for grazing animals. Intensive degradation of alpine grasslands in recent decades has mainly impacted the upper root-mat/soil horizon, with severe consequences for nutrient uptake in these nutrient-limited ecosystems. We used ^{15}N labelling to identify the role of individual soil layers for N-uptake by *Kobresia pygmaea* – the dominating plant in the degraded Tibetan pasture ecosystems. We hypothesized a very efficient N-uptake corresponding mainly to the vertical distribution of living roots (topsoil > subsoil). We assume that *K. pygmaea* develops a very dense root mat, which has to be maintained by small aboveground biomass, to enable this efficient N-uptake. Consequently, a higher N-investment into roots compared to shoots was hypothesized.

The ^{15}N recovery in the whole plants (~70%) indicated very efficient N-uptake from the upper injection depths (0-5 cm). The highest ^{15}N amounts were recovered in root biomass, whereby ^{15}N recovery in roots strongly decreased with depth. In contrast, ^{15}N recovery in shoots was generally low (~18%) and independent of the ^{15}N injection depth. This clearly shows that the low N demand of *Kobresia* shoots can be easily covered by N-uptake from any depth. Less living root biomass in lower versus upper soil was compensated by a higher specific activity of roots for N-uptake. The ^{15}N allocation into roots was on average 1.7 times higher than that into shoots, which agreed well with the very high R/S ratio. Increasing root biomass is an efficient strategy of *K. pygmaea* to compete for belowground resources at depths and periods with available resources. This implies high C costs to maintain root biomass (~6.0 kg DM m^{-2}), which must be covered by a very low amount of photosynthetically active shoots (0.3 kg DM m^{-2}). It also suggests that *Kobresia* grasslands react extremely sensitively towards changes in climate and management that disrupt this above-/belowground trade-off mechanism.

2.2.2 Introduction

The Tibetan Plateau (TP) is the world’s largest alpine grassland ecosystem and is also one of the largest pastoral high altitude ecosystems, with year-round grazing of yaks, sheep and goats of the Tibetan nomads. The grazing lawns of the TP are 2–4 cm in height and are dominated by the Cyperaceae *Kobresia pygmaea* (C.B. CLARKE). The *K. pygmaea* ecosystem covers an area of approximately 450,000 km² and is thought to derive at least partly from human activity by moderate grazing pressure and partial deforestation during the Holocene (Miehe and others 2009; Miehe and others 2014). The *Kobresia* ecosystems are important both regionally and globally by providing grazing ground (Gao and others 2014), their impact on the Asian climate system (Boos and Kuang 2010) and their high storage of carbon (C) and nitrogen (N) with regard to climate change (Genxu and others 2002; Yang and others 2008; Liu and others 2012).

Plant growth in alpine ecosystems is limited by unfavourable environmental conditions: low temperature, water scarcity, high solar radiation and nutrient deficiency (Callaway and others 2002; Körner 2003; Hermans and others 2006). Alpine plants compete under these stressful conditions by developing specific strategies to ensure survival and reproduction (Choler 2005; Onipchenko and others 2009). Livestock grazing is an additional stress factor in many alpine ecosystems, changing the vegetation and soils (Heitkamp and others 2014; Sylvester and others 2014). This requires the plants to acquire and utilise resources very efficiently.

Kobresia pygmaea develops very compact root mats that vary in thickness between 5 and 30 cm (Kaiser and others 2008; Miehe and others 2008). These root mats protect against mechanical degradation by trampling and also support rapid regrowth following grazing events (Miehe and others 2011). Nonetheless, large grassland areas of the TP are already degraded (Holzner and Kriechbaum 2001; Harris 2010). Grassland ecosystems on the TP react extremely sensitively towards increasing grazing pressure and climate change (Du 2004), but the drivers and mechanisms of grassland degradation and the impacts due to a changing environment remain unclear (Chen and others 2013). A few studies have shown that increasing temperature and intensified livestock management accelerate C and N mineralisation (Gao and others 2008; Yang and others 2013). Therefore, both N availability for plants and N loss via leaching might increase (Klein and others 2004; Gao and others 2007).

Nitrogen limits net primary production in many terrestrial ecosystems (Vitousek and Howarth 1991; LeBauer and Treseder 2008), and variations in N-availability can therefore have large impacts on plant growth and ecosystem recovery, especially in ecosystems such as alpine grasslands (Xu and others 2014). Nitrogen limitation mainly occurs due to low deposition rates, a high proportion of immobilised N in organic form, and a low N-mineralisation and N-fixation rate caused by low temperature and a short vegetation period (Wang and others 2005; Xu and others 2006; Lü and Tian 2007; Liu and others 2011; Zhang and others 2012). Moreover, the dung of the main herbivore, the yak, is completely collected by nomads and serves as their only fuel source (Rhode and others 2007). As an obvious sign of N deficiency, many *K. pygmaea* grasslands are coloured green-yellowish, which contrasts with the fertilized grounds around settlements and cattle resting places (Stumpp and others 2005; Wesche and Ronnenberg 2010). Grassland degradation has been extensive in recent decades and has destroyed mainly the upper root-mat/soil horizon (Wang and others 2005; Babel et al. 2014). This makes the recapture of nutrients by roots from deeper soil layers potentially important.

Little is known about the development and future response of these sensitive grasslands against the background of climate and land-use changes. Understanding the drivers of degradation requires demonstrating the mechanisms of nutrient partitioning within the soil–plant system and their uptake in non-degraded grasslands. Here, we attempt to fill this gap in our knowledge using a ^{15}N-labelling experiment. Nitrogen uptake and N allocation were investigated within the soil–plant system in non-degraded *K. pygmaea* grasslands; ^{15}N-urea was injected into the soil into six depths and ^{15}N was analysed in samples of shoots, roots and soil after 45 days. We hypothesize that the ^{15}N-uptake of shoots, roots and total plant biomass strongly depends on the vertical distribution of living root biomass (topsoil > subsoil). Consequently, decreasing ^{15}N recovery rates are expected when ^{15}N tracer is injected into deeper soil (Hypothesis 1). Since alpine *Kobresia* pastures are assumed to be N limited, we further expect that *K. pygmaea* has developed specific mechanisms for very efficient N-uptake reflected by high ^{15}N recovery rates in total plant biomass (Hypothesis 2). We further hypothesize the ^{15}N incorporation into root biomass will be much higher than into shoot biomass to guarantee an efficient N-uptake. This would involve higher below- than aboveground investments and also be reflected by high R/S ratios (root to shoot ratio) for alpine *Kobresia* pastures (Hypothesis 3).

Due to the long-term moderate grazing history of *Kobresia* pastures, we assume that K. *pygmaea* developed a very efficient trade-off between the allocations of assimilates between roots and shoots. Nonetheless, this implies that this ecosystem might react extremely sensitively towards changes in climate and management that potentially disrupt this trade-off mechanism. This can presumably explain why degradation during the last decades strongly affected this ecosystem.

2.2.3 Materials and methods

2.2.3.1 Site description

The study was conducted within the vegetation period from June to September 2012 at the *Kobresia* Ecosystem Monitoring Area research station (KEMA) on a gently inclined alpine grassland pasture (Xizang, China; 31°16'45''N, 92°59'37''E; 4,410 m a.s.l., inclination of 2–5%, Babel and others 2014). The site is located in the core area of *K. pygmaea* distribution (Miehe and others 2008). *Carex* spp., *Festuca* spp., *K. humilis*, *Poa* spp., *Stipa purpurea* and *Trisetum* spp. are present in addition to *K. pygmaea*, which is the dominant and eponymous species (covering up to 98% of the root-mat surface).

The mean summer precipitation (June–September) of the area (Climate station Nagqu, 4,507 m a.s.l.) is 272 mm, ranging from 21 to 442 mm (Miehe and others 2011). The pasture quality is highly dependent on the onset and duration of the summer rain. Although the vegetation period lasts from mid-May to mid-September, the greening of the pastures can be delayed until early August. Winter snowfall is comparably low. The mean maximum temperature of the warmest month (July) is 15.1°C (Miehe and others 2011; Miehe and others 2014). During the 45-day experiment, a mean air temperature of 10.4°C and a total precipitation of 162 mm were recorded. Forty-five percent of this precipitation fell within four days at the beginning of this experiment.

Soils are classified as Stagnic Eutric Cambisol (Humic, IUSS Working Group WRB 2006) and developed on a Holocene loess layer of variable thickness (0–30 cm), overlying a glacial moraine. The mineral soil (0–25 cm) consisted of 50.4 ± 1.3% sand, 33.0 ± 0.9% silt and 16.6 ± 0.7% clay and is therefore defined as loam. Soils were free of carbonates (0–25 cm) and showed mean pH values (H_2O) of 6.85 ± 0.03, which marginally changed with depth. The top-soils were characterized by dense *Kobresia* root mats (up to 15 cm thick, Figure SII-1). These root mats consisted mainly of mineral particles, humified organic matter and large amounts of dead and living roots. Thus, soils store high amounts of C and N (soil and roots in 0–25 cm: 15.2 ± 0.43 kg C m^{-2} and 1.0 ± 0.03 kg N m^{-2}, Figure SII-1). A detailed description of general soil and root characteristics is provided in Table S1 (supplement).

Traditionally, the site was used as a grazing ground for livestock (yaks, sheep) from January to April, and large numbers of small mammals (mainly the Plateau Pika, *Ochotona curzoniae*) compete with livestock for plant biomass resources.

2.2.3.2 Labelling and sampling

The ^{15}N labelling experiment started on 20 July 2012 and lasted for 45 days. Plots (15 × 15 cm) that were dominated by *K. pygmaea* were randomly selected and a total amount of 2.6 mg ^{15}N was added as urea to each plot (99 atom% ^{15}N, Sigma Aldrich). The ^{15}N urea was injected into the soil at six depths, representing treatments within this field experiment (treatments = input depths: 0.5 cm, 2.5 cm, 7.5 cm, 12.5 cm, 17.5 cm and 22.5 cm, Figure SII-1). For each injection depth, four replicate plots were sampled, yielding a total of 24 plots. To ensure equal distribution of tracer in each depth, we used a uniform labelling grid with 16 injection points and pierced the root mats with a small metal pin. One mL of ^{15}N-labelled urea solution was injected using a dispensing pipette. During the experiment, grazing was excluded by choosing plots within a fenced area.

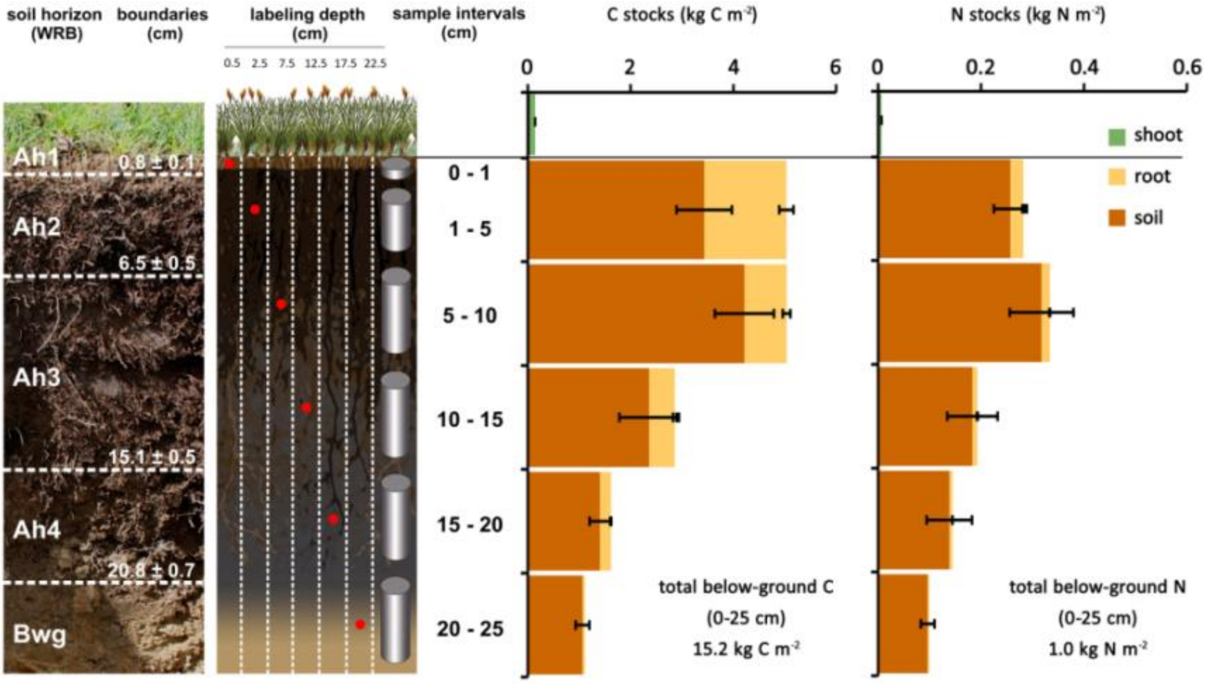

Figure SII-1: Characteristics of the upper 25 cm of soils and an overview of the applied study design at the KEMA study sites. The image shows the appropriate soil horizons and their boundaries (n = 4), summarizes the applied experiment and its design, with dots marking the selected injection depths, and illustrates the C and N stocks for shoots, roots and soil, with standard errors (n = 24).

Samples of shoots, roots and soil were taken from each plot 45 days after ^{15}N addition. Root and soil samples were collected at sample intervals of 0–1 cm, 1–5 cm, 5–10 cm, 10–15 cm, 15–20 cm and 20–25 cm depth (Figure SII-1). Four soil pits (30 cm length × 30 cm width × 40 cm depth) were established adjacent to the plots to determine root and soil characteristics. Samples for ^{15}N natural abundance, pH, soil texture, bulk density, living and dead root biomass were taken at the corresponding sample depth intervals. Soil samples were sieved (2 mm), and the separated roots were washed in distilled water. The shoot biomass was cut directly on the plots in an area of 25 cm^2. Eight control samples for shoot biomass and for ^{15}N natural abundance were cut next to the soil pits. All samples (shoots, roots, soil) were dried and then milled.

2.2.3.3 Analyses and calculations

Basic plant and soil characteristics: Bulk density was determined from dried (105°C) undisturbed soil cores (van Reeuwijk 2002). Carbon and N stocks (kg m^{-2}) were calculated by multiplying the C and N contents with the bulk soil densities and thickness of each layer. Soil pH was measured by mixing dried sieved soil samples (45°C) with deionised water in a ratio (*v*/*v*) of 1.0 to 2.5 (van Reeuwijk 2002). A combined sieving (particle size: 2,000–20 µm) and sedimentation procedure (particle size < 20 µm) was carried out to determine particle size distribution after pre-treatment with 30% H_2O_2 and 4% Na-dithionite-citrate (van Reeuwijk 2002). Root biomass was obtained by taking volume-based soil cores, which were separated into living and dead roots. Each single root was divided by morphological criteria: the colour of the root and its core, elasticity and consistency (Hertel and Leuschner 2002). The shoot and root biomass is represented as dry matter content (DM) throughout.

^{15}N analysis and calculations: To determine the total C and N contents and stable isotope signatures of nitrogen ($\delta^{15}N$), samples of shoots, roots and soil were analysed using an isotope ratio mass spectrometer (Delta plus, Conflo III, Thermo Electron Cooperation, Bremen, Germany) coupled to an elemental analyser (NA1500, Fisons instruments, Milano, Italy). The $\delta^{15}N$ signature was calculated using the isotope ratio of each sample ($R_{sample} = {}^{15}N/{}^{14}N$) and recalculated as ^{15}N atom%. The incorporation of tracer-derived N into soil, shoots and roots was estimated by an isotope mixing model (Robinson 2001). To avoid confusion, we used the terms tracer N-uptake (N_{upt}) for plant N pools and tracer-N incorporation (N_{inc}) for the soil N pool:

$$\text{tracer } N_{\text{upt.-N}}\text{. or tracer } N_{\text{inc.-N.}} = N_{\text{stock}} \times \frac{\text{atom\% } ^{15}N_{\text{labeled}} - \text{atom\% } ^{15}N_{\text{NA}}}{\text{atom\% } ^{15}N_{\text{Tracer}} - \text{atom\%} ^{15}N_{\text{NA}}} \times 1000 \qquad (1)$$

where N_{stock} is the total N (g N m^{-2}), atom% $^{15}N_{\text{labelled}}$ is the content of ^{15}N atoms in the sample, atom% $^{15}N_{\text{NA}}$ is the content of ^{15}N atoms in the control samples, and atom% $^{15}N_{\text{Tracer}}$ is the content of ^{15}N atoms in the ^{15}N urea tracer. In the final step, the proportion of total input (^{15}N recovery) was calculated by relating the ^{15}N-uptake of plant compartments and the ^{15}N incorporation of soil to the amount of total ^{15}N injected into individual soil depths.

The specific root activity (SRA in mg ^{15}N g DM living root^{-1}) describes the relative plant N-uptake per mass unit living roots from the input layer and was calculated as follows:

$$\text{SRA} = \frac{\text{plant } N_{\text{upt.-N}}}{\text{LRB}} \times f_{\text{DC}} \qquad (2)$$

where plant N-uptake (mg ^{15}N m^{-2}) is the total amount of tracer-N incorporated in plants (roots and shoots), LRB is the amount of living root biomass (g DM living roots m^{-2}), and f_{DC} is a depth correction factor to ensure an equal amount of tracer in each input layer (0.2 for 0–1 cm; 0.8 for 1–4 cm).

2.3.3.4 Statistics

Statistical analyses were carried out with PASW Statistic 18 (IBM SPSS Statistics) and R version 3.0.3 (R Development Core Team). Soil and plant characteristics are illustrated by means and standard errors (mean ± SE). In general a significance level of $p < 0.05$ was used. Significance of treatment effects was tested by a one-way ANOVA after testing for normality (Shapiro-Wilk-test, $p > 0.05$) and for the homogeneity of variances (Levene-test, $p > 0.05$). In cases of non-normal distribution, data were log- or root-transformed and retested with the Shapiro-Wilk-test. The ANOVAs were followed by post-hoc tests for multiple comparisons using the Tukey-test, or LSD-test, if the homogeneity of variances was not given. In a few cases, normality was not achieved and the non-parametric Kruskal-Wallis ANOVA was performed. Subsequently, multiple comparisons coupled with the Benjamini-Yekutieli correction were performed. To analyse the relationships between various investigated plant and soil characteristics, regression analysis was used. In some cases, variables could be better explained by combining a set of predictors and, thus, a step-wise multiple linear regression analysis (MLRA) was implemented. The MLRA results were interpreted by using the total explained variance and changes in R^2.

2.2.4 Results

2.2.4.1 ^{15}N partitioning in the shoot-root system

The total belowground biomass was 5.98 ± 0.23 kg DM m^{-2} and was therefore 20 times higher than shoot biomass (0.3 ± 0.02 kg DM m^{-2}). Total, living and dead root biomass (TRB, LRB and DRB, respectively) decreased linearly with depth (Figure SII-2 a), whereas specific root activity (SRA) tended to increase with depth (Figure SII-2 b). Dead roots dominated over living roots (ratio: 0.4–0.9) in the uppermost 15 cm, but the ratio narrowed and remained constant below 15 cm (ratio: 1.1).

For the ^{15}N recovery in shoots and roots, we assumed a strong relationship with the vertical distribution of root biomass. Accordingly, we expected the highest ^{15}N recovery from the upper layers, where living root biomass was highest (H1).

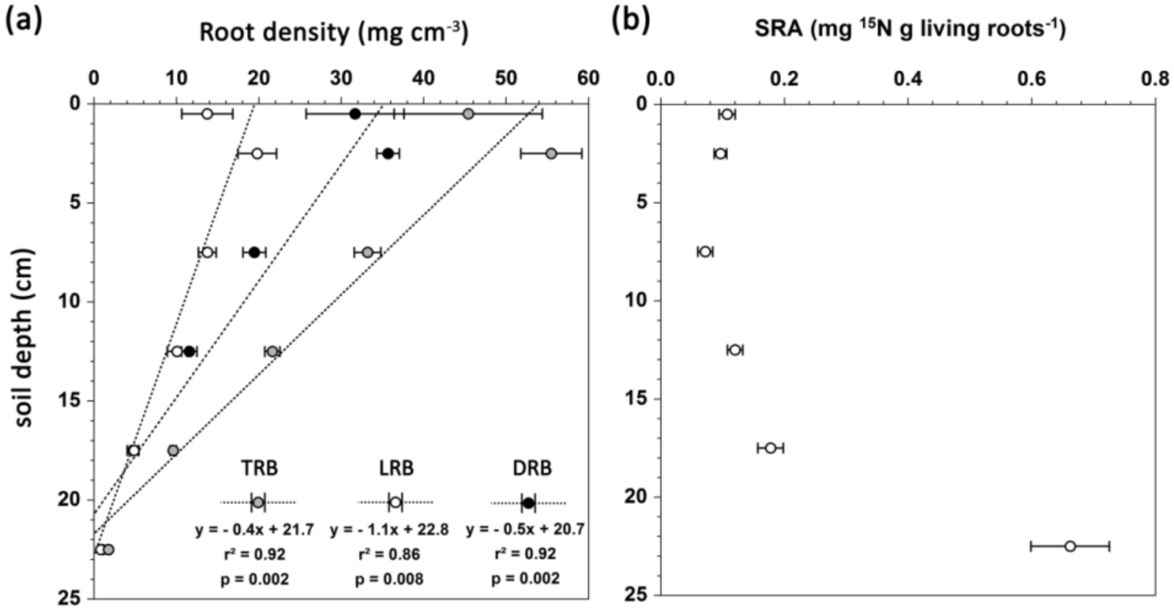

Figure SII-2: Relationship between soil depth and **(a)** total, living or dead root biomass (TRB, LRB and DRB, respectively) and **(b)** specific root activity (SRA). Values are means and standard errors (n = 4).

^{15}N recovery in shoot biomass: The ^{15}N recovery in shoot biomass was 18.1 ± 1.3%. There was no significant relationship between ^{15}N injection depth and ^{15}N recovery in shoots (Figure SII-3). Linear regression between the N-uptake of shoots with the LRB ($r^2 = 0.10$, p = 0.11) and SRA ($r^2 = 0.19$, $p = 0.03$) showed weak relationships. However, the relationship was strongly improved by combining LRB and SRA into one model ($r^2 = 0.44$, $p < 0.001$, Figure SII-4). This demonstrates that both LRB and SRA had an important role for aboveground N-acquisition from deeper soil.

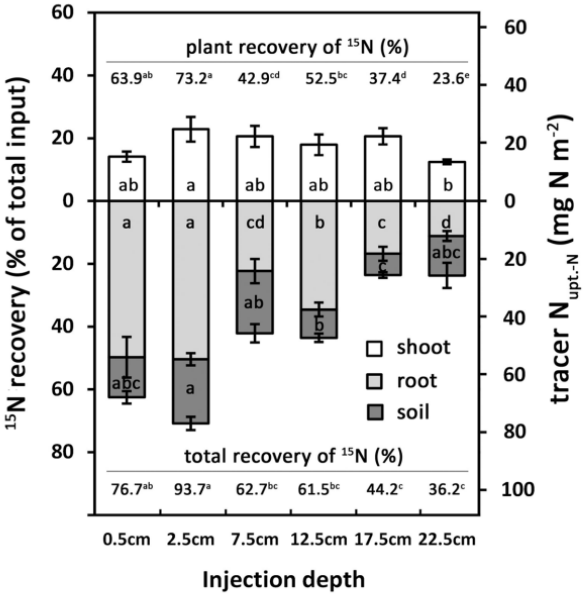

Figure SII-3: The ^{15}N recovery and N-uptake for shoots, roots and soil, depending on injection depth. Values are means and standard errors (n = 4). Lowercase letters (a–e) indicate significant differences between the injection depths ($p < 0.05$).

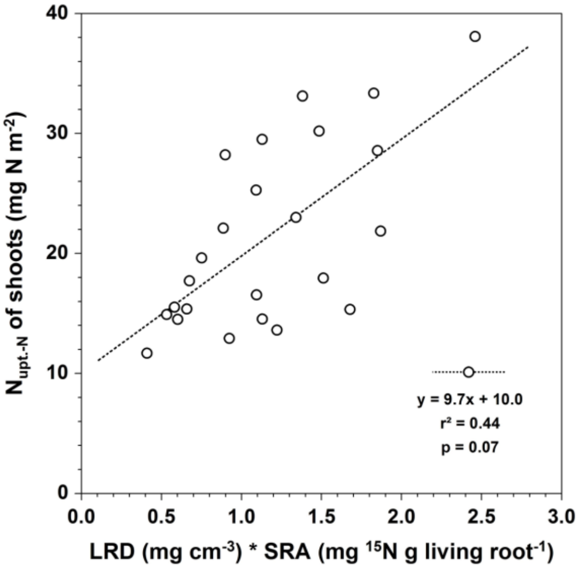

Figure SII-4: The product of living root density (LRD) and the specific root activity (SRA) to explain shoot N-uptake. Data were used from the ^{15}N-input layer (n = 24).

^{15}N recovery in root biomass: The ^{15}N recovery in roots averaged 30.8 ± 3.4%. Total ^{15}N recovery decreased with increasing injection depth. The highest ^{15}N amount was recovered when tracer was injected at 0.5 cm and 2.5 cm depths, whereas the lowest ^{15}N-recovery was obtained at 17.5 cm and 22.5 cm (Figure SII-3).

Considering single injection depths we found most ^{15}N in root biomass at the depths of tracer input. To a lesser extent, ^{15}N was recovered in vertical overlying layers, but ^{15}N recovery decreased with vertical distance from the injection depth (except for the deepest sample at 22.5 cm, Figure SII-5 a). We further recorded a higher ^{15}N recovery for layers with a high root biomass and found the LRB to be the most important predictor to explain root N-uptake ($r^2 = 0.63$, $p < 0.001$).

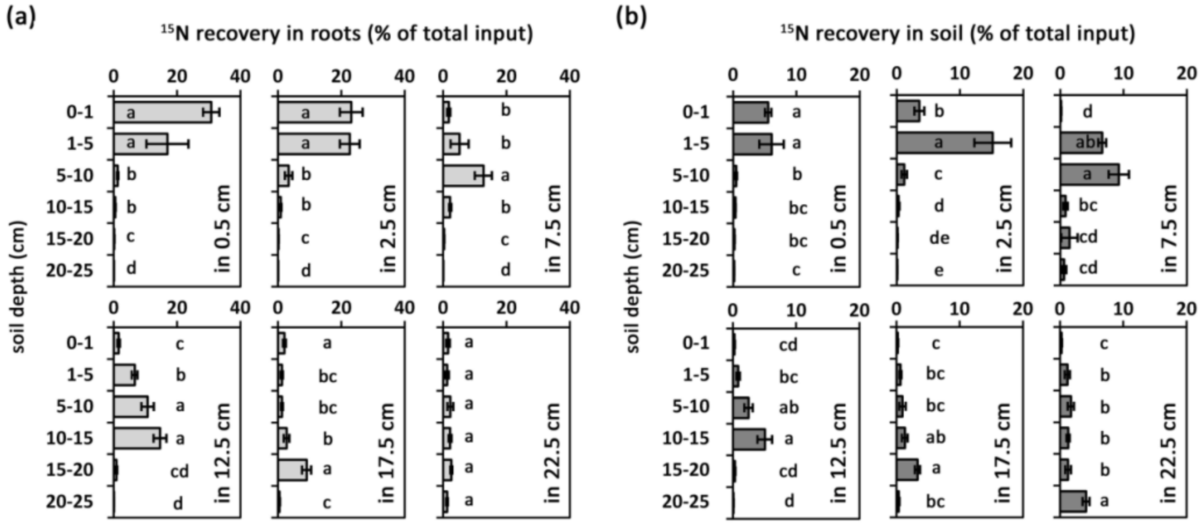

Figure SII-5: The ^{15}N recovery in **(a)** soil and **(b)** roots at the six sample intervals depending on injection depth (at 0.5 cm, 2.5 cm, 7.5 cm, 12.5 cm, 17.5 cm or 22.5 cm), 45 days after labelling. Values are means and standard errors (n = 4). Lowercase letters (a–e) indicate significant differences between the sample intervals ($p < 0.05$).

2.2.4.2 ^{15}N partitioning in the plant-soil system

^{15}N recovery in total plant: We used the ^{15}N recovery in total plant biomass to test the efficiency of ^{15}N-uptake of *K. pygmaea* after 45 days. We hypothesised generally high ^{15}N-uptake efficiency in this N-limited grassland (H2). A high ^{15}N recovery (~70%) occurred when ^{15}N was injected within the first 5 cm. The ^{15}N recovery in plant biomass decreased with ^{15}N injection depth, mainly due to a decreasing ^{15}N recovery in roots (Figure SII-3). On average, 48.9 ± 3.9% of ^{15}N was recovered in root and shoot biomass together. This was more than the ^{15}N remaining in soil (0 – 25 cm) or which was lost after 45 days.

^{15}N recovery in soil: The lowest ^{15}N portion was recovered in soil, independent of the injection depth (Figure SII-3). The vertical distribution of ^{15}N in soil indicated that ^{15}N was also mainly present at the depths of injection (Figure SII-5). To a lesser extent, however, ^{15}N was also recovered in vertical overlying soil layers, reflecting mainly upwards N transport.

^{15}N loss: The amount of ^{15}N which was not recovered in soil or in plant biomass after 45 days was defined as short-term ^{15}N loss. It was 37.5 ± 4.7% of the total input and increased when the tracer was injected into deeper soil layers (Figure SII-3). Almost no ^{15}N was lost from the 2.5 cm injection depth, whereas the highest loss occurred from 22.5 cm. A MLRA showed that 82.2% of the variance was explained by a set of predictors including LRB (explaining 67.8% of the variance), SRA (3.3%), SOC content (4.4%) and clay content (6.7%). This showed that ^{15}N was mainly lost when the potential for root uptake and N immobilization was low. Consequently, injected ^{15}N leached deeper than 25 cm and was thus not recovered.

To consider for the long-term N loss, we used the natural abundance of δ^{15}N in the reference soil (without ^{15}N labelling). The δ^{15}N value increased exponentially with increasing depth ($r^2 = 0.93$, $p < 0.001$), indicating greater N losses by nitrate leaching and nitrous oxide emissions from deeper soil (Amundson and others 2003; Hobbie and Quimette 2009). In addition, we demonstrate a significant relationship ($r^2 = 0.45$, $p < 0.001$) between ^{15}N loss after tracer application (short-term loss) and the natural-occurring δ^{15}N in soil (long-term loss).

2.2.4.3 Comparisons between below- and aboveground investments

In line with an efficient N-uptake, we further assume higher below- than aboveground investments (H3). We therefore used the R/S ratio as long-term indicator and the ratio of ^{15}N in root-to-shoot as short-term indicator to compare above- and belowground investments. We observed a very high R/S ratio of 20.0. Further, the root ^{15}N-uptake was on average 1.7 times higher than shoot ^{15}N-uptake. The ratio exponentially decreased with increasing injection depth and exceeded 1.0 in the upper root mats, but was less than 1.0 if ^{15}N was injected at 17.5 cm or deeper (Figure SII-6).

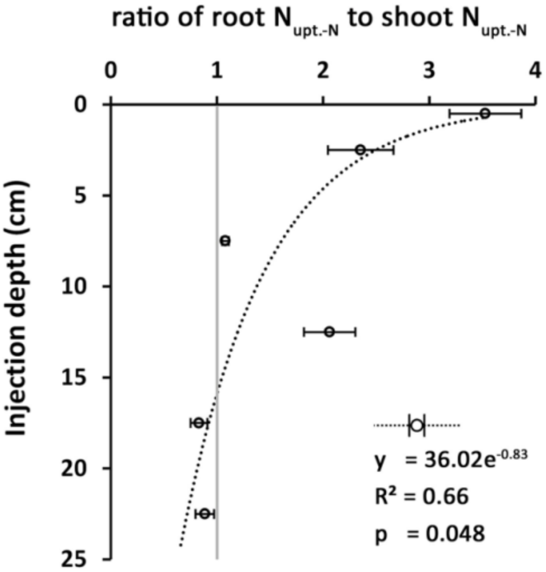

Figure SI-6: Comparison between above- and belowground investments using the ratio of root-to-shoot N-uptake depending on injection depth. Values are means and standard errors (n = 4). The solid grey line is the 1/1 ratio and illustrates balanced above- and belowground investments.

2.2.5 Discussion

2.2.5.1 ^{15}N partitioning in shoots and roots

We recorded a mean shoot biomass of 0.30 kg DM m^{-2}, which fully agrees with the value of 0.29 kg DM m^{-2} reported by Wang and others (2008) for alpine *Kobresia* grasslands. The ^{15}N recovery in shoots was independent of injection depth (Figure SII-3), which indicates that aboveground N-requirements can be entirely met from any part of the soil profile. Furthermore, aboveground N-demands tend to be small (mean shoot ^{15}N recovery: 18.1%) and thus agreed well with the low aboveground net primary productivity reported for alpine grasslands (Knapp and Smith 2001). This partly contradicted our hypothesis (H1), because we expected that shoot N-uptake would be higher from the upper parts of the root mats, where living root biomass was highest. However, there was no significant relationship between living root biomass and shoot N-uptake. Nevertheless, by combining living root biomass and the specific root activity, we observed a highly significant relationship (Figure SII-4). This demonstrates that a higher specific root activity in deeper soil (Figure SII-2 b) compensated for a lower living root biomass there (Figure SII-2 a).

We assume that *K. pygmaea* prioritized aboveground N-transfer to develop and/or maintain assimilation tissue. This may be crucial for balancing the belowground C-costs and to recover from grazing events. In agreement with this, Cao and others (2004) found a strong increase in shoot biomass at the beginning of the growing season (June), with a maximum in September.

In contrast to shoot biomass, total root biomass was remarkably high (5.98 kg DM m^{-2}). The root biomass was also higher than the common range of 1.5–3.7 kg DM m^{-2} reported in several earlier studies on the alpine TP (Luo and others 2005; Wang and others 2008; Xu and others 2011; Li and others 2011). We observed a trend for decreasing ^{15}N recovery in roots with depth (Figure SII-5 a). This was associated by a decrease of living root biomass ($r^2 = 0.63$ $p < 0.001$). Since ^{15}N-uptake of roots was mainly controlled by the vertical distribution of living root biomass, we could confirm our hypothesis (H1) in this respect.

This finding indicated that N-uptake of roots was mainly associated with the upper soil, where a high proportion of SOM serves as a nutrient sink (Figure SII-1). Soil organic matter in cool mountain environments often serves as a sink and storage for nutrients (Vitousek and others 2010). The environmental conditions in such ecosystems are highly variable and alternately favour or inhibit decomposition, nutrient release and subsequent uptake by plants at a high temporal resolution. Higher temperatures especially favour decomposition in the topsoil (Swift and others 1979; Heitkamp and others 2012) and promote energy-intensive processes such as nutrient uptake (Bassirirad 2000). The general nutrient sink may therefore also serve temporally as a source, when environmental conditions favour mineralisation of SOM. Consequently, *K. pygmaea* roots preferentially grew into patches with higher nutrient availability.

2.2.5.2 Challenges for Kobresia pygmaea in a N-limited ecosystem

As a long-term consequence of moderate grazing (Miehe and others 2008), we assumed that *K. pygmaea* adopted specific mechanisms for very efficient resource uptake in this N-limited ecosystem (Xu and others 2014). To test this, we used the ^{15}N recovery of total plant biomass to reflect the ^{15}N-uptake efficiency (H2). The ^{15}N-uptake efficiency was particularly high when tracer was injected into the upper root mats (^{15}N recovery ≈ 70%, Figure SII-3) and thus confirmed our hypothesis (H2) of a very efficient N-uptake. The high ^{15}N-uptake efficiency was consistent with previous studies (Yuan and others 2006; Liu and others 2013), which showed that the N-use efficiency and N-uptake efficiency of grassland plants increased when N-limitation occurred.

Importantly, ^{15}N-uptake efficiency decreased with injection depth and was lowest in deeper soil (^{15}N recovery ≈ 30%, Figure SI-3). On average 48.9 % of ^{15}N were recovered in plant biomass, which was significantly higher than that which remained in the soil or was lost after 45 days. We suggest that the decreasing ^{15}N-uptake efficiency with depth was mainly explained by high ^{15}N loss from deeper soil. Most of this loss probably occurred over a short period (25–28 July 2012) directly after labelling. During this period, about 60 mm precipitation fell within four days and soil volumetric water contents showed that the soil was saturated, indicating a high probability of ^{15}N leaching. Stronger ^{15}N loss in deeper soil was mainly explained by less root N-uptake and less N immobilization by SOM and soil minerals. The MLRA demonstrated that decreasing living root biomass, SOC and clay contents are the main factors that explain the total variance in ^{15}N losses.

We also found increasing δ^{15}N natural abundance in non-labeled soil with increasing depth, which agreed well with trends found by Zhou and others (2014) for alpine meadows (TP) considering a depth down to 20 cm. The higher δ^{15}N values with depth indicate a preferential removal of ^{14}N over ^{15}N and consequently reflect long-term N loss (Amundson and others 2003). As a consequence of decomposition and nitrification the microbial fractionation favours the forming of ^{15}N-depleted N forms (Hobbie and Quimette 2009). These, in turn, get lost via leaching and outgassing especially from deeper soil and cause an increase of the $\delta^{15}N$ values. In contrast the very efficient recapture and recycling of N from the upper soil by *K. pygmaea* diminishes the increasing $\delta^{15}N$ shift in 0-5 cm. Accordingly, long-term N loss (^{15}N of natural abundance) and our short-term N loss (^{15}N loss after labeling) are in good agreement.

We further hypothesized that *K. pygmaea* shows far higher belowground than aboveground investments (H3) as a mechanism for an efficient N-uptake. We demonstrated that root N-uptake was on average 1.7 times higher than shoot N-uptake, thus confirming our hypothesis (3). Nonetheless, when comparing the ratio of root-to-shoot N-uptake for a single injection depth, this ratio decreased exponentially (Figure SII-6). This shows that the belowground investment, in contrast to above-ground investments, strongly decreased with soil depth. The ratio was relatively high above a depth of 5 cm but then equalised in deeper soil (ratio of 1-2), It was in good agreement with the vertical pattern of ^{15}N recovery in plant biomass, with the highest ^{15}N-uptake efficiency within the first 5 cm (Figure SII-3). We suggest that *K. pygmaea* mainly concentrates root growth and/or root support in patches where SOM decomposition releases nutrients for plant uptake.

The underlying causes for the generally higher belowground investment (especially within the first 5 cm) might be a strong resource competition of *K. pygmaea* with other plants and microbes (Song and others 2007; Xu and others 2011; Kuzyakov and Xu 2013). In these shallow-rooted grassland ecosystems, competition pressure is intensive due to naturally occurring limitations of N and other nutrients (Xu and others 2014), increasing water stress (especially in terms of global warming; Dorji and others 2013), the lack of time to acquire resources in the short growing season (Körner, 2003) and the simultaneous needs of consumers (microbes and plants) (Lipson and others 1999; Song and others 2007). In a previous study, Kuzyakov and Xu (2013) showed for alpine *Kobresia* meadows that plants outcompete microbes for N-uptake when root biomass exceeds 4.1 kg m^{-2}. The root biomass in the *K. pygmaea* grassland was 1.5 times higher in our study, indicating an advantage of plants over microbes regarding N-uptake.

We therefore conclude that a crucial strategy of *K. pygmaea* is the establishment of a dense root network to improve resource uptake and storage for future needs. A high belowground resource storage and N-uptake by *K. pygmaea* becomes particularly important when physical stress via grazing, dry spells or short-term nutrient limitations by leaching increase. The high belowground investment prior to stress events potentially promotes rapid regrowth following the disturbance. This, in turn, provides *K. pygmaea* with a competitive advantage over other plants species and helps explain its very broad distribution and dominance on the TP.

2.2.5.3 Implications for a vulnerable grassland ecosystem

The high belowground investments are in good agreement with a high root-to-shoot ratio, which therefore can be considered as a long-term indicator for high belowground investment in *Kobresia* grasslands. The R/S ratio was distinctly higher than that of non-alpine grasslands (R/S: 0.7–4.5, (Jackson and others 1996; Mokany and others 2006) and also than that reported in most other previous studies conducted on the TP (R/S: 6–11, Wang and others 2008; Yang and others 2009; Wang and others 2010). Most studies, however, were conducted on alpine grasslands with a variable degree of degradation; the value found in this study is comparable to the mean of non-degraded *Kobresia* grasslands (R/S: 20.3, Li and others 2008). The high R/S ratios in alpine *Kobresia* grasslands were reported to be mainly driven by environmental conditions such as a low annual mean temperature, low N availability and grazing pressure (Davidson 1969; Wilson 1988; Gao and others 2007; Li and others 2008). We suggest that *K. pygmaea* optimises C-allocation in order to minimise resource limitation, which presumably explains the high R/S ratios of 20.0. This further indicates a very sensitive balance of resource allocation between shoot and root biomass.

To compete in this harsh environment, plants face two challenges: firstly, available belowground resources must be captured efficiently at specific depths and times when they are available. The most efficient way to do this is to increase living root biomass, resulting in high root densities especially in the upper root-mat layers (Figure SII-2 a). Secondly, the enormous root biomass requires high C-maintenance costs, which must be covered by comparably low amounts of photosynthetically active aboveground plant parts. The latter was proven by Ingrisch and others (2014), who showed for the same study site that 70% of the ^{13}C was allocated to roots 15 days after CO_2 pulse labelling. From the belowground C-allocation, about 2/3 and 1/3 was recovered in 0-5 cm and 5-15 cm, respectively. This agrees well with our results because we also found highest belowground investment and highest ^{15}N recovery in the upper layer (0–5 cm).

Plant C-economy implies that roots will only be maintained or re-supplied with C when resources are available within the growing season (Hermans and others 2006). Consequently, the R/S ratio has to be re-adjusted (e.g. by root senescence) after resource exploitation to improve the C-balance between the acquisition of below- and aboveground resources (Chapin III and others 2011). Accordingly, root biomass varied seasonally with highest peaks in the growing season (July to September) in alpine lightly grazed *Kobresia* grassland on the TP (Cao and others 2004; Wu and others 2011).

The very high R/S ratio indicates that the C balance of *Kobresia* pastures might be critical and vulnerable to changes in climate and management. For instance a continuing removal of aboveground biomass under high grazing pressure will reduce the partitioning of assimilates to belowground biomass which, in turn, decreases the uptake of belowground resources and might trigger grassland degradation. Increasing grazing pressure, which disturbs the sensitive balance between below- and aboveground processes, might be one important driver leading to the disappearance of *Kobresia* cover and its turf-bearing root mats.

2.2.6 Conclusions

We have illustrated some mechanisms for efficient nutrient acquisition by *Kobresia pygmaea* that partly explain its dominance on the TP. *Kobresia pygmaea* has developed efficient above- and belowground trade-offs to counterbalance resource limitation by N and probably some other nutrients such as P. These trade-offs include a high investment into root biomass, especially in the topsoil, to compete for resources with other plants and microbes (Song and others 2007; Xu and others 2011; Kuzyakov and Xu 2013). This requires high belowground C maintenance costs, which must be covered by photosynthetically active shoots. To develop shoot biomass, the required N is taken up from the entire rooting zone. In particular, an increasing specific root activity with increasing depth compensated for the decreasing living root biomass for N-uptake. We therefore assume that *K. pygmaea* can recover very rapidly following moderate grazing events and can supply the high belowground C demand. The higher R/S ratio, however, also indicates that this efficient above- belowground trade-off might react extremely vulnerable to changes in climate and management. This study therefore provides the basis for further investigations and predictions concerning the future responses of *Kobresia* grasslands to changes in pasture management.

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2.2.8 References

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2.3 Study III: Mechanisms and consequences of Tibetan grassland degradation

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2.3.1 First paragraph

Kobresia grasslands store tremendous amounts of soil organic carbon (SOC)[1,2], are an important grazing ground for local herdsmen[3,4], host a major portion of the regional terrestrial biodiversity[5,6], and supply large areas of SE Asia with water[7] – all threatened by large-scale soil degradation on the Tibetan Plateau. Nonetheless, the patterns and mechanisms of pasture degradation, visible across the entire Tibetan Plateau, remain unknown.

Here we (a) provide a novel degradation concept combining anthropogenic and natural impacts and (b) demonstrate the mechanisms for associated SOC loss. We show that soil drought and frost lead to polygonal cracking of the *Kobresia* turf, already weakened by overgrazing. This induces gradual erosion by wind and water, extends the cracks and removes the upper carbon-enriched soil. Erosion-derived SOC loss amounts to 5 kg C m^{-2} and is aggravated by decreasing root C-input and increasing SOC mineralization (ca. 2.5 kg C m^{-2} combined). Mineralization-driven SOC loss was reflected in a negative $\delta^{13}C$ shift of SOC going from intact to severely degraded stages, and was caused by a relative enrichment of ^{13}C-depleted lignin. In sum, degradation triggered high SOC loss from this ecosystem with profound consequences for carbon sequestration, atmospheric CO_2, water quality and ecosystem stability.

2.3.2 Main part

The Tibetan Plateau (TP) hosts the world's largest high-altitude grasslands, contributing 2.5% to global SOC stocks[1] over less than 2% of the Earth's total terrestrial area. The TP also provides extensive grazing grounds, influences the Asian monsoon climate system, and is the source of the water supply for large parts of Asia[7,8]. Approximately one fifth of the TP is covered by *Kobresia* grasslands[9]. *Kobresia pygmaea* forms a grazing lawn only 2 to 4 cm high, thus harbouring a low shoot biomass but developing very compact root mats (root to shoot ratio: > 20)[10]. Such grasslands host unique plant and animal species[5,6], contributing to regional biodiversity. Palaeo-records from soil and lake sediments indicate a livestock-induced origin of these *Kobresia* pastures since the mid-Holocene Climatic Optimum and following yak domestication[11,12]. The grazing lawns are induced by long, moderate grazing history increasing the belowground C allocation and root biomass itself[2,13]. A dense root network is a species-specific trait of *K. pygmaea*. It protects against trampling, ensures efficient nutrient recapture[10] and makes *K. pygmaea* very competitive compared to other plant species[14].

Despite high uncertainties for degradation estimations[13], about 30% of the Tibetan grasslands are classified as degraded[6], and degradation has drastically increased in recent decades[4,7]. Overgrazing has promoted grassland degradation due to heavy trampling and disruption of belowground allocation of photosynthates from shoots.[10,13,15] These anthropogenic impacts are amplified by frequent freeze-thaw cycles, recurrent droughts, high wind speeds, sloping land, and very strong solar radiation[16,17]. Degradation leads to an immense export of soil and a major decline in SOC storage[5], for which the exact mechanisms remain unclear. In the *K. pygmaea* core area, we studied natural and anthropogenic effects on pasture degradation to discover new mechanisms and associated processes of soil organic carbon (SOC) loss. A new pasture degradation concept was developed and the proposed degradation stages were analyzed for physical, chemical and biological properties.

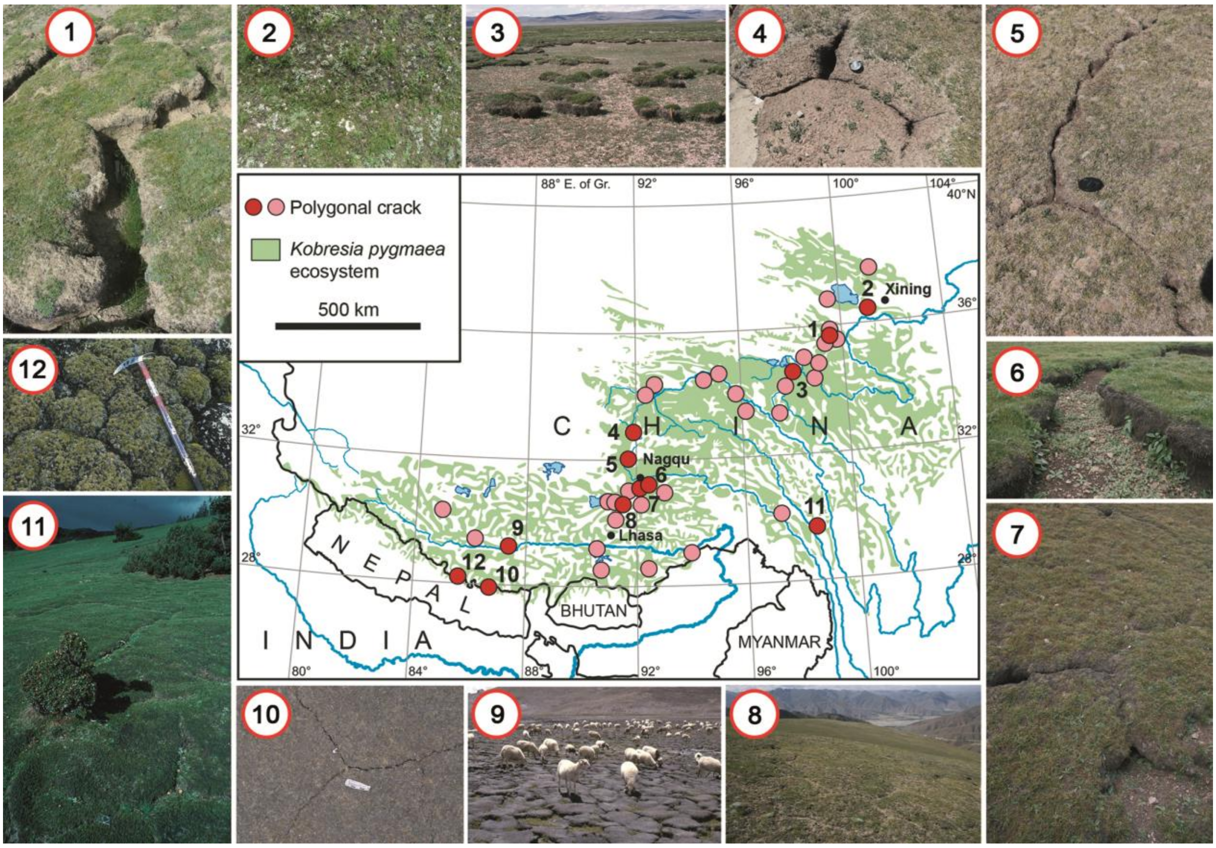

Figure SIII-1: Selected examples of polygonal cracking and extension on the TP. Red dots show locations of polygonal cracks based on observations during field trips on the Tibetan Plateau and the Himalaya between 1982 and 2015. This indicates the widespread distribution of this specific degradation phenomenon, not its actual distribution. Photo credits: E. Seeber (1, 2), G. Miehe (3, 4, 5, 9, 11, 12), P-M. Schleuss (6, 7, 8) and R. Bäumler (10). Cartography: C. Enderle, Data source: Miehe et al. 2008[3].

2.3.3 Concept of soil degradation

Polygonal cracks in the *Kobresia* turf are a common but still not explained phenomenon between the Qilian Shan in the north and the Himalayas in the south (Fig. SIII-1). We identified six successional degradation stages from intact *Kobresia* root mats (S0), to stages with increasing extent of surface cracks (S1-4) to bare soil patches (S5), where the root mats have totally disappeared. Here we report a mechanistic concept of pasture degradation, accounting for man-made factors and natural amplifications (Fig. SIII-2).

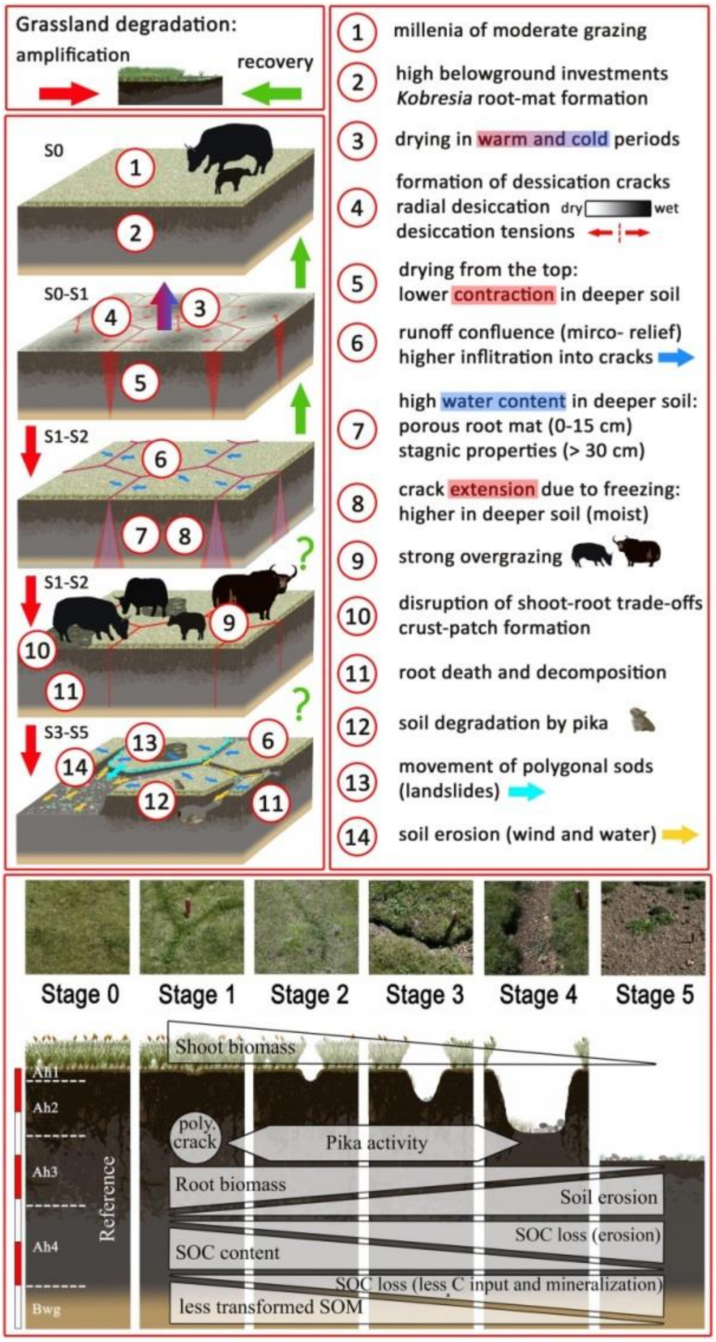

Figure SIII-2: **(a)** Simplified overview of the degradation sequence from the intact (S0) to the severely degraded stage (S5) and **(b)** the anthropogenically induced and naturally occurring driving forces behind *Kobresia* ecosystem degradation. Numbers and arrows describe the main biotic and abiotic mechanisms. The hierarchical order does not necessarily imply a rigid pathway: some steps can be simultaneous, be reversed, repeated or fail to appear in a certain period. The white/red scale on the left is 30 cm with 5 cm increments. Polygons summarize main degradation mechanisms with focus on SOC stocks according to the hypotheses.

Strong overgrazing by livestock and small mammals is the prerequisite for grassland degradation because permanent removal of shoot biomass decreases the belowground assimilate input, reduces plant growth, and hinders grassland recovery[10,13,15]. Furthermore, overpopulation of herbivores causes widespread damage due to trampling, scrubbing and burrowing[6,18]. Nevertheless, the polygonal cracks reflect that degradation is reinforced by natural abiotic impacts[19] (S1, Fig. SIII-1, -2). Repeated drying/rewetting and freezing/thawing cycles lead to soil contraction and expansion, gradually cracking the *Kobresia* turf. This occurs during droughts, both when summer monsoon rains are delayed and in dry winter times with very low temperatures.

Once the *Kobresia* turf cracks, it forms a micro-relief (S1, Fig. SIII-2, Extended Data Table 1). This increases moisture in the initial cracks due to confluence of surface runoff and stronger infiltration, explaining the slightly higher shoot biomass of S1 (Extended Data Table 1). A sharp decrease of the penetration resistance within the upper 30 cm from S0 to S2 clearly demonstrated crack expansion during freezing (Fig. SIII-3a). A combination of moist soil at the beginning of the frost season and diurnal frost events exacerbates polygonal cracking. Presumably, the higher bulk density promotes soil expansion/contraction, especially at 10-20 cm, whereas the porous and densely rooted topsoil, with a much lower bulk density, provides enough pore space for volume changes without severe damage (Tab 1 Ext). The decreasing vegetation cover and biomass (above- and belowground) from S1 to S5 indicated plant die-off following polygonal cracking (Fig. SIII-2b, Table 1). Root death and decomposition then expands the surface cracks (S1, S2) and promote erosion (S3 to S4). Crack expansion is aggravated by small mammals (Plateau pikas, *Ochotona curzoniae*) using the existing cracks to better access the underlying *Kobresia* turf[18]. Erosion on the TP is often promoted by the sloped landscape and the soil texture, consisting mainly of easy erodible particles (study site: fine sand 40%, silt 33%)[10]. The loss of the fine soil results in an accumulation of coarser material, as indicated by the stone cover on the bare soil patches (Fig. SIII-1, -2). Erosion, stimulated by hilly landscapes, low vegetation protection, fast winds and intense rains is a pressing problem on the TP and in surrounding regions. It reduces pasture quality, worsening the livelihood of local herdsmen; loads rivers and water basins with sediments; pollutes the SE Asian headwaters, which supply billions of people with clean water; and is the origin of dust pollution, a growing problem in Asian megacities.

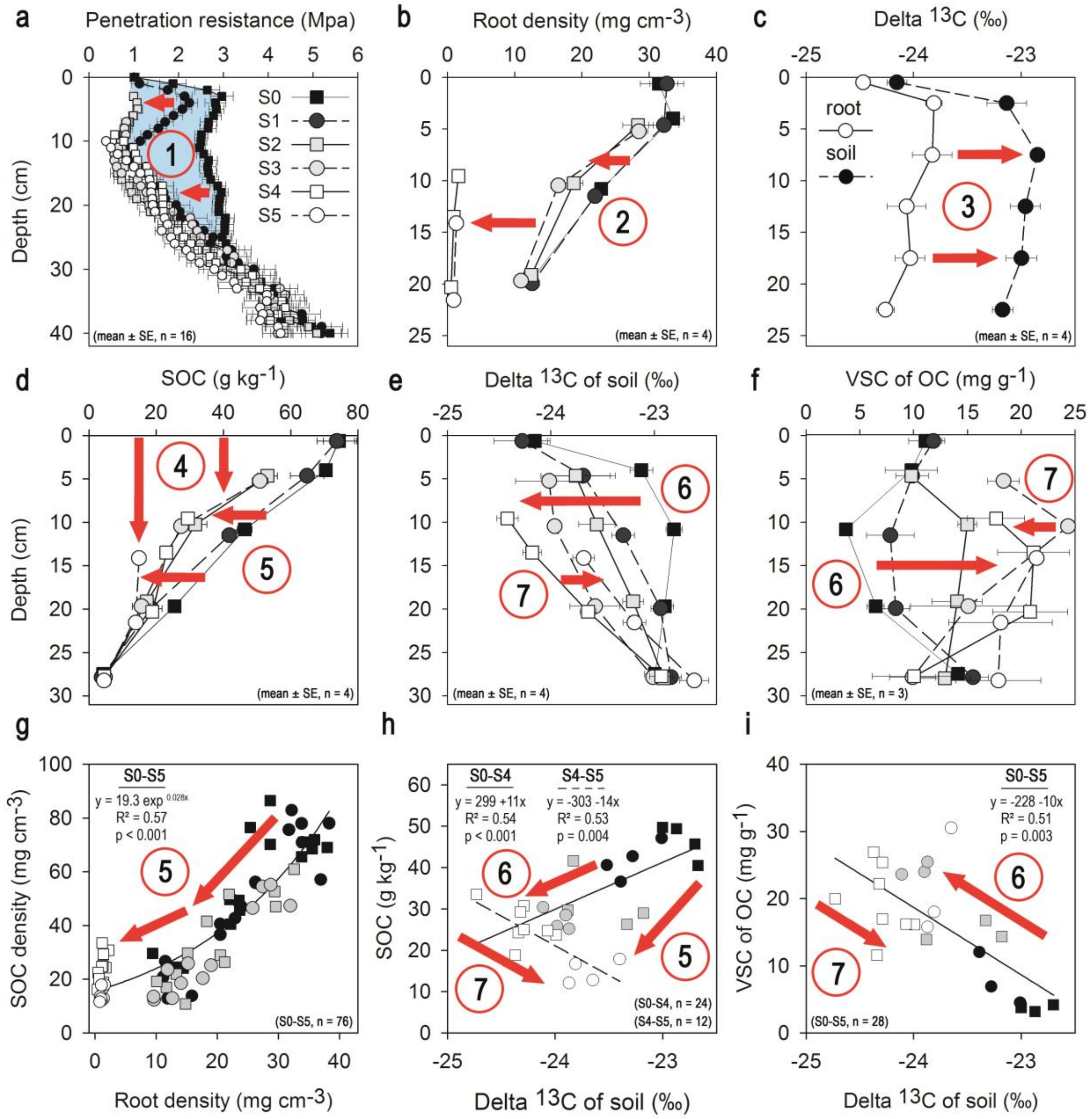

Figure SIII-3: Soil properties and processes in the depth profile depending on status of degradation: (**a)** penetration resistance, **(b)** root density, **(c)** δ^{13}C of SOC and roots**, (d)** SOC content, **(e)** δ^{13}C of SOC and **(f)** content of lignin monomers: vanillyl, syringyl, and cinnamyl (VSC). All parameters (means ± SE) are presented for each soil horizon (center), except for the δ^{13}C between soil and root and the penetration resistance, which are shown in 5 and 1 cm increments, respectively. Statistics are shown in Extended Data Table 1. Degradation changes the patterns of root density, SOC content, the δ^{13}C value and the lignin derivates (VSC) based on the example of the Ah3 horizon **(g, h, i)**. The pattern along the degradation sequence can be explained by the following processes: (1) cracking by desiccation and frost, (2) root death and decomposition, (3) kinetic ^{13}C fractionation from root decomposition, (4) erosion-derived SOC loss, (5) SOC loss from less root C input and SOC mineralization, (6) relative lignin accumulation and $\delta^{13}C_{SOC}$ decrease (S0-S3), (7) lignin degradation and $^{13}C_{SOC}$ enrichment (S4-S5).

Table 1: Basic soil and plant characteristics with successive degradation

	Degradation stage					
	S0	**S1**	**S2**	**S3**	**S4**	**S5**
horizontal crack (cm)						
	-	4.0 (0.9)^{c}	6.6 (0.6)^{bc}	10.3 (1.9)^{ab}	17 (1.2)^{a}	-
vertical crack (cm)						
	-	0.6 (0.1)^{e}	2.0 (0.3)^{d}	5.8 (0.3)^{c}	8.0 (0.4)^{b}	10.4 (0.8)^{a}
vegetation cover (%)						
	95 (0.6)^{a}	92 (1.0)^{ab}	79 (3.5)^{b}	30 (3.0)^{c}	24 (2.9)^{c}	9 (0.9)^{d}
shoot biomass (g m^{-2})						
	179 (11)^{ab}	210 (8)^{a}	70 (4)^{bc}	41 (5)^{c}	48 (11)^{cd}	22 (1)^{d}
root biomass in 0-25 cm (kg m^{-2})						
	5.2 (0.12)^{a}	5.4 (0.06)^{a}	4.1 (0.33)^{b}	3.2 (0.42)^{b}	0.15 (0.02)^{c}	0.17 (0.01)^{c}
Root density (mg cm^{-3})						
Ah1	31 (2.8)^{a}	33 (2.5)^{a}				
Ah2	34 (1.7)^{ab}	32 (2.2)^{a}	28 (2.3)^{b}	28 (1.3)^{c}		
Ah3	23 (0.4)^{a}	22 (0.9)^{ab}	19 (1.4)^{bc}	16 (1.1)^{ab}	1.5 (0.2)^{d}	1.3 (0.1)^{cd}
Ah4	12 (1.1)^{a}	13 (1.1)^{ab}	12 (1.0)^{ab}	11 (0.8)^{ab}	0.6 (0.1)^{bc}	0.9 (0.1)^{c}
Bulk density (mg cm^{-3})						
Ah1	0.62 (0.01)^{a}	0.72 (0.14)^{a}				
Ah2	0.72 (0.07)^{a}	0.77 (0.09)^{a}	0.68 (0.01)^{a}	0.84 (0.00)^{a}		
Ah3	1.03 (0.06)^{a}	1.03 (0.06)^{a}	0.96 (0.01)^{ab}	0.82 (0.10)^{b}	0.98 (0.07)^{a}	1.24 (0.06)^{c}
Ah4	1.19 (0.02)^{ab}	1.06 (0.12)^{b}	1.13 (0.01)^{b}	1.24 (0.05)^{ab}	1.26 (0.07)^{ab}	1.37 (0.02)^{a}
Bwg	1.54 (0.02)^{a}	1.54 (0.04)^{a}	1.43 (0.01)^{a}	1.51 (0.08)^{a}	1.59 (0.06)^{a}	1.59 (0.03)^{a}
SOC (g C kg^{-1})						
Ah1	74 (4.6)^{a}	74 (6.0)^{a}				
Ah2	70 (0.7)^{a}	65 (5.0)^{ab}	53 (2.9)^{bc}	51 (4.6)^{c}		
Ah3	46 (2.1)^{a}	42 (2.2)^{a}	32 (3.4)^{b}	27 (4.6)^{b}	26 (2.3)^{b}	15 (1.4)^{c}
Ah4	25 (1.4)^{a}	19 (3.2)^{ab}	17 (2.4)^{ab}	13 (4.6)^{b}	19 (1.5)^{ab}	14 (1.4)^{b}
Bwg	4 (0.4)^{a}	4 (0.4)^{a}	5 (4.6)^{a}	5 (1.0)^{a}	5 (0.3)^{a}	4 (0.5)^{a}
$\delta^{13}C$ of SOC (‰)						
Ah1	-24.16 (0.12)^{a}	-24.28 (0.27)^{a}				
Ah2	-23.13 (0.11)^{a}	-23.69 (0.31)^{a}	-23.76 (0.34)^{a}	-24.02 (0.32)^{a}		
Ah3	-22.81 (0.08)^{a}	-23.30 (0.11)^{bc}	-23.56 (0.18)^{c}	-23.97 (0.18)^{d}	-24.30 (0.11)^{e}	-23.68 (0.10)^{cd}
Ah4	-22.90 (0.08)^{a}	-22.94 (0.09)^{a}	-23.21 (0.10)^{ab}	-23.58 (0.10)^{b}	-23.64 (0.08)^{b}	-23.19 (0.11)^{ab}
Bwg	-23.00 (0.10)^{a}	-22.84 (0.10)^{ab}	-22.91 (0.11)^{ab}	-23.01 (0.11)^{a}	-22.93 (0.11)^{a}	-22.62 (0.14)^{b}
VSC of OC (mg g^{-1})						
Ah1	11.1 (1.6)^{a}	11.8 (1.1)^{a}				
Ah2	9.8 (2.4)^{b}	9.9 (1.5)^{b}	9.8 (0.6)^{b}	18.3 (1.5)^{a}		
Ah3	3.7 (0.3)^{c}	6.4 (0.9)^{bc}	15.0 (0.9)^{abc}	24.3 (0.6)^{a}	19.4 (3.0)^{a}	21.4 (4.6)^{ab}
Ah4	6.5 (0.8)^{c}	8.3 (1.3)^{bc}	14.0 (2.3)^{abc}	15.1 (5.4)^{abc}	20.8 (3.5)^{a}	18.1 (4.8)^{ab}
Bwg	14.1 (1.6)^{a}	15.5 (1.5)^{a}	12.9 (2.4)^{a}	9.9 (2.1)^{a}	10.1 (3.9)^{a}	17.9 (3.9)^{a}

Values are mean ± SE. Lowercase letters indicate significant differences between degradation stages ($p < 0.05$). Missing values with increasing degradation result from erosion removing the upper soil horizons.

2.3.4 Effects of soil degradation on SOC stocks

The SOC stocks sharply declined with increasing degradation from S0 to S5 (Fig. SIII-4a). The SOC stock was on average 70% lower for bare soil patches (S5) versus intact *Kobresia* root mats (S0), corresponding to a loss of 7.5 kg C m^{-2} (Fig. SIII-4a,b). Bare soil constitutes 19% of the study site surface[9], implying an overall average SOC loss of 1.4 kg C m^{-2}. Assuming that about 20% of the *Kobresia* grasslands (450,000 km²)[3] have suffered similar degradation, about 0.6 Pg C has been lost in total. Two thirds of this high SOC loss resulted from erosion and one third from decreasing root C input and SOC decomposition (Fig SIII-4b).

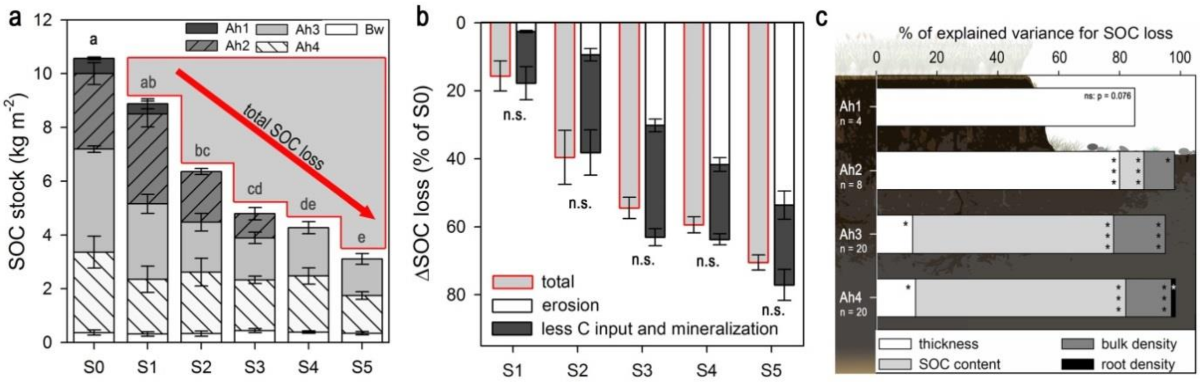

Figure SIII-4: Soil organic carbon (SOC) stocks and losses with increasing degradation. Total SOC stocks in intact soil (S0) and under each crack (S1-S5) down to 30 cm depending on horizons **(a)** and SOC losses by erosion and by less C input and SOC mineralization **(b)**. Contributions of soil horizon thickness, SOC content, bulk density and root density to SOC loss **(c)**. Lowercase letters show significance of differences for the SOC stock between degradation stages. The absence of significant differences (n.s.) between the total SOC loss (red frame) and the sum of the erosion- and mineralization-derived SOC losses reflect realistic estimations. Contribution of single predictors to SOC loss was calculated by a multiple linear regression analysis. Only significant predictions were considered (*** → $p < 0.001$ and * → $p < 0.05$). For the Ah1 horizons, no predictor showed a significant contribution due to the small number of repetitions (this horizon is absent for S2-S5).

SOC loss from erosion: Water and wind erosion causes complete loss of the upper, most fertile and C-enriched soil (S5 in 0-10 cm: ~85 kg soil per m^{-2}) and a preferential removal of fine mineral particles (clay and fine silt), which contribute most to SOC storage due to their high specific surface area and sorption capacity[20]. The declining vegetation cover and increased runoff confluence in the extended surface cracks (S4, S5) favors erosion of topsoil horizons (0-10 cm) and causes an SOC loss of ca. 40-50% (Fig. SIII-4b,c). Moreover, the trench expansion (S5) increases the vulnerability to wind erosion[4,16].

Losses by decreased root C input and SOC mineralization: We hypothesized high SOC losses due to decreasing root C input and SOC mineralization (Fig. SIII-3d). We found very similar vertical patterns of δ^{13}C values for SOC and roots in non-degraded *Kobresia* soil (Fig. SIII-3c), showing that the SOC input depends heavily on the amount of root biomass[21], particularly due to rhizodeposition and root decomposition[22]. For the *Kobresia* grasslands, 20-times-higher root than shoot biomass is common[10]. Accordingly, roots provide the highest C input in this ecosystem[2]. A close correlation between SOC density and root density across all degradation stages confirmed our hypothesis of decreasing C input with degradation (Fig. SIII-3g).

The mineralization-driven SOC loss was identified by the vertical patterns of the δ^{13}C values, which decreased from S0 to S4 within the upper 20 cm, but then increased from S4 to S5 (Fig. SIII-3e). We expected a continuous δ^{13}C increase across the whole S0-S5 sequence due to kinetic isotope fractionation[23], but an accumulation of more recalcitrant, ^{13}C-depleted lignin components[24] caused a negative δ^{13}C shift from S0 to S4 and clearly indicated SOC decomposition. The content of lignin monomers – vanillyl, syringyl, cinnamyl (VSC) – increased from S0 to S4, indicating selective lignin accumulation, but then decreased to S5, demonstrating lignin degradation (Fig. SIII-3f). Indeed, the δ^{13}C changes in the Ah3 horizon were closely related to the shift in VSC throughout the degradation sequence (Fig. SIII-3i). Two mechanisms explain the VSC and δ^{13}C patterns with increasing degradation: (a) an increasing lignin input following root death and decomposition and (b) a preferential loss of easily available substances, e.g. carbohydrates (with higher δ^{13}C).

First, root death and litter decomposition increase the lignin input from S0 to S4. Nonetheless, the root litter inputs do not lead to increased, but rather decreased bulk SOC content, showing that most of the root litter is not stabilized in the soil. Our interpretation is that the high root litter input stimulates microbes to decompose the more complex SOC pool (root litter priming)[25]. Such priming effects can be triggered by the high C/N ratio of the roots, which is 3-4 times higher than that of the soil. This stimulates microbes to decompose organic substances to obtain N (N mining)[26] in this N-limited ecosystem.

Second, preferential decomposition of easily available substances over more complex ones[27] enriches lignin relative to the SOC pool. The lignin components decreased again for S4 and S5 (Fig. SIII-3e), resulting (a) in a ^{13}C enrichment (Fig. SIII-3i) but also (b) in a simultaneous decrease of SOC content (Fig. SIII-3d, h). Once most of the root litter and easily available SOC substances have been decomposed (S1-S3), resistant organic materials such as lignin become degraded (Fig. SIII-3e, h, i). In conclusion, the combined effects of lower root C input and SOC mineralization induced high SOC losses with degradation, especially from the Ah3 and Ah4 horizons, and thus confirmed our hypothesis of mineralization-derived SOC loss.

2.3.5 Fate of Tibetan pastures: Overgrazing versus Climate Change

Despite the harsh climate and natural impacts, the grasslands on the TP were in equilibrium for millennia. Overgrazing and climate change have shifted the age-old balance and induced pasture degradation. However, underlying climate-related mechanisms have been less investigated because the changes are slow (compared to overgrazing) and the causal network is more complex. The precipitation predictions for the TP show no clear trend, but an increasing variability[28]. This means a higher risk of extreme dry and wet periods and thus an increasing potential for desiccation and frost cracks. The *Kobresia* ecosystem, however, covers a huge spatial and altitudinal range (~3000 - 6000 m a.s.l.)[3] and, as a whole, experiences widely varying temperature and precipitation regimes. This makes climatic changes of the last 50 years[28,29] relatively small compared to the overall range of precipitation (mean annual precipitation: 300-1000 mm) and temperature (mean temperature of the warmest month 13.6-17.6 °C) for the whole *Kobresia* ecosystem[3]. Consequently, climate-change-induced degradation and associated SOC losses presumably played a minor role compared to land-use intensification in recent decades. We conclude that soil degradation induced by overgrazing exacerbates consequences from the local to global scale: slight degradation (S1, S2) decreases mainly pasture quality and impairs the livelihood of Tibetan herdsmen (local), while further erosion (S3 to S5) affects the Asian headwaters and landscapes (regional), and mineralization releases high CO_2 amounts, contributing to climate change (global). Since extreme events are predicted to increase in frequency under future climate scenarios, the natural triggers of degradation will also become more severe. Consequently, even a low level of anthropogenic pressure may gain importance as a force behind ecosystem degradation.

2.3.6 Methods

2.3.6.1 Site description

The study was conducted on sites near Nagqu (Tibet, China; 31°16'45''N, 92°59'37''E) in late summer 2013. The study site was located on gently inclined slopes (2-5%) at 4,484 m a.s.l. in the core area of the *K. pygmaea* ecosystem[3]. The vegetation here consists mainly of *K. pygmaea*, which covers up to 61% of the surface. Other grasses, sedges or dwarf rosette plants (*Carex ivanoviae*, *Carex* spp., *Festuca* spp., *Kobresia pusilla*, *Poa* spp., *Stipa purpurea*, *Trisetum* spp.) rarely cover more than 40%. The growing season is strongly restricted by temperature and water availability. In the best case it lasts from mid-May to mid-September, but varies strongly depending on the onset and duration of the summer monsoon. Mean annual precipitation is 431 mm with roughly 80% summer rains. Mean annual mean temperature is -1.5 °C; the mean maximum temperature of the warmest month (July) is +15.1 °C[9].

A characteristic feature of *Kobresia* pastures is their very compact root mats, with an average thickness of 15 cm at the study site. They consist mainly of living and dead *K. pygmaea* roots and rhizomes, leaf bases, high amounts of SOC, and mineral particles. The soil, a Stagnic Eutric Cambisol (Humic), developed on a loess layer overlying glacial sediments and contained 50% sand, 33% silt and 17% clay in the topsoil (0-25 cm). The topsoil is free of carbonates but has high pH values (pH in H_2O: 6.8)[10].

Large areas in the study region are impaired by grassland degradation. In total, 45% of the surface area is already degraded[9]. The site is used as winter pasture for yaks, sheep and goats from January to April. Besides livestock, large numbers of Plateau Pika occur on the sites. The latter have a considerable impact on the plant cover through their burrowing activity, especially the soil thrown out of their burrows, covering and destroying the *Kobresia* turf.

2.3.6.2 Study and sampling design

All six stages (S0-S5) were selected within an area of about 25,000 m² to ensure equal environmental conditions. Each stage was sampled in four field replicates each. The vertical and horizontal extent of the surface cracks were measured for each plot (Extended Data Table 1). Furthermore, the vegetation cover and the aboveground biomass were collected in the cracks (Extended Data Table 1). In general, the intact *Kobresia* turf (S0) provides a high penetration resistance mainly due to the integrity of the root mat. Due to the polygonal patterns of the initial cracks (S1, Fig. SIII-1, 2) degradation starts via contraction/expansion due to desiccation and frost impacts, slightly opening the *Kobresia* turf. Further cracking is expected to initiate root death and mineralization, strongly compromising penetration resistance (measured by penetrologger in 1 cm increments and 4 replicates per plot, Eijkelkamp Agrisearch Equipment).

Soil sampling was conducted using soil pits (30 cm length × 30 cm width × 40 cm depth). First, horizons were classified and then soil and roots were sampled for each horizon directly below the cracks. Bulk density and root biomass were determined in undisturbed soil samples. Because > 95% roots occurred in the upper 25 cm[10], we did not sample for root biomass in the Bwg-horizon (below 25 cm). Additional soil samples were taken from each horizon for further analyses.

2.3.6.3 Analyses and calculations

Plant and soil analyses: Bulk density and root density were determined by dividing the dry soil mass (dried at 105 °C for 24 hours) and the dry root biomass (60 °C) by the volume of an undisturbed sampling core. To illustrate the root biomass, root density was expressed per soil volume (mg cm^{-3}). For further analyses, soil and roots were separated by sieving (2 mm) and the roots subsequently washed with distilled water. Soil and root samples were dried at 60 °C and milled. Total SOC content and the stable isotope signature ($\delta^{13}C$) were analyzed using an isotopic mass spectrometer (Delta plus, Conflo III, Thermo Electron Cooperation, Bremen, Germany) coupled to an elemental analyzer (NA 1500, Fisons instruments, Milano, Italy). Measurements were conducted at the Centre for Stable Isotope Research and Analysis (KOSI) of the University of Göttingen. The $\delta^{13}C$ was calculated using the isotope ratio of each sample ($R_{sample} = {}^{13}C/{}^{12}C$) and relating it to the international standard R_{PDP} (${}^{13}C/{}^{12}C$ in Pee Dee Belemnite).

The SOC stocks (in kg C m^{-2}) for the upper 30 cm were determined by multiplying the SOC content (in g C kg^{-1}) with the bulk soil density (in g cm^{-3}) and the thickness of the soil horizons (in m). SOC losses (in %) were calculated for each degradation stage and horizon and were related to the mean C stock of the reference stage (S0). The erosion-derived SOC loss for the upper horizon was estimated by considering the topsoil removal (extent of vertical soil cracks) of all degraded soil profiles (S1-S5) and multiplying it with the SOC content and bulk density of the reference (S0). To calculate the mineralization-derived SOC loss, we assumed that mineralization of SOC and roots will affect both SOC content and bulk density. Thus we used the SOC content and bulk density from each degraded stage (S1-S5) and multiplied it with the mean thickness of each horizon (down to 30cm) from the reference site (S0).

Lignin phenols were depolymerized using the CuO-oxidation method[30]. The lignin phenols were analyzed on a Varian 220 gas chromatograph mass spectrometer (GC-MS). Vanillyl and syringyl units were calculated from the corresponding aldehydes, ketones and carboxylic acids. Cinnamyl units were derived from the sum of p-coumaric acid and ferulic acid. The sum of the three structural units (VSC = V+S+C) is considered to reflect the lignin phenol content in a sample.

2.3.6.4 Statistical analyses

Statistical analyses were done using PASW Statistics (IBM SPSS Statistics) and the R version 3.0.3 (R Development Core Team). Soil and plant characteristics are presented as means and standard errors (mean ± SE). Significance of treatment effects (S0-S5) were tested by a one-way ANOVA at $p < 0.05$. Prior to this, we checked for normality and homogeneity of variance using the Shapiro-Wilk-test and Levene-test, respectively. Post-hoc multiple comparisons were carried out using the LSD ANOVA, if normality was given. In cases of non-normal distribution, the non-parametric Kruskal-Wallis test was implemented coupled with a Bonferroni correction. To detect relationships between various plant and soil characteristics, we used linear and non-linear regressions. Additionally, a step-wise multiple linear regression analysis was used to determine the contribution of various predictors to explain a certain independent variable (i.e. SOC loss). To interpret the contribution of a single predictor, we used the R^2 change. Correlations were deemed significant for single and multiple regressions at $p < 0.05$.

2.3.7 Acknowledgements

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2.4 Study IV: Degradation-driven nutrient losses of the Tibetan Kobresia pastures

In preparation for submission to *Global Change Biology*

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2.4.1 Abstract

The Tibetan *Kobresia* pastures have been increasingly affected by large-scale soil degradation since the last decades, which has impaired several important ecosystem functions. We present empirical experimental data from field surveys in the highlands and new analyses in the *Kobresia* core area to demonstrate the consequences of the degradation for this vulnerable ecosystem. We derived a conceptual model of degradation processes that incorporates anthropogenic impacts and natural amplifications and explores the effects of erosion and leaching on nitrogen (N) and phosphorus (P) stocks. Six successional degradation stages were selected: from intact *Kobresia* root mats (S0), to stages with increasing extent of surface cracks (S1-4) to bare soil patches (S5), where the root mats have totally disappeared. Increased degradation strongly decreased soil N and P stocks (by 0.63 kg N m^{-2} and 0.062 kg P m^{-2}), with respective losses at the most degraded sites of 45% and 35% by erosion and 20% and 15% by leaching. Degradation induced a decoupling of element losses because erosion removed relatively more N than P from the soil due to a narrowing N/P ratio with depth. Besides, mineralization followed by leaching induced higher N losses compared to P losses due to differences in their mobility and contributed to decoupling of these element losses. Degradation therefore, not only has reduced soil fertility, hampering ecosystem regeneration, but also has shifted N and P stoichiometry to stronger N limitation in the remaining soil. Our conceptual model offers mechanistic insight into the degradation processes of *Kobresia* pastures that have reduced pasture quality, undermined pastoral livelihoods, and polluted Tibetan surface waters.

2.4.2 Introduction

The Tibetan Plateau, the highest plateau on Earth, has a total area of 2.5 million km² (Lu *et al.* 2004), of which approximately 1.5 million km² are covered with grasslands (Ma *et al.* 2016). One third of this is occupied by the world's largest pastoral alpine ecosystem, the *Kobresia pygmaea* pastures (Fig. 1, also called Tibetan alpine meadows, (Miehe *et al.* 2008). It hosts more than 30 sedges of the *Kobresia* group and is a hot-spot for Cyperaceae diversity (Zhang & Noltie, 2010). The name giving species, *K. pygmaea*, is particularly dominant.

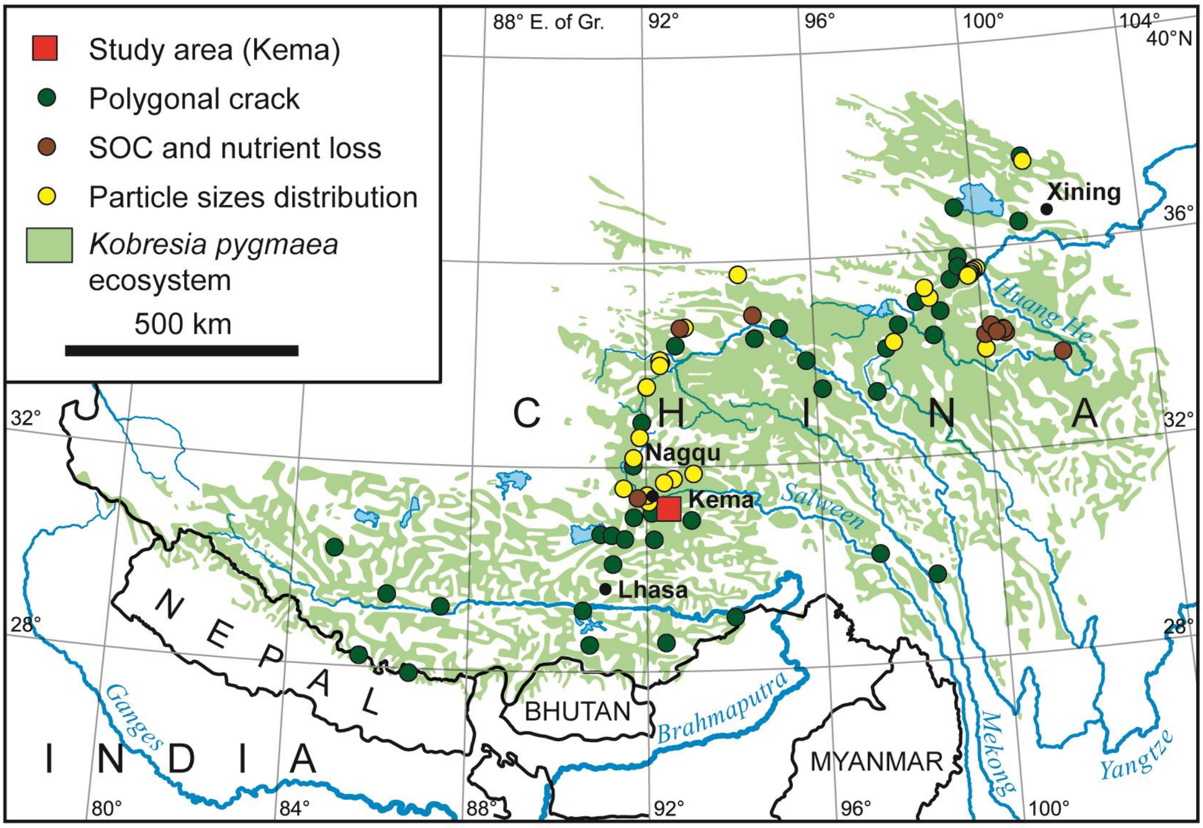

Figure SIV-1: Geographical distribution of *Kobresia* ecosystem, polygonal degradation patterns, soil texture profiles and studies on SOC, N and P losses on the Tibetan Plateau. Green dots show locations of polygonal cracks based on observations during field trips on the Tibetan Plateau and the Himalaya between 1982 and 2015. This indicates the overall distribution of this specific degradation phenomenon, not its actual distribution. Yellow dots represent the locations of soil profiles used for soil texture triangle. Brown dots represent studies on SOC, N and P losses following degradation extension. The red square indicates the location of the KEMA study site, where field work was carried out. Cartography: C. Enderle, Data source: Miehe et al. 2008[3].

The *Kobresia* ecosystem provides grazing grounds for roughly 12 million yaks and 30 million goats and sheep, directly supporting the livelihood of five million humans (Suttie *et al.* 2005). This ecosystem regulates the Asian Monsoon system (Boos & Kuang 2010) and covers the watersheds of major rivers suppling clean water for large parts of SE Asia (Huang *et al.* 2008; Qiu 2016). The dominant soil types of the *Kobresia* grasslands are: Cambisols, Regosols, Leptosols, Gleysols, Histosols, Phaeozems, Kastanozems.

It is still a matter of debate since when the pastures of the Tibetan Plateau are subjected to husbandry (Miehe et al. 2016), but the domestication of yaks has been dated back to 7.3 ka BP (Qiu *et al.* 2015), sheep domestication even to 8.6 ka BP (Miehe et al. 2016). Large herds of wild herbivores have grazed in these grasslands even longer. This long history of grazing led to a dynamic grazing-driven equilibrium system (Sheehy *et al.* 2006; Miehe *et al.* 2011) with a well-adapted set of species. Recent studies showed, that moderate, long-term grazing by wild and later by domestic ungulates favored plant species with preferential belowground C allocation (Hafner *et al.* 2012; Ingrisch *et al.* 2015), such as *Kobresia pygmaea*. This species produces a very dense root mat (Gao *et al.* 2008; Miehe *et al.* 2008) with high organic matter accumulation, and correspondingly high stocks of nutrients such as nitrogen (N) and phosphorus (P).

In cool environments, with low rates of chemical weathering, nutrients are mainly released by mineralization of accumulated organic matter, which in turn is limited by the moisture regime and low temperatures as well (Hobbie *et al.* 2002; Körner 2003). Thus N and P are mainly present in dead and living organic matter and are often, although not universally, growth limiting in Tibetan grasslands (He *et al.* 2008; Jiang *et al.* 2012; Xu *et al.* 2014). *Kobresia pygmaea* develops dense root systems, which increase the species' competitiveness with respect to nutrient uptake compared to other plant species and microorganisms (Kuzyakov & Xu 2013; Schleuss *et al.* 2015). This is especially important during the growing season, when greater moisture and warmer temperatures favor organic matter mineralization, but competition for nutrients is simultaneously high. On the other hand, the very high root to shoot biomass ratio (R/S ≈ 20, (Li *et al.* 2008; Schleuss *et al.* 2015) with small shoot fraction results in a high sensitivity to overgrazing. Removal of photosynthetically active shoots by overgrazing diminishes the belowground allocation of assimilates (Trlica & Rittenhouse 1993);(Li *et al.* 2013; McSherry & Ritchie 2013). If this occurs too frequently, the large belowground maintenance costs cannot be covered, causing a dieback of the plants (Hermans *et al.* 2006; Chapin *et al.* 2011). As a consequence, a roughly threefold increase of the grazing intensity in recent decades (shown for sheep numbers from 1960 to 2000 for several sites of the Tibetan Plateau, (Zhou *et al.* 2005) has put this ecosystem under immense pressure have led to pasture degradation (Holzner and Krichbaum 2002).

Degradation of the *Kobresia* pasture is nowadays widespread, occurring from Qilian Shan in the North to the Himalayas in the South (Fig. SIV-1). Here, degradation is defined as a process of pasture deterioration and a decrease of forage production caused by disadvantageous natural factors and improper utilization (Liu *et al.* 2006). It has usually been attributed to the increasing grazing activities promoting grassland degradation due to (a) trampling and (b) overgrazing (Li *et al.* 2013). Besides anthropogenic impacts, degradation is amplified by several harsh environmental conditions: low temperature, heavy rainfall events, droughts, high wind speed, sloping land, freeze-thaw cycles, high solar radiation (Callaway *et al.* 2002; Körner 2003; Shang *et al.* 2008). Up to now it remains unclear how the degradation is connected to climate change or is solely triggered by overgrazing and natural-occurring impacts. It is challenging to identify the climate change induced amplification of grassland degradation, because these mechanisms are less investigated, the changes are slow and the causal network is more complex. Most ecological studies are local and short-term, but climate change encompasses much larger temporal and spatial scales (Walther *et al.* 2002). Currently, the precipitation predictions on TP do not show a clear trend, with exception of increasing variability (Zhai *et al.* 2005; Wang *et al.* 2008a), meaning a higher risk of extreme dry and wet years and thus an increasing potential for degradation.

Within this paper we present a conceptual framework summarizing man-made and natural impacts on Kobresia pasture degradation to understand the implications for nutrient storage and losses. In particular, we link losses of nitrogen (N) and phosphorus (P) to the degradation stages by considering mechanisms of both physical degradation (erosion) and biochemical degradation (organic matter mineralization, followed by leaching). We hypothesize that, in addition to soil erosion, leaching has been a major contributor to losses of N and P (Hypothesis 1). Leaching, however, requires a positive water balance over several days, allowing water infiltration deeper than the main rooting zone. We expected a positive water balance despite the limited precipitation and partly high evapotranspiration in this semi-humid ecosystem (Hypothesis 2). With respect to total nutrient stocks, we expect that erosion and leaching both has resulted in unbalanced losses of elements, and consequently we expect decreasing slopes of regressions when losses are considered (Hypothesis 3). This because, erosion begins at the soil surface, and the stoichiometric ratios (C:N:P) narrow with soil depth. A relatively higher erosion loss of C > N > P is therefore expected on a total stock basis. Further, mineralization has released C as CO_2 into the atmosphere, whereas nutrients remain in the soil; because of differences in mobility, N is leached more strongly than P (Fig. SIV-2).

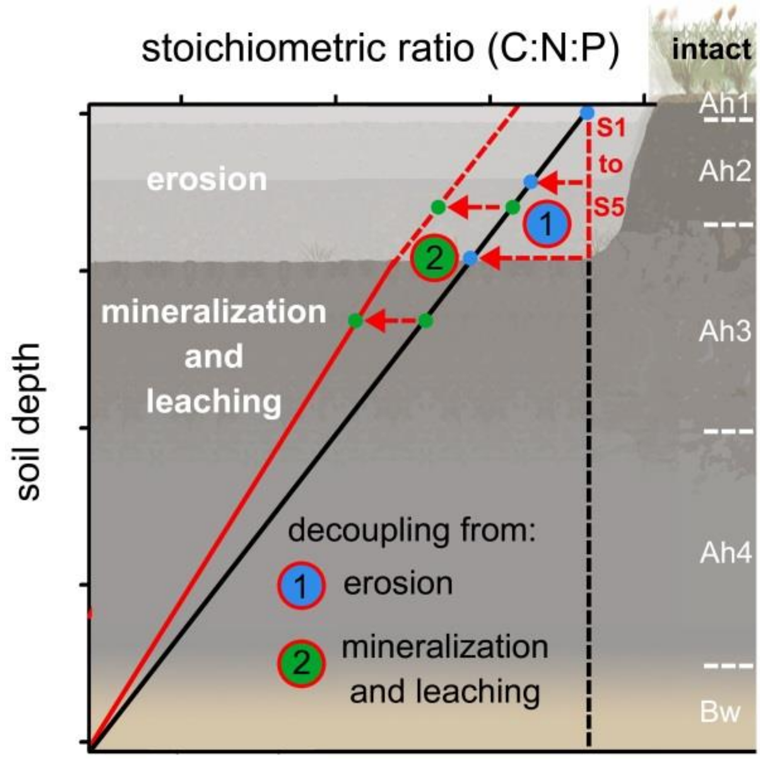

Figure SIV-2: Concept for the decoupling of carbon (C), nitrogen (N) and phosphorus (P) losses from leaching and erosion according to the 3rd hypothesis. The solid black and red lines indicate the stoichiometric ratios on a stock basis from the intact and degraded stages, respectively. *Decoupling of erosion:* erosion removes the topsoil and cause a relative higher loss of C > N > P compared to the deeper soil horizons. *Decoupling from mineralization and leaching*: C is released as CO_2 back to the atmosphere, whereas nutrients remain in the soil. Based on the chemical properties and interactions in the soil N and P are then leached to different extends (N > P).

To test these hypotheses, we selected a degradation sequence from intact Kobresia root mats (S1) to stages with extended surface cracks (S4) and bare soil patches (S5) (Fig. SIV-3) . Soils were sampled at various depths from each of the degradation stages (S0-S5), and soil properties were analyzed. A simple model of the soil water balance was used to assess the frequency of potential leaching conditions. This was validated with on-site lysimeter measurements.

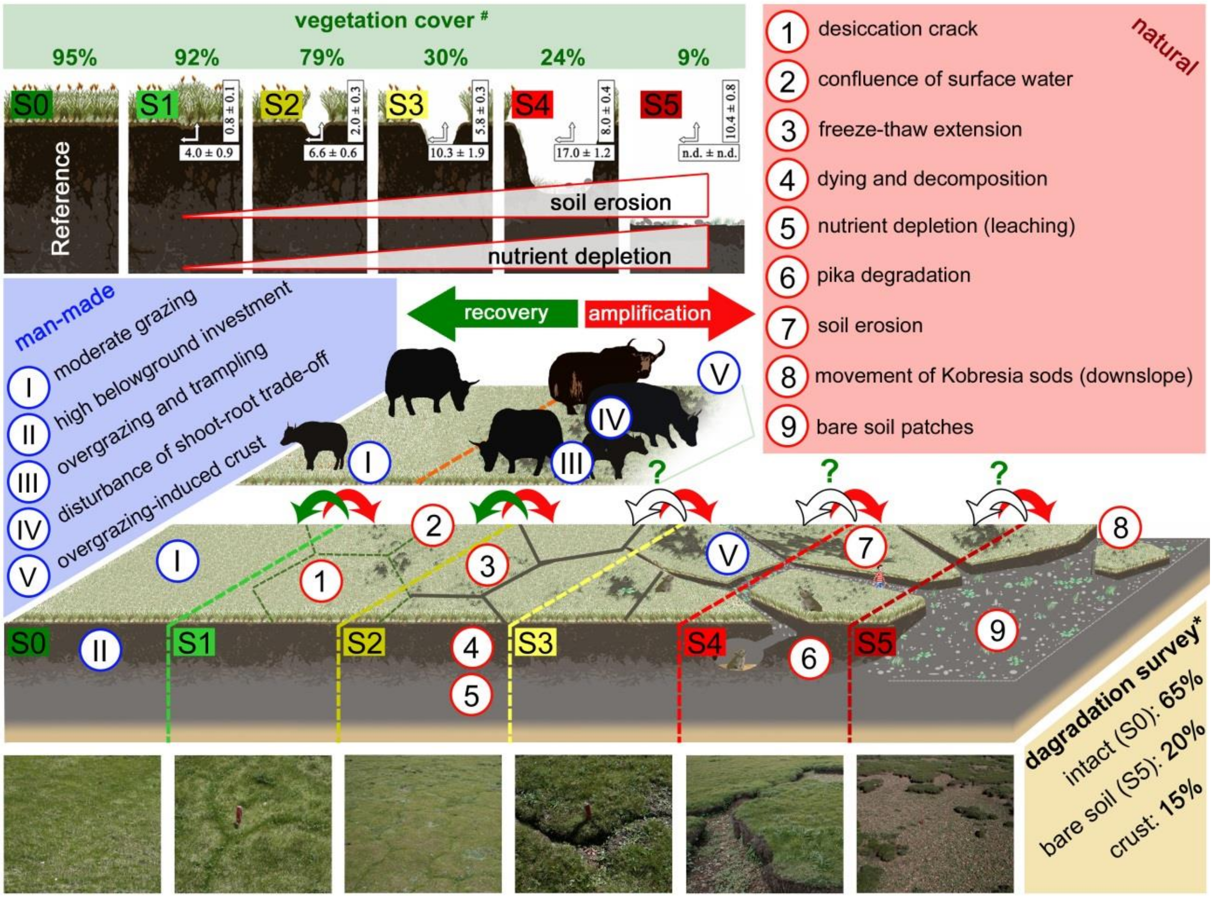

Figure SIV-3: Schematic overview of the degradation sequence from the intact (S0) to the severely degraded stage (S5) including man-made and natural-induced impacts on the *Kobresia* ecosystem degradation. Numbers describe the main biotic and abiotic mechanisms (man-made in blue and natural in red). The hierarchical order from S0 to S5 does not necessarily imply a rigid pathway: some steps can be simultaneous, be reversed, repeated or fail to appear in a certain period or location. Red and green arrows indicate the overgrazing-induced amplifications or pasture recovery under a moderate grazing regime, whereby it is still unclear if degradation is irreversible at a certain stage (white arrows). Data of vertical and horizontal extend of the cracks, the vegetation cover and degradation survey are inserted as well (Data source: *Babel et al. 2014, #Schleuss et al. unpublished).

2.4.3 Materials and methods

2.4.3.1 Site description

The empirical part of the study was conducted on the *Kobresia* Ecosystem Monitoring Area (KEMA) near the small village of Kema in the Nagqu Prefecture of the Tibetan Autonomous region (31°16'45''N, 92°59'37''E, Fig. SIV-1). Due to the high altitude of ca. 4410 m a.s.l., a cold and semi-humid climate predominates. Annual mean temperature is -0.9°C with 15.6 °C for the warmest month (July). Annual mean precipitation is 430 mm, most of it falling during the growing season (~270 mm, Nagqu climate station, ca. 20 km distance, (Miehe *et al.* 2011; Babel *et al.* 2014). The growing season normally lasts from mid-May to mid-September (Babel et al. 2014). The vegetation is dominated by*Kobresia pygmaea*, which covers up to 60% of the surface. The sedge forms very dense root-mats (*Kobresia* turf), which developed on a thin loess layer parent material (mainly metamorphites) loosen by cryoclastics. The soils are classified as Stagnic Eutric Cambisols (Humic) (IUSS Working Group, WRB 2006) and are characterized by a loamy texture (consisting of sand 50%, silt 33%, clay 17% in 0-25 cm, S0) and high SOC stocks (S0: ~11 kg C m² in 0-30 cm). Although the soils are decarbonated in the upper 30 cm, high pH values (pH H_2O 6.5) and high CEC predominate. Calcium and magnesium are the main exchangeable cations, comprising about 80% of the CEC.

The sites are mainly used as spring pastures for yak and sheep from April to June, with exceptional winter grazing in years with heavy snowfall. Large numbers of small mammals (Plateau Pika, *Ochotona curzoniae*) also occur on the sites. An *in situ* degradation survey showed that these pastures are moderately degraded, meaning that 65% of the surface was in intact condition (S0), 15% was dead *Kobresia* turf, and the root-mat was completely destroyed (S5) in the remaining 20% (Fig. SIV-3, (Babel *et al.* 2014).

2.4.3.2 Study design and sampling

We selected a degradation sequence including six stages from intact (reference site, S0) to strongly degraded sites (bare soil, S5). Each stage was replicated four times, resulting in 24 plots. Sites were selected within an area of ca. 25,000 m² to ensure similar environmental conditions, with degradation stages assigned according to the horizontal and vertical extent of the surface cracks. The aboveground biomass was sampled on each plot directly in a defined area (75 cm²). To sample for soil characteristics and root biomass down to 30 cm soil, pits were dug (30 cm length × 30 cm width × 40 cm depth). The soil profiles were sampled according to soil horizons. We took two intact soil cores from each horizon to determine the bulk density and root biomass, whereas non-volumetric samples were taken for analysis of carbon and nutrients. Hardly any roots occurred deeper than 25 cm, so we did not sample for root biomass in the Bwg horizon (Schleuss *et al.* 2015).

2.4.3.3 Analyses and calculations

Bulk soil density and root density were determined from soil cores after drying soil at 105 °C and root biomass samples at 60 °C (van Reeuwijk 2002). Soil, root- and shoot biomass are presented on a dry matter basis throughout. Grain size analysis was done by combined pipette and sieving method (seven fractions, Koehn, DIN 19683-1) after digestion of organic matter with H_2O_2. Total soil C and N contents were analysed using an elemental analyser (NA1500, Fisons instruments, Milano, Italy). Phosphorous was extracted by HNO_3 digestion from air-dried soil. The HNO_3 dissolves the organic matter yet affects only the surfaces of the silicate structures. Hence, it does not strictly represent the total element content of P in the soil, but a major proportion of it. The effective cation exchange capacity was analysed by percolating with unbuffered 1 M NH_4Cl and cations (Ca, Mg, K, Na, Al, Fe and Mn) were measured in percolates. After digestion or extraction, solutions were measured with ICP-OES (Optima 4300 DV, Perkin Elmer Instruments, Norwalk, USA). Carbon and nutrient stocks (in kg per m²) were calculated by multiplying the element content (in g of element per kg soil) by the bulk soil densities (kg soil per m^3) and thickness of each horizon (m). We presented the nutrient stocks (0-30 cm) of each degradation stage (S1-S5) in percent of the mean stock of the reference stage (S0).

Disentangling erosion and leaching losses: We separated N and P losses caused by physical and chemical degradation (i.e. erosion versus leaching-driven N and P losses) by attributing the nutrient depletion from remaining soil horizons (below the surface crack) to leaching. Losses by gaseous emissions from the upper well aerated-topsoil in terms of N (i.e. N_2O, N_2, NO_X) were assumed to be negligible

On the other hand, the loss of surface soil and its nutrients was attributed to erosion. The erosion-driven element loss was estimated by measuring the topsoil removal (volume of vertical soil cracks) from each degraded soil profile (S1-S5) and multiplying this by the average element content and bulk density of the missing horizons as they occurred in the undegraded sites (S0). This is an approximate measure, since topsoil horizons may have been affected by N and P leaching before erosion. It is a conservative approach, however, because these uncertainties tend toward an underestimation of leaching relative to erosion losses. Comparing the total N and P losses with the sum of modelled data for erosion and depletion showed no significant differences.

Water balance of the intact Kobresia pygmaea pasture: Daily water balance (evapotranspiration ET, infiltration INF, and soil water content SWC) of the *Kobresia pygmaea* pasture at the Kema research station was monitored with microlysimeters in the periods June 23rd to September 5th in 2010 and July 23rd to September 3rd in 2012. The microlysimeters consisted of intact soil monoliths enclosed in plexi-glass tubes (15 cm diameter) with a wick drainage system allowing for realistic determination of infiltration rates (Coners et al 2016). Installation depth of the microlysimeters (30 cm) covered the main rooting zone.

To assess the potential for leaching events, we calculated a simple water balance model for the intact stage (S0). For the estimation of the infiltration probability for a given day, three parameters are needed: (i) cumulative amount of precipitation of the preceding period, (ii) evapotranspirative water loss during this period, (iii) water uptake capacity of the soil, and (iii) water content of saturated soil (field capacity). The cumulative precipitation was calculated from daily precipitation rates measured at Nagqu meteorological station (31.483N, 92.067E, National Climatic Data Center www.ncdc.noaa.gov/). Microlysimeter measurements at Kema research station (Babel *et al.* 2014; Coners *et al.* 2016) revealed a minimum evaporatranspirative loss to the atmosphere of 2mm d^{-1} and lower and upper limits of soil water contents of 13 vol% and 30 vol%, respectively. The corresponding water storage in the upper 30 cm was 40 and 90 mm, respectively. Thus, water uptake capacity in our model was assumed to be 50 mm between dry and saturated soil. Precipitation exceeding this value cannot be stored in the soil and will leach into deeper soil horizons. At a given daily evapotranspiration rate of 2mm d^{-1}, even a fully saturated soil would be fully depleted after 25 days. For subsequent calculations, this period was shortened to 15 days based on preceding optimizing model runs looking for the best fit of calculated versus estimated leaching events based on microlysimeter measurements in 2010 and 2012.

2.4.3.4 Statistical analyses

Data are presented with mean and standard error throughout ($n=4$). To determine significant differences ($p < 0.05$) between various plant and soil characteristics, a one-way ANOVA was implemented with corresponding horizons compared between degradation stages. We first checked for normality (Shapiro-Wilk test) and homogeneity of variance (Levene test). Post hoc multiple comparisons were implemented using the Fishers least significant difference (LSD). When normality and homogeneity of variance was not given, data were log-transformed or analysed with the non-parametric Kruskal-Wallis test coupled with a Bonferroni correction for multiple comparisons. Single linear and non-linear regressions to identify relationships between several soil characteristics were deemed significant at $p < 0.05$.

2.4.4 Results

2.4.4.1 Nutrient losses with intensified degradation

Relevance of soil organic matter and decreasing nutrient contents: Soils at the KEMA research sites had high organic matter contents, including C, N and P. SOC content declined markedly with intensified degradation from S0 to S5. The effective CEC (sum of cations) correlated closely with the SOC content (R^2= 0.82, $p<0.01$). In contrast, soil mineral components consisted of 50% sand and 20% coarse silt, both having low surface charge for retaining nutrients. The y-intercept revealed that only 25% of the effective CEC was contributed by minerals, while 75% were attributed to SOC (Fig. SIV-4a).

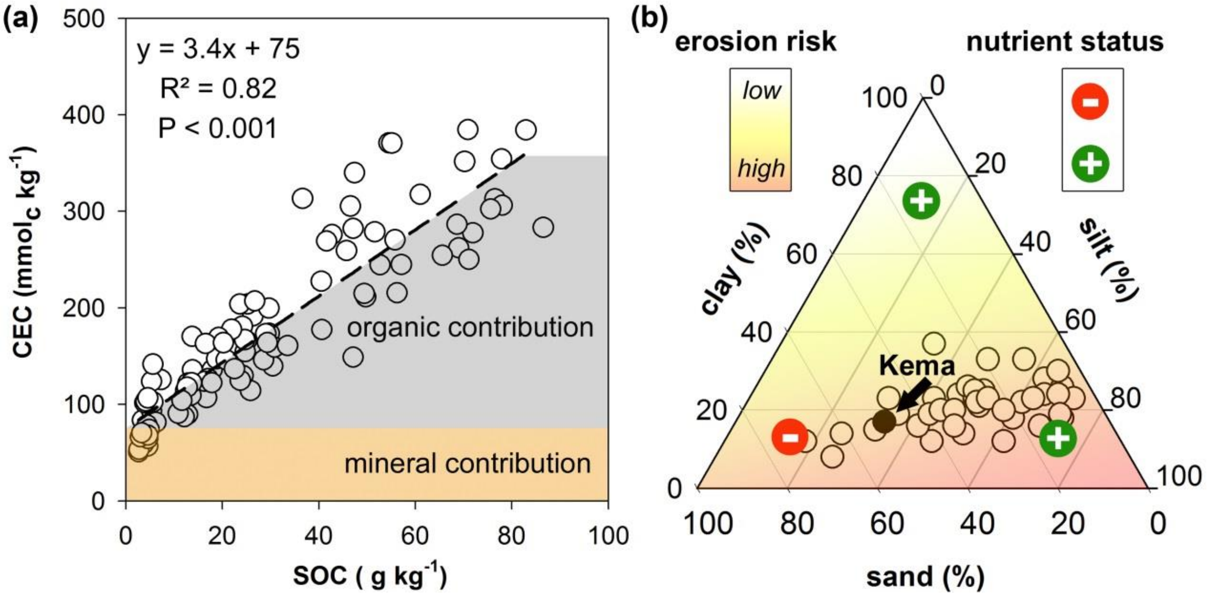

Figure SIV-4: **(a)** Relationship between soil organic carbon content (SOC) and effective cation exchange capacity (CEC) to deduce mineral particles and organic matter contribution to nutrient availability and **(b)** particle size distribution of 61 soil profiles distributed on the Tibetan Plateau. Soil texture is presented for the topsoil horizons from 0-30 cm. The risk for soil erosion from low to high (white to yellow to red) was assumed to increase from a clayey to sandy to silty textures. The nutrient status (+, -) was expected to decrease with coarser soil textures.

We quantified total N, total P and exchangeable base cations (Ca, Mg, K, Na) for each horizon of each degradation stage (S0-S5). All nutrients decreased with intensified degradation (Fig. SIV-5). In the erosion-unaffected Ah3 horizon, N and P contents decreased by ~2.8 mg N g^{-1} soil (i.e. loss of ~65%) and by ~0.17 mg P g^{-1} soil (loss of ~30%) from S0 to

S5, respectively. Base cations decreased to the same extent, i.e. Ca (~100 $mmol_c\ kg^{-1}$), Mg (~20 $mmol_c\ kg^{-1}$), K (~1 $mmol_c\ kg^{-1}$) and Na (~0.8 $mmol_c\ kg^{-1}$). However, here we focus on the fate of total N and P contents because these elements limit the productivity of the *Kobresia* ecosystem, whereas base cations are often sufficiently available as was shown by mean of fertilization studies.

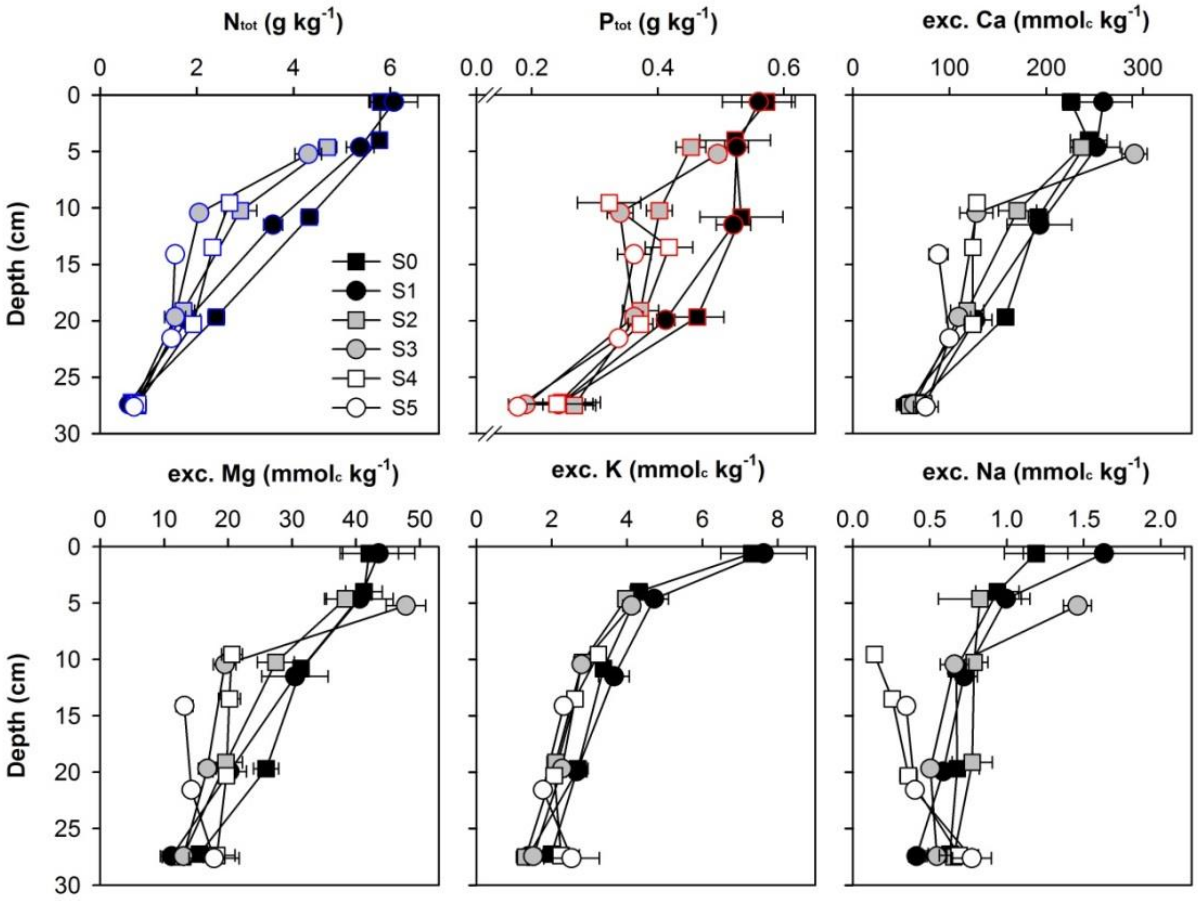

Figure SIV-5: Decreasing soil nutrients contents from the intact (S0) to the severe degraded stage (S5). Nitrogen (N) and phosphorous (P) contents are shown as total contents, whereas the base cations such as calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na) are represented as exchangeable nutrients. All data points are means with standard error (n=4).

N and P stocks and losses: Accounting for both (a) removal of the upper soil horizons and (b) decreasing nutrient contents revealed a steady decrease of total N and P stocks from the intact (S0) to the most degraded stage (S5) (Fig. SIV-6). Losses were restricted to the upper 25 cm (Ah1-Ah4), whereas the Bw horizon showed similar stocks from S0 to S5. On the bare soil patches (S5), 65% (~0.63 kg N m^{-2}) and 43% (~0.062 P kg m^{-2}) of total N and P were lost from the upper 30 cm of soil compared to the reference stage (S0).

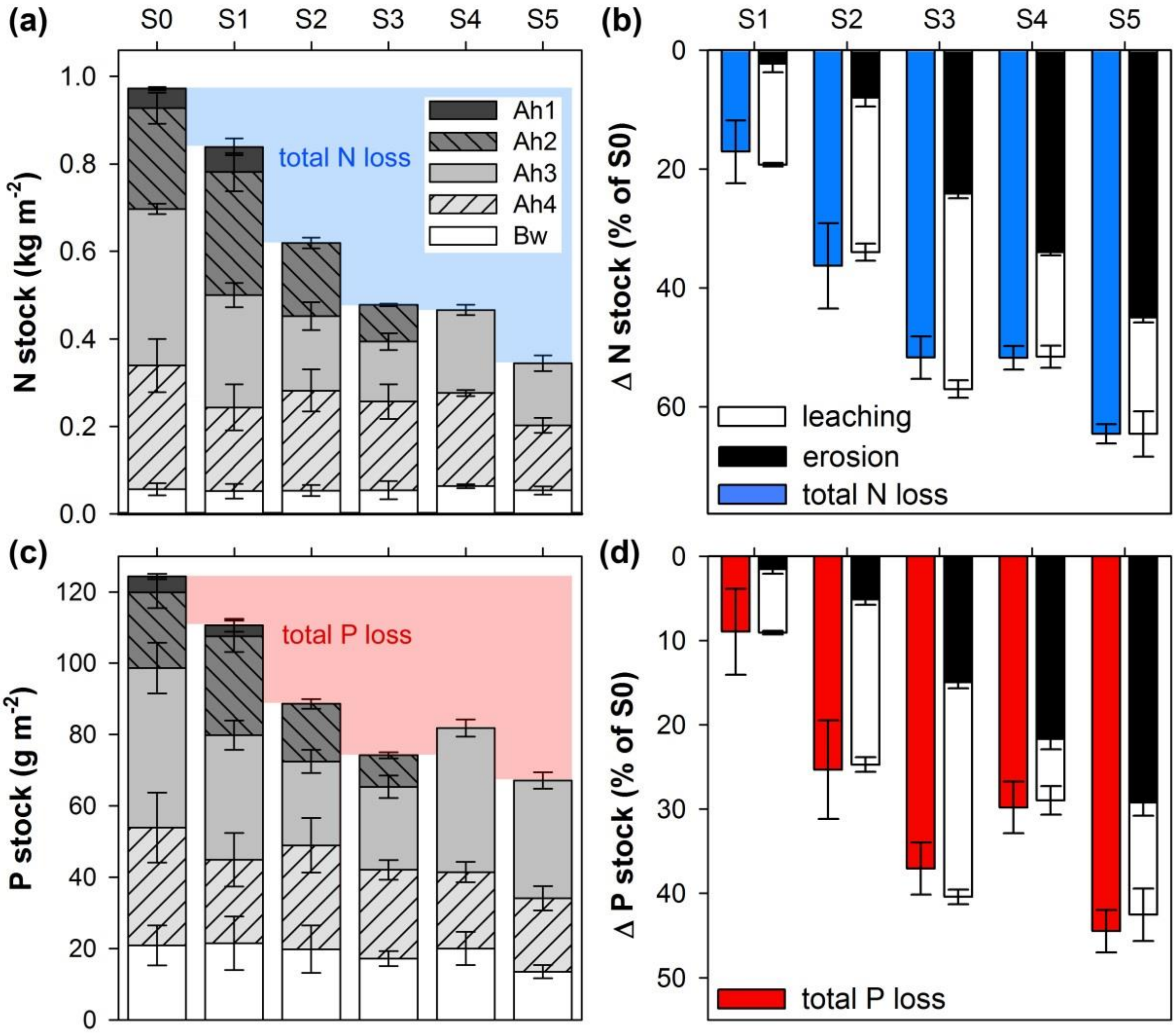

Figure SIV-6: Total nitrogen (N) and phosphorous (P) stocks and losses with increasing degradation; **(a & b)** show N and P stocks in intact soil (S0) and under each crack (S1-S5) down to 30 cm depending on horizons and **(c & d)** reflect the differentiation of N and P losses from erosion and leaching. Lowercase letters show significance of differences for the N and P stocks between degradation stages (a & b). The absence of significant differences (n.s.) between the total N and P losses (blue and red columns) and the sum of the erosion- and leaching-derived N and P losses reflect correct estimations (c & d).

2.4.4.2 Disentangling erosion and leaching losses

Erosion-driven nutrient losses were calculated on the basis of the missing surface soil horizons, and losses from erosion-unaffected horizons were attributed to mineralization and leaching. For the most degraded stage (S5), erosion accounted for two thirds of nutrient loss and leaching for one third, with leaching losses being relatively more prominent in the less degraded stages (S1-S3).

N and P losses from erosion: In the most degraded stage (S5) about 85 kg soil m^{-2} (corresponding to soil layer of 30 cm) was lost to erosion. The erosion-derived losses increased with intensified degradation and were particularly high in the severely degraded stages (S4-S5) (Fig. SIV-6a-b). By S5, about 0.44 kg N m^{-2} (~45% of S0) and about 0.42 kg P m^{-2} (~29% of S0) had been lost to erosion.

N and P losses from leaching: Nutrient leaching requires (a) the presence of N and P in its soluble forms (i.e. DON, nitrate and phosphate formed during organic matter mineralization) and (b) periods when infiltration reaches deeper than the main rooting zone. Both requirements were met: First, organic matter mineralization was indicated by decreasing SOC contents in uneroded horizons from S1 to S5. Second, a water balance model and lysimeter data indicated that leaching below 30 cm can occur (see following section). Losses of N and P contents (Fig. SIV-5) were indeed evident in uneroded horizons, decreasing nutrient stocks (Fig. SIV-6). Particularly in the less degraded stages (S2-S3) stocks decreased by 26-33% for N and by 20-26% for P via leaching (Fig. SIV-6). In the most degraded stage (S5) leaching contributed 0.19 kg N m^{-2} (~20% of S0) and about 19.2 g P m^{-2} (13% of S0) to depletion of N and P stocks, respectively. Thus, we conclude that leaching is indeed an essential contributor to N and P loss in this pastoral ecosystem, which might be pronounced in summer during heavy rainfall events and during snow melting in early spring when plant uptake is low.

2.4.4.3 A water budget to verify leaching potential

A water budget model for the intact stage (S0) estimated that water infiltrated deeper than 30 cm during a period of only 10 to 30 days per year, mainly during the growing season (Fig. SIV-7b). During these infiltration events, nutrients can be leached from the rooting zone. The modelled probability for leaching events was confirmed by direct infiltration measurements on site with micro-lysimeters (Fig. SIV-7c).

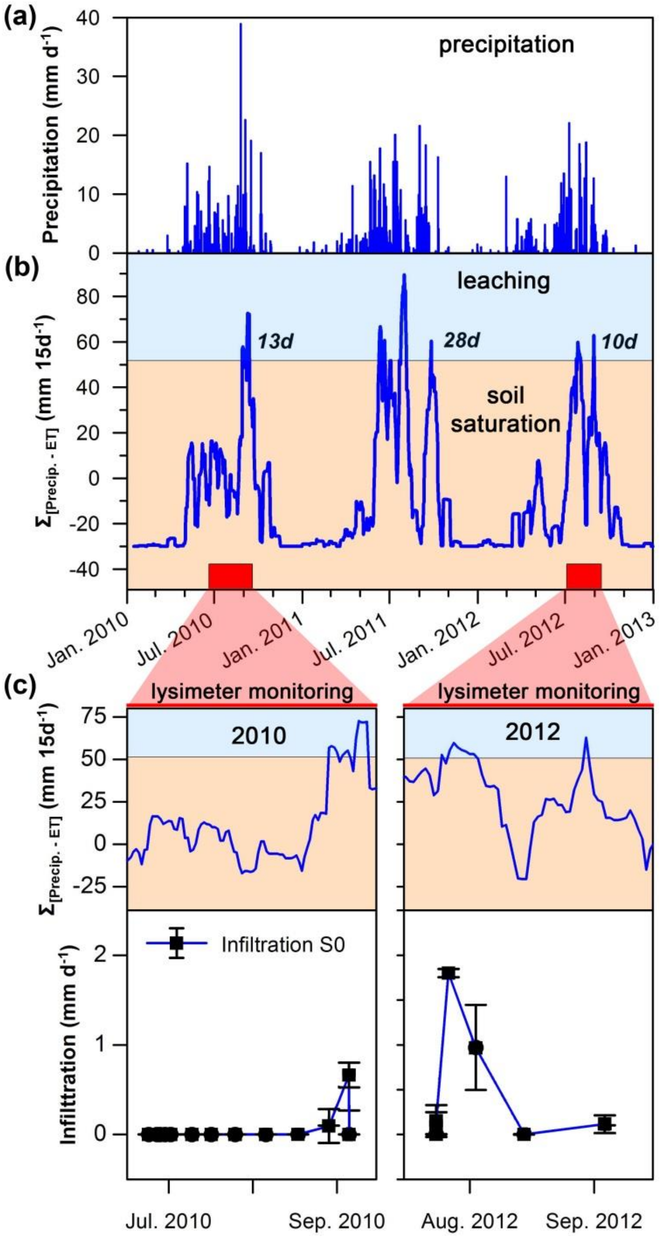

Figure SIV-7: Estimation of leaching events during 2010, 2011 and 2012 at Kema/Nagqu. Shown are: **(a)** the daily precipitation rate [mm d^{-1}) based on climatic data at Naqu, **(b)** the 15-day water balance giving the sum of the 15 day's precipitation and its correction by the daily (number indicate days with probable water infiltration per growing season) and **(c)** the infiltration rate [mm d^{-1}] from intact *Kobresia pygmaea* root mat and bare soil patches at Kema research station. Infiltration was monitored with microlysimters in the periods June 23rd to July 23rd in 2010 and July 23rd to September 3rd in 2012.

Calculated annual leachate sums from the water balance model (58, 138, and 56 mm a^{-1} in the year 2010, 2011, and 2012, respectively) indicated that roughly 10-25% of the annual precipitation infiltrated below the rooting zone. This mainly happened during short periods of several days to weeks. Within the rest of the frost-free season the high evapotranspiration rates cause a positive water budget (Coners *et al.* 2016) and consequently lowers the risk for leaching events.

While the model, even with our very conservative parameters, predicts leaching (meaning: water movement below the rooting zone) of 4.4, 5.8, and 4.4 mm d^{-1}, (based on rain data for years 2010, 2011, and 2012, respectively), results from micro-lysimeters hardly reach 2 mm d^{-1}. Therefore, we suggest that during periods of strong precipitation, larger quantities of water run off on the surface (promoted by micro-relief); and infiltrated into the surface cracks. This, in turn, may have strongly intensified leaching of N and P in the degraded stages. Since the water balance model and field measurements both confirmed that hydrological conditions can induce nutrient leaching to below the root zone within short periods over the frost-free season, it confirmed our second hypothesis.

2.4.4.4 Unbalanced losses of C, N and P from erosion and leaching

The decreases in N stocks from S1 to S5 were marginally lower than the decreases in SOC stocks (fit slightly above the 1/1 trend-line), whereas the P stocks were clearly more resistant to loss. This resulted in imbalance between total losses of C and N compared to P (Fig. SIV-8c). Unbalanced N and P losses from erosion: Erosion is a bulk transport process and should remove elements equally, but the stoichiometric ratios (C:N:P) decreased with depth (Fig. SIV-9). This caused relatively higher losses of C > N > P on a total stock basis, confirming our third hypothesis with respect to erosion. This is clearly evident in the highly correlated plot of N versus P loss (Fig. SIV-8d, $R^2 = 0.98$), which lies well above the 1/1 trend-line.

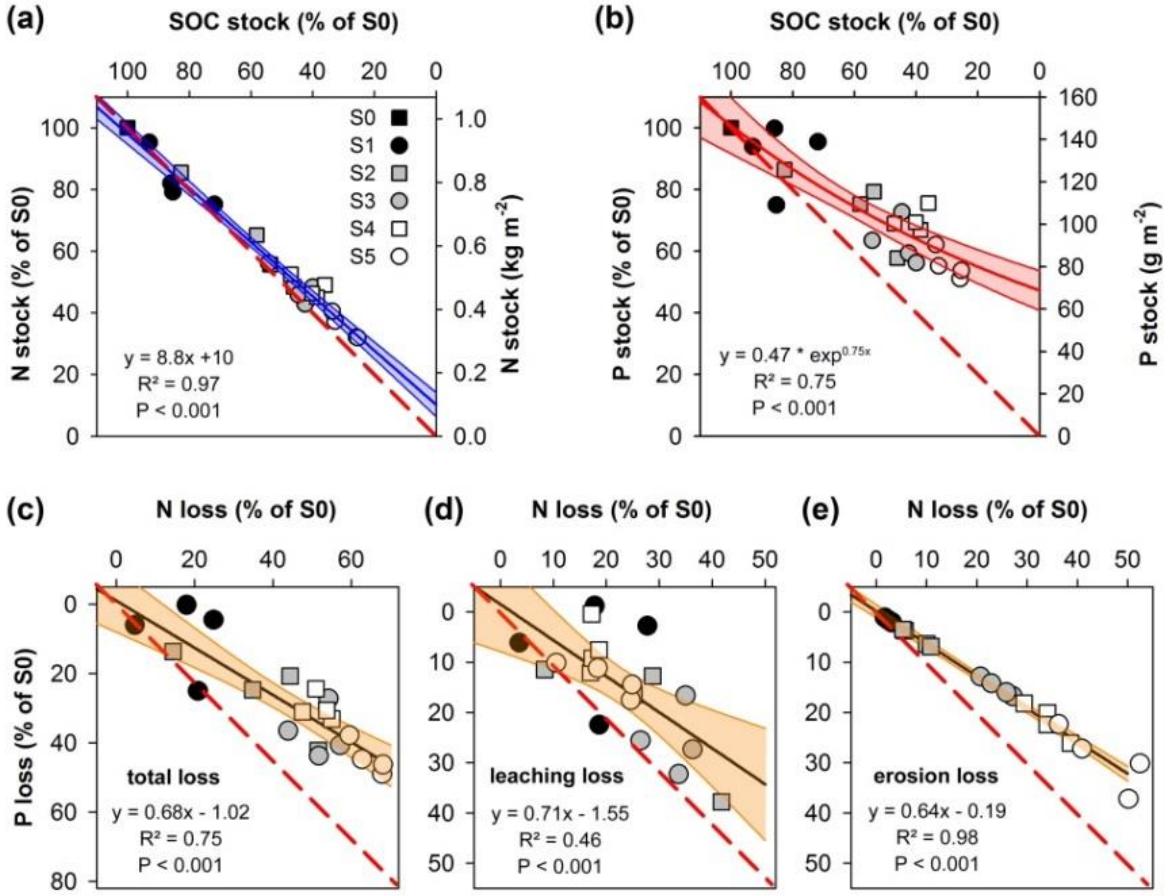

Figure SIV-8: Unbalanced losses of carbon (C), nitrogen (N) and phosphorous (P) in the total soil profile depending on degradation stage and postulated mechanisms. **(a-b)** show the decoupling of N and P stocks from SOC stocks, **(c)** shows the decoupling of total N versus P loss, **(d)** shows the decoupling of estimated leaching-driven N versus P loss, and **(e)** shows the decoupling of estimated erosion-derived N versus P loss. The blue (for N), red (for P) and orange (for both) areas show the 95% confidence intervals of the applied fits (n=20)

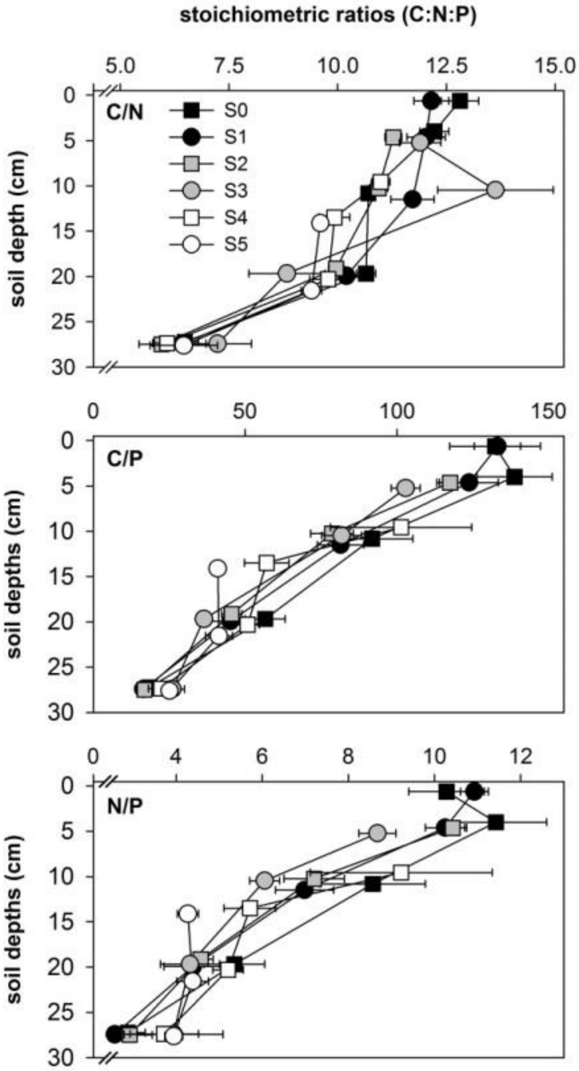

Figure SIV-9: Stoichiometric ratios (C:N:P) with intensified degradation (S0 to S5) depending on soil depths. Shown are means with standard errors (n=4) for (a) C/N ratio, (b) C/P ratio and (c) N/P ratio.

Unbalanced N and P losses from leaching: We also observed unbalanced losses of N and P through leaching, although this was less strong (about 46% of explained variance) than for erosion. The SOC content in each erosion-unaffected horizon, representing progressive mineralization from S1 to S5, was related to N and P content (Fig. SIV-10). Consequently, N and P contents decreased in these horizons as the SOC content declined, but the decrease in N content was greater than that of P (Fig. SIV-10a-c). Unbalanced losses of C, N and P during degradation from S0 to S5 were therefore evident for both leaching and erosion mechanisms considered separately, and for the total nutrient stocks overall.

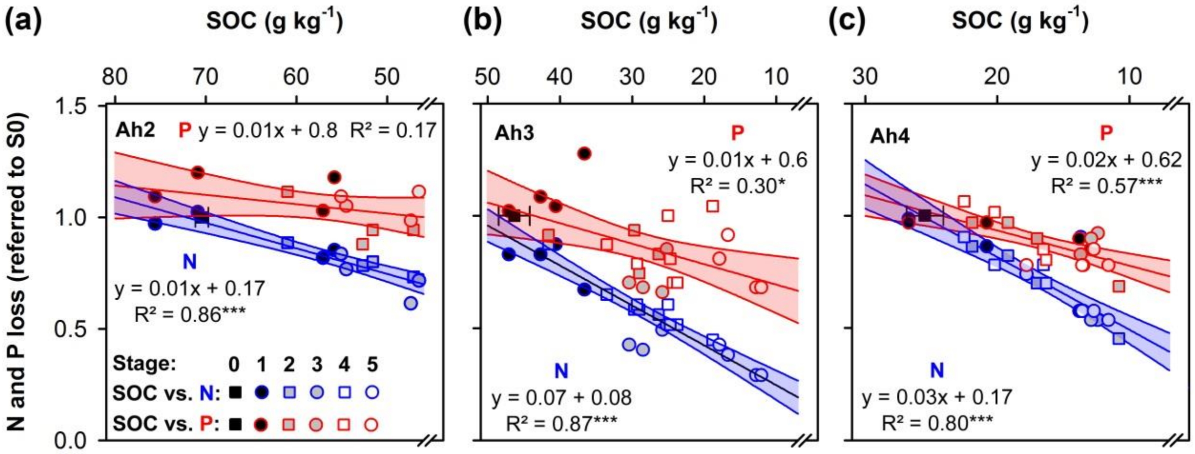

Figure SIV-10: Unbalanced losses of nitrogen (N) and phosphorus (P) contents in the Ah2, Ah3 and Ah4 horizon depending on degradation stage. N and P contents of the degradation stages are standardized to the reference stage (S0) to enable a comparison between both on the same scale. The reference stage is represented with the black square including the standard error for SOC variability. The red and blue areas show the 95% confidence intervals of the linear fits. Asterisks indicate significance of regressions with * for $P < 0.05$ and *** for $P < 0.001$. Since only N and P contents of the erosion-unaffected soil horizons were considered [(Ah2: S1-S3; n=12), (Ah3: S1-S5; n=24), (Ah4: S1-S5; n= 20)] the decoupling can be solely attributed to leaching losses.

2.4.5 Discussion

2.4.5.1 Concept of degradation

We have incorporated degradation factors into a more comprehensive conceptual model of *Kobresia* pasture degradation, accounting for important biotic and abiotic interactions (Fig. SIV-3). The model describes a gradual degradation sequence with five stages from intact (S0) to severely degraded (S5), in which the root mat has entirely disappeared.

The model postulates that a high grazing activity is a key factors for inducing degradation. Trampling by livestock directly damages the protective *Kobresia* turf, and heavy grazing removes the photosynthetically active shoots, which disrupts the belowground allocation of assimilates (Trlica & Rittenhouse 1993; Hermans *et al.* 2006; McSherry & Ritchie 2013). Over the long-term this has promoted the dying of the *Kobresia* turf, and the formation of vegetation-free patches of dead root mat, covered with blue-green algae and crustose lichens (Fig. SIV-11e-f, (Unteregelsbacher *et al.* 2012). Additional images of the degradation factors and stages are provided in the supplementary material (Fig. SIV-11).

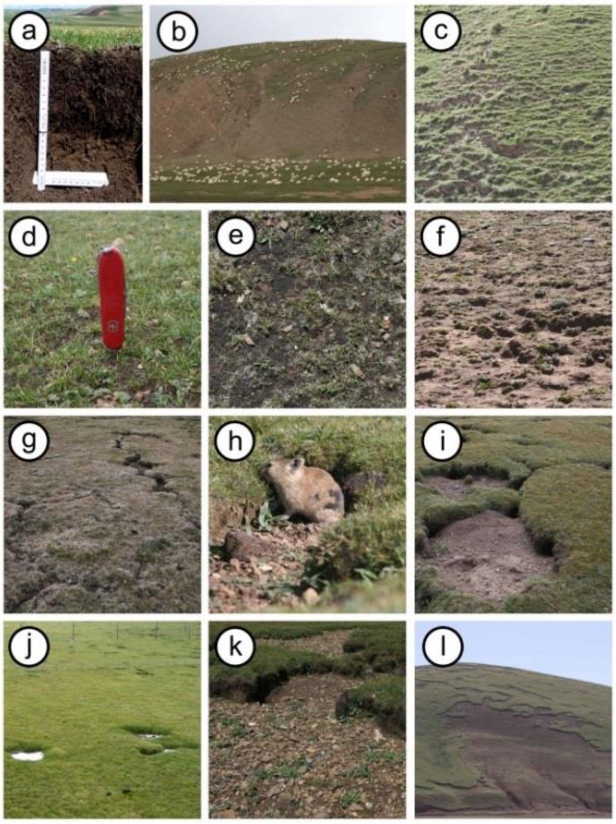

Figure SIV-11: Pictures of degradation patterns and mechanisms in the *Kobresia* ecosystem: **(a)** intact Kobresia root mat, **(b-c)** overgrazing and trampling damages, **(d-e)** overgrazing-induced or natural dying of the *Kobresia* turf associated with formation lichen cover **(f)** extensive decomposition of the *Kobresia* turf, **(g)** polygonal cracking and the formation of a micro-relief, **(h-i)** pika degradation via grazing and burrowing, **(j)** surface water following a strong rain event, **(k)** accumulation of stones and gravel following water and wind erosion and **(l)** downslope- sliding sods of the *Kobresia* turf.

Patterned ground with sharp polygonal cracks indicate desiccation or frost impacts (Walker *et al.* 2008; Lehmkuhl 2016), promoted by high evaporation due to very low relative humidity, low air pressure (~ 500 hPa) and temperature extremes in winter and summer ((Shenbin *et al.* 2006). As a consequence plants die along the cracks (above- and belowground, Fig. SIV-12) due to desiccation or frost impacts.

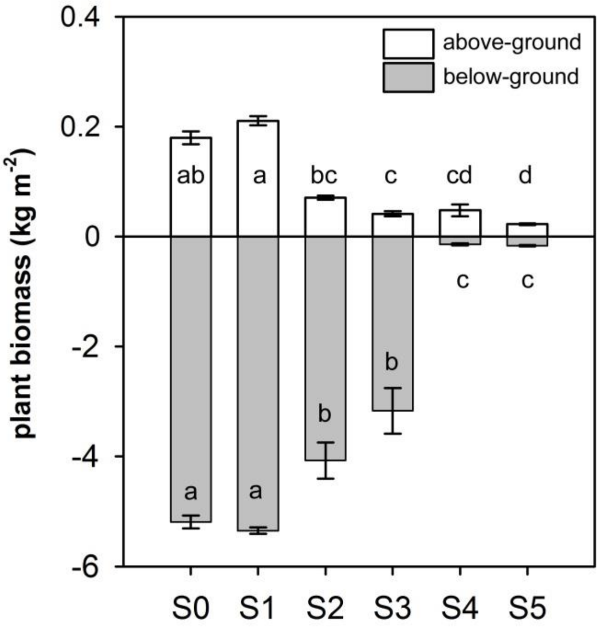

Figure SIV-12: Above- and belowground biomass with increasing degradation from S0 to S5. Shown are means with standard errors (n=4). Lowercase letters show significance of differences between degradation stages. Note that above-and below-ground biomass are represented on different scales (BGB 10^0 and AGB 10^{-1}).

The misbalance of C in and output then initiate the gradual decay of the *Kobresia* turf (S1 to S4). This forms a micro-relief and enables a confluence of surface water during rainfall events, which increase the moisture in the initial cracks. Moist soil at the beginning of the frost season in combination with strong diurnal frost events leads to expansion during freezing, extending the surface cracks (S1, S2). The soil is then exposed to the forces of water and wind, and erosion widens the polygonal cracks (S2-S4) until only bare soil remains (S5). A relative accumulation of gravel on the surface of the cracks (erosion pavement) reflects the removal of fine soil fractions during erosion. Soil erosion on the Tibetan Plateau is strongly facilitated by the predominantly loamy to silt loam soil texture, high relief energy due hilly landscapes, intense summer precipitation events, high wind velocities, snow melting in spring, and burrowing small mammals, which use the extended cracks to access the underside of the root mats (Pech *et al.* 2007; Harris 2010; Lehnert *et al.* 2015).

2.4.5.2 Nutrient losses

Intensified degradation has disturbed the equilibrium state of the intact *Kobresia* ecosystem with regard to the C and nutrient cycles (Babel et al. 2014) and induces high SOC losses across the whole ecosystem (Fig. SIV-3a).

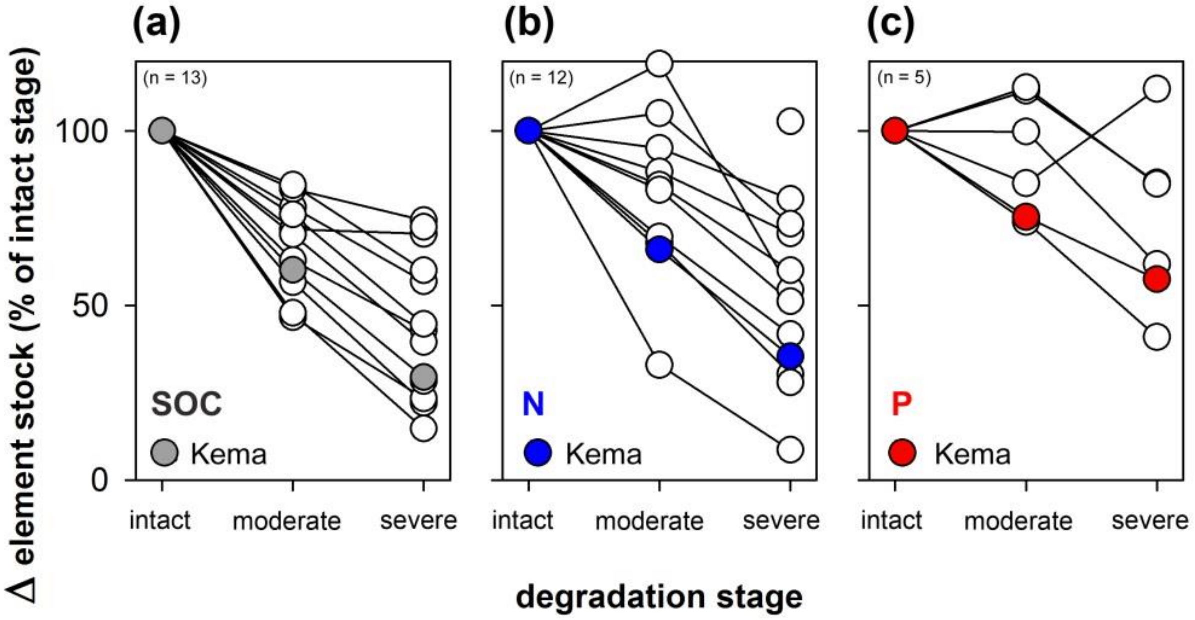

Figure SIV-13: Literature overview of degradation-derived soil organic carbon (SOC), total nitrogen (N) and total phosphorous (P) losses in the *Kobresia* ecosystem. Element stocks of **(a)** SOC, **(b)** N and **(c)** P were referred to the intact stage, because definitions about degradation (intact, moderate, and severe) as well as sampling depths differ between studies. The colored circles (SOC in grey, N in blue, P in red) represent the element losses at the KEMA research site.

SOC loss strongly compromises nutrient availability, due to its broad impact on soil chemical and physical properties (Jobbagy & Jackson 2000). In contrast, mineral-associated nutrients in the *Kobresia* ecosystem are less important in terms of soil fertility due to the high proportions of aeolian coarse silt and sand, which mainly consist of nutrient-poor quartz (Pye 1995). The high N and P losses found in this study are nevertheless in the upper range compared to other studies from the *Kobresia* ecosystem, where severe degradation typically has caused average losses of 45% for N and 23% for P (Fig. SIV-13b-c). Overall, the diminished C and nutrient stocks across the whole ecosystem indicate a strong reduction of soil fertility and probably also of the ecosystem's capacity for revegetation and recovery.

This compromises pasture quality and threatens the livelihood of millions of Tibetan herders (Niu *et al.* 2016; Qiu 2016). These impacts are amplified by the progressive losses of available grazing ground, while stocking rates continue to increase (Zhou *et al.* 2005).

Losses from erosion: Erosion removes the upper, most fertile and organic-matter-enriched soil, leading to high N and P losses, especially in the severely degraded stages (S3-S5, Fig. SIV-6a-b). At our study sites, the most degraded stage (S5) had lost 85 kg of soil per square meter, including SOC (~5 kg m^{-2}), N (~0.43 kg m^{-2}), and P (~0.044 kg m^{-2}). Although most of these nutrients were incorporated into SOM and are not directly plant-available (Hobbie *et al.* 2002; Vitousek *et al.* 2010), this nutrient pool provided a long-term potential reservoir for plant nutrition.

Losses from leaching: In the erosion-unaffected horizons (Ah2 for S0 to S2, Ah3 and Ah4 for S0 to S5), N and P contents decreased with intensified degradation from S1 to S5 (Fig. SIV-5a-b) contributing to the decline in nutrient stocks (Fig. SIV-6a-b). These decreasing nutrient stocks are explained by mineralization of organic matter, followed by leaching. Degradation stimulates mineralization through the following processes: First, trampling, overgrazing and polygonal cracking cause a dying of the *Kobresia* turf and facilitate the decay of the root mat. This releases nutrients such as N and P into the soil environment. The decreasing plant biomass from S1 to S5 (Fig. SIV-12) presumably reduces nutrient demand below supply. Consequently, nutrients accumulate in the soil solution and are prone to leaching. For the most degraded of our field sites (S5), leaching contributed about one third of total N and P losses. However, this approach neglects that the eroded soil horizons have likely already been affected by leaching. The hypothesized significance of leaching was therefore confirmed, and the extent of leaching could in fact be even larger than calculated here.

The importance of leaching in this semi-arid ecosystem was verified by a modeled water balance for intact *Kobresia* pasture (Fig. SIV-7b). Even though intensive rain events occur at a low frequency on the Tibetan Plateau (~10-20%, (Maussion *et al.* 2014), our water balance model resulted in 10-28 days per growing season (2010-2013) during which the precipitation exceeded the threshold for infiltration of water below the rooting zone. Direct micro-lysimeter measurements temporally matched the modeled leaching events (Fig. SIV-7c). Since most of the root biomass in *Kobresia* pastures is located in the topsoil (0-10 cm: 86-

88%; 10-20 cm: 8-10%; 20-30 cm: 2-4%, (Wang *et al.* 2008b), it is likely that the mobile nutrients are exported from the plant-soil system with the infiltration water. However, this model was applied for the intact pasture (S0), thus leaching losses are potentially even higher in the degraded stages, where water supply (micro-relief) and infiltration (cracking) is enhanced.

2.4.5.3 Unbalanced losses of elements

Disentangling nutrient losses by erosion and leaching demonstrated that erosion removes relatively more N than P from the soil profile. This is due to the decreasing N/P ratio with depth (Fig. SIV-9). Consequently, erosion of the upper horizons causes higher proportional N than P losses, when total stocks down to 30 cm are considered. The erosion dependent unbalanced N and P losses are amplified by mineralization and leaching. First, mineralization releases C back to the atmosphere as CO_2, but in relative terms have accumulated nutrients such as N and P in the soil (Zech *et al.* 1997). These are then leached to different extents (N > P), depending on (a) microbial transformation (between organic and inorganic forms) and (b) their chemical behavior, including mobility, sorption, solubility and precipitation in the soil. N is leached in its soluble and mobile forms. In fact, DON and NO_3^- are the dominant forms leached from dying and dead *Kobresia* root-mats, where plant N uptake is low (Liu *et al.* 2016). Contributions by gaseous N losses were not considered, since these are assumed to play a minor role compared to N leaching due to the well aeration of the permeable topsoil that hampers denitrification processes (Lu *et al.* 2012). The lower P than N losses are presumably caused by the lower solubility and mobility of phosphate, its stronger sorption, and precipitation as calcium-phosphates (Tunesi *et al.* 1999). The formation of calcium-phosphates is likely, because in these formerly calcareous soils with continuous loess deposition, still more than 80% of effective CEC is occupied by exchangeable Ca^{2+}. In sum, the unbalanced nutrient losses alter the relative availability of N and P, leading to changed nutrients stoichiometry of the ecosystem. This, in turn, potentially alters plant community composition with marked implications for ecosystem functions in the medium term (Vitousek *et al.* 2010). However, increasing N deposition (Kang *et al.* 2002; Bobbink *et al.* 2010) as well as asymbiotic N fixation by microorganisms and symbiotic N fixation by lichens or legumes (Zielke *et al.* 2005; Yang *et al.* 2011) may reverse these limitations in the long-term.

2.4.5.4 Implications of pasture degradation

Degradation of the Tibetan *Kobresia* pastures has caused high losses of N, P and base cations. However, soil erosion has been frequently reported to initiate SOC and nutrient losses for Tibetan grasslands (Wang *et al.* 2012; Lu *et al.* 2014; Su *et al.* 2015), yet this study has demonstrated that chemical degradation, involving mineralization of organic matter and leaching of nutrients, is an important mechanism for nutrient losses, alongside erosion. Around 20% of the surface was covered with bare soil patches at the study sites (S5, (Babel *et al.* 2014). Assuming that 20% (~90.000 km^2) of the *Kobresia* pasture ecosystem (450.000 km^{-2}, (Miehe *et al.* 2008) has suffered similar degradation from erosion (Babel *et al.* 2014)and that comparable soil conditions prevail throughout, overall losses amount to 38 PG of soil, including SOC (0.43 PG), N (37 TG) and P (3.5 TG). The exact extent and potential fate of these losses is unknown, but they have likely been loaded into rivers and water basins, polluting the Tibetan headwaters. Since the *Kobresia* ecosystem is the source of some major rivers (i.e. Huang He, Yangtze, Mekong, Fig. SIV-1), degradation might have enhanced ecological and economic consequences even on larger scales. Sediment loads might have increased the risk for flooding events, trouble the functioning of dams for energy production or flood control, and in combination with input of other pollutants (i.e. nutrients, heavy metals, organics) decrease faunal fresh-water quality and overall may have impaired clean water supply at least for many people in the upper reaches of the rivers. (Lu & Higgitt 1998; Fu *et al.* 2003; Ren *et al.* 2007; Huang *et al.* 2008). However, studies focusing on river sedimentation and water quality of the Yangtze indicate that both sediment loads and water pollution has decreased in the last decades (Yang *et al.* 2002; Müller *et al.* 2008). It may suggest that degradation rates have peaked in earlier decades but most likely are still extensive.

Nevertheless, the sites still not have recovered and thus ongoing degradation, even if less intensive, is contributing to increasing nutrient losses from erosion and leaching. This has strongly compromised soil fertility and reduced pasture quality. Moreover, the unbalanced losses of N and P (N > P) have altered prevailing N and P limitations of growth and could impede natural or managed grassland restorations. In the long-term, further degradation of this pastoral ecosystem will likely be intensified; because of the 1) large population that is dependent on livestock products (Suttie *et al.* 2005; Qiu 2016), 2) increasing stocking rates (Zhou *et al.* 2005) and 3) diminishing availability of quality grazing ground following degradation (Harris 2010). This is worsened by a concentration of livestock grazing around cities and villages (Zhou *et al.* 2005) induced by sedentarization programmes for the Tibetan nomads since 1960s (Ptackova 2011; Li & Li 2012). The best approach to maintain soil fertility and other important functions of the very vulnerable *Kobresia* ecosystem is to lower livestock densities by limiting numbers, and perhaps more importantly improve mobility. This was the status quo for the traditional migratory rangeland management, which proved sustainable for millennia.

2.4.6 Acknowledgements

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2.5 Study V: Carbon and nitrogen losses from soil depend on degradation of Tibetan Kobresia pastures

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2.5.1 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 (SOC) 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_2 efflux and leaching of dissolved organic C and N, NH_4^+ and NO_3^- 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 CO_2 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_2 efflux (0.38 ± 0.1 µg C g^{-1} h^{-1}) because CO_2 was assimilated via photosynthesis. Nighttime CO_2 efflux positively correlated with soil moisture for living and dead root mats. It indicates that increasing precipitation might accelerate C losses due to enhanced SOC decomposition. Furthermore, dead root mat had the highest average NO_3^- loss (23 ± 2.6 mg N L^{-1}) from leaching compared to 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.

2.5.2 Introduction

Globally, grasslands occupy an area of about 24 million km² (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 (Yayneshet *et al*., 2009; Schönbach *et al*., 2011; Bilotta *et al*., 2007). Fire, permafrost and drought were also considered as factors which may influence soil structure and C storage (Pereira *et al*., 2014; Liu & Diamond, 2005; Novara *et al*., 2013; Yang *et al*., 2010). A reversal of grassland degradation, however, can be induced by changing management options i.e. by planting legumes or shifting to organic farming (Parras-Alcántara *et al*., 2015; Hu *et al*., 2015).

The Tibetan Plateau (TP) covers up to 2.5 million km^2 and hosts the largest montane and alpine grasslands of the world. As the only dominant *Cyperaceae* mats in southeastern humid TP (450,000 km²), 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 to other plant species because its belowground reserves ensure a rapid regrowth following grazing and the recapture of nutrients such as N is very efficient (Schleuss *et al*., 2015).

Due to 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_2 partial pressure, strong temporal and spatial precipitation variations and steep slopes) (Fan *et al*., 2011; Liu-Zeng *et al*., 2008; Ren *et al*., 1997; 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*., 2004). 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 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, i.e. 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 nitrogen (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 (Yu & Jia, 2014; Peng *et al*., 2015; Canadell *et al*., 2010; Follet *et al*., 2012). 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 (Fig. SV-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_2 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_2 and counterbalances C losses (Ingrisch *et al*., 2015). We also investigated the effect of soil moisture on nighttime CO_2 efflux and hypothesized that CO_2 efflux from living and dead *K. pygmaea* root mats will strongly increase with higher soil moisture because it stimulates SOC mineralization (Mukhopadhyay & Maiti, 2014).

2.5.3 Material and Methods

2.5.3.1 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 *Kobresia 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, Miehe *et al.*, 2011). The growing season ranges from May to October and mainly depends on the on- and off-set of the summer monsoon (Miehe *et al.*, 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_2O) 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 (Miehe *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^{-2}. Besides *Kobresia 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. Around 65% of the area is covered by living *Kobresia* root mats, while the remaining parts are occupied by dead root mats (16%) and bare soil patches (19%) (Babel *et al.*, 2014). 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).

2.5.3.2 Soil sampling and preparation

Samples were randomly selected within an area of about 25,000 m² 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 (Fig. SV-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 (Fig. SV-1, middle). Since the dying stage was still living before sampling but died during transport or storage, they had the same initial soil characteristics compared to the intact stage i.e. 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_2-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 to the living and dying stages because of long-term degradation in the field: i.e. 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 respectively. 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.

2.5.3.3 Experimental set-up

Six samples from each root mat were selected to conduct the experiment. These samples were put in incubation boxes (Fig. SV-1, left) allowing simultaneous analyses of CO_2 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 µm m^{-2} s^{-1} and kept in the darkness for 10 h.

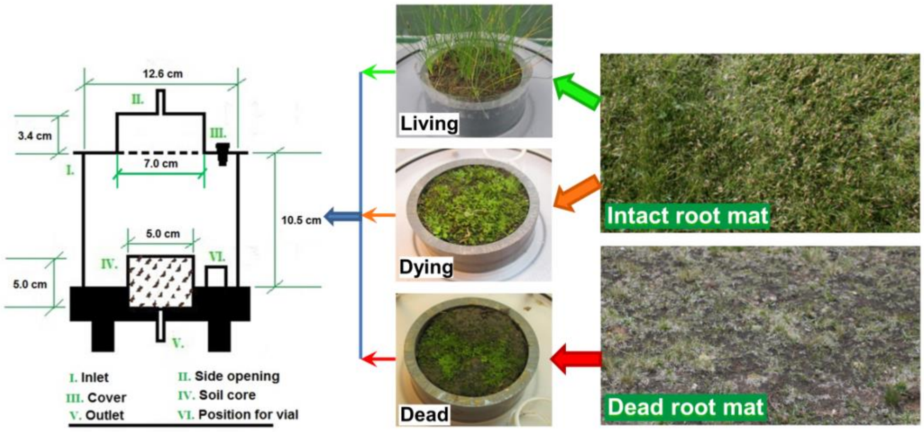

Figure SV-1: Longitudinal section of chamber (left) and origin of three Kobresia root mat types (right). “Living” = living root mat; “Dying” = dying root mat; “Dead” = dead root mat.

The first experiment was conducted to assess CO_2-C loss and leaching of dissolved C and N. Living, dying and dead root mats were included. Daytime and nighttime CO_2 efflux was measured separately. To measure the CO_2 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_2. 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_2 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 (Fig. SV-1, left). After taking the leachate samples, the cover of the incubation box was opened again for ensuring photosynthesis. This two-day collection of CO_2 efflux and leachate was repeated weekly and lasted in total nine weeks.

The second experiment focused on the effect of soil moisture on nighttime CO_2 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_2 efflux was measured every two days. Vials with 3 ml 1.0 M NaOH solution were placed into the incubation box to trap CO_2. This second experiment included living and dead root mats and lasted for 17 days.

To measure CO_2 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 (TC), total nitrogen (TN) and dissolved inorganic carbon (DIC) using a multi N/C 2100s analyzer (Analytik Jena Inc, Germany). Dissolved inorganic nitrogen (DIN: NH_4^+ and NO_3^-) 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 DIC and DIN from TC and TN. Microbial biomass carbon (MBC) and nitrogen (MBN) were determined by the fumigation-extraction method (Brookes *et al.*, 1985; Vance *et al.*, 1987). SOC contents in soils were also separately determined after the incubation using the elemental analyzer (Vario Max CN, Hanau, Germany).

2.5.3.4 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_2 efflux was analyzed using linear regression. The cumulative CO_2-C for all replicates during this experiment was correlated to their final SOC contents. All analyses were conducted using STATISTICA 10.0 (StatSoft Inc.).

2.5.4 Results

2.5.4.1 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 content of the root biomass did not differ significantly from each other (Table 1). 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_2 efflux and DOC concentration in the leachate (Fig. SV-2). Living root mat had an average aboveground biomass of 215 ± 2.2 g m^{-2}.

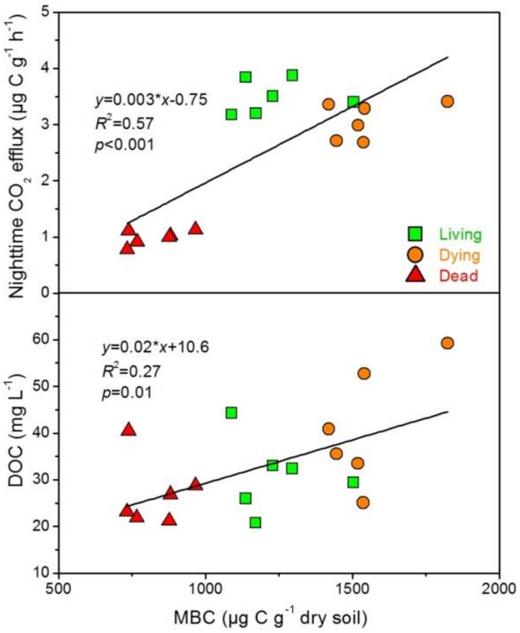

Figure SV-2: Relations between microbial biomass carbon (MBC) and nighttime CO_2 efflux (top) and DOC concentration in the leachate (bottom) at Day 114. “Living” = living root mat; “Dying” = dying root mat; “Dead” = dead root mat.

Table 1: Distribution of carbon and nitrogen in pools of soil, root and microbial biomass

Root mats	Soil			Root			MBC (mg C g^{-1} dry soil)	MBN (mg N g^{-1} 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							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.

2.5.4.2 CO_2 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_2 efflux. It was roughly 1.2 and 3.1 times higher compared to living and dead root mats, respectively (Fig. SV-3, top). Nighttime CO_2 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_2 efflux did not differ significantly from that of dying root mat. The cumulative CO_2-C for all replicates during this experiment was positively related to their final SOC contents (Fig. SV-4, $p<0.05$).

Daytime CO_2 efflux of living root mat was the lowest (Fig. SV-3, bottom), confirming our second hypothesis about the strong CO_2 assimilation by living *Kobresia.* The average daytime CO_2 efflux of living root mat was even 6 and 2 times lower than dying and dead root mats, respectively. The trend of daytime CO_2 efflux for the three root mat types was stable during the two months.

Overall, the dying of *K. pygmaea* induced the significantly highest CO_2-C losses, whereas the presence of living *K. pygmaea*, in reverse, showed a strong CO_2-C uptake by photosynthesis.

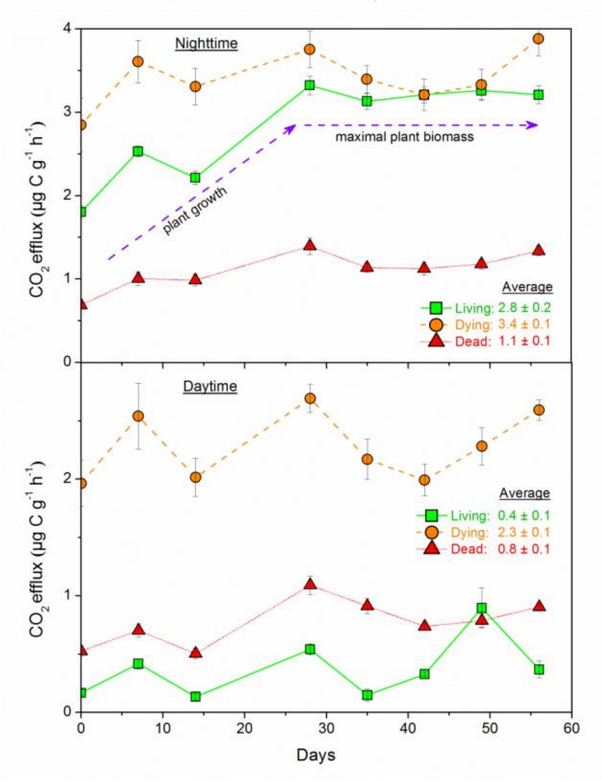

Figure SV-3: Nighttime (top) and daytime (bottom) CO_2 efflux of three Kobresia root mat types. “Living” = living root mat; “Dying” = dying root mat; “Dead” = dead root mat. Error bars represent standard error (n=6).

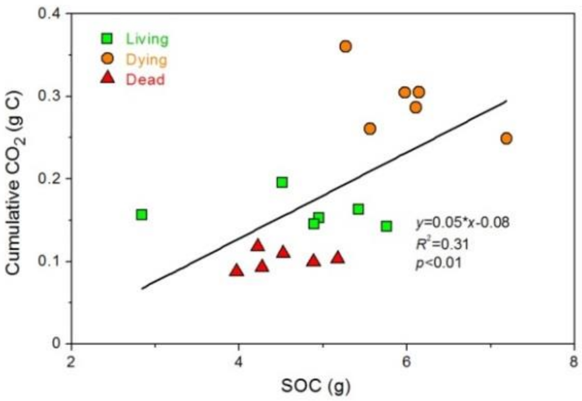

Figure SV-4: Correlation between cumulative CO_2-C for all replicates and their final soil organic carbon (SOC) contents. “Living” = living root mat; “Dying” = dying root mat; “Dead” = dead root mat.

2.5.4.3 Effects of soil moisture on nighttime CO_2 efflux

A strong positive relation between nighttime CO_2 efflux and soil moisture was obtained for living and dead root mats considering the total duration of the second experiment (Fig. SV-5, *p*=0.001). This confirmed our third hypothesis. Moreover, nighttime CO_2 efflux was the higher under the increased soil moisture level (70% vs 100% WHC) for living and dead root mats (Fig. SV-6). Soil moisture of living root mat was also higher than dead root mat. After the first rewetting at Day 11, CO_2 efflux of living and dead root mats increased. The CO_2 efflux of living root mat continued to increase from Day 11 to Day 13 (*p*=0.04), although soil moisture decreased.

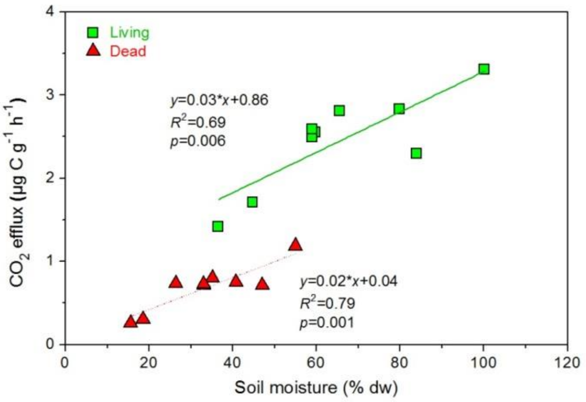

Figure SV-5: Correlation between soil moisture content (% dw) and nighttime CO_2 efflux during the second experiment. “Living” = living root mat; “Dead” = dead root mat.

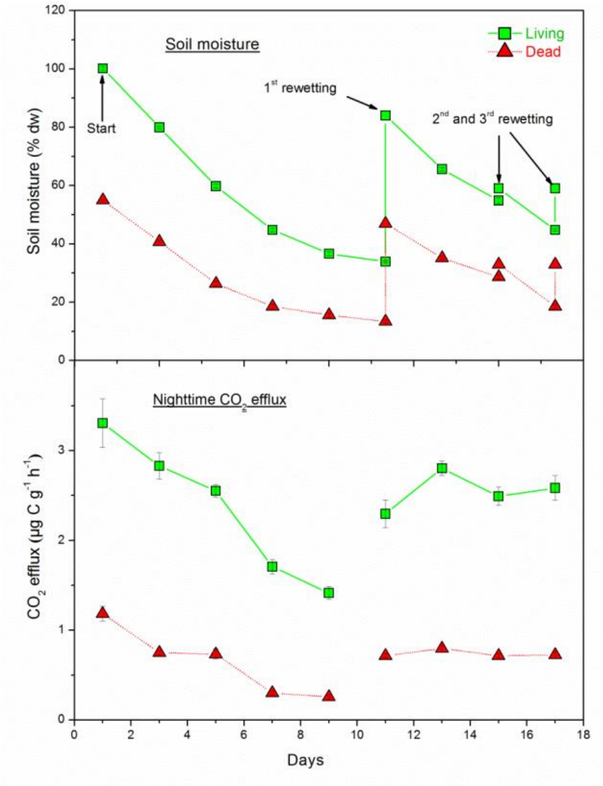

Figure SV-6: Change of soil moisture content (top) and response of nighttime CO_2 efflux (bottom) in living and dead root mats to increased moisture. "Living" = living root mat; "Dying" = dying root mat; "Dead" = dead root mat. Soil moisture content is expressed as percent of dry weight (% dw). When 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).

2.5.4.4 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 to living and dead root mats (Fig. SV-7, top and middle). This was consistent with our first hypothesis. However, the NO_3^- concentration was highest from the dead root mat compared to the living and dying stages (Fig. SV-7, bottom). It strongly decreased over time but was significant higher throughout the experiment. The NO_3^- 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_3^- was leached from the living stage (Fig. SV-7, bottom). The NH_4^+ 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_3^- loss from leaching.

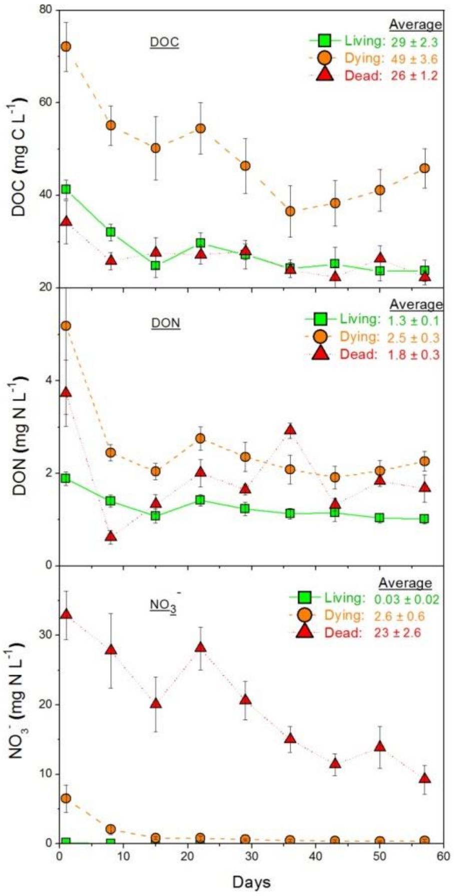

Figure SV-7: Concentrations of DOC (top), DON (middle) and NO_3--N (bottom) in the leachate of three Kobresia root mat types during the leaching experiment. “Living” = living root mat; “Dying” = dying root mat; “Dead” = dead root mat. Error bars represent standard error (n=6).

2.5.5 Discussion

2.5.5.1 C loss from soil respiration

The nighttime CO_2 efflux was highest from the dying, slightly lower from living and lowest from dead *Kobresia* root mat throughout the incubation period (Fig. SV-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 1), indicating that the higher C-availability stimulated microbial respiration (Cleveland *et al.*, 2007). This finding was supported by a positive correlation of cumulative CO_2-C for all degradation stages and their SOC contents (Fig. SV-4). The positive relation between MBC and nighttime CO_2 efflux also supported this finding (Fig. SV-2, top).

The CO_2 efflux was slightly higher for the dying versus living root mat. This was especially pronounced in the first four weeks. We suggest that an additional supply of root litter following plant death was respired and slightly increased the CO_2 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 1).

Nighttime CO_2 efflux from living root mat increased within the first four weeks due to 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_2 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_2 efflux after Day 28.

2.5.5.2 Effects of photosynthesis on CO_2 losses

To consider for the photosynthetic C input with regard to SOC loss, we included daytime CO_2 efflux measurements and hypothesized that living root mat strongly mitigated C loss from *Kobresia* pastures. Daytime CO_2 efflux of living root mat was 6 times lower than that of dying stage due to CO_2 assimilation via photosynthesis. It mitigated the C loss from soil respiration compared to 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_2 fixation during the growing season (Ingrisch *et al*., 2015; Peng *et al*., 2014). 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_2 efflux increased during plant growth within the first four weeks, whereas the daytime CO_2 efflux remained on a constant low level for the living stage (Fig. SV-3). It demonstrates that the increasing CO_2 uptake during plant growth was offset by a higher CO_2 release from soil respiration (Suter *et al*., 2002).

2.5.5.3 Soil respiration as influenced by soil moisture

The effect of changing soil moisture on soil respiration (nighttime CO_2 efflux) for living and dead root mats was tested in the second experiment. Soil moisture was positively correlated with nighttime CO_2 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^{-2} for living and 2.5 g m^{-2} 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 (Fig. SV-6, top).

Surprisingly, nighttime CO_2 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_2 efflux. This lag was longer than that for most other grassland ecosystems (Kuzyakov & Gavrichkova, 2010).

When soil moisture was kept at around 100% dw on the first day, nighttime CO_2 efflux remained at a relatively high level for living and dead root mats (Fig. SV-6). This contrasted to some studies showing that SOC decomposition and CO_2 production decreased under a high soil moisture level because oxygen diffusion into the soil was inhibited (Ganjurjav *et al*., 2014; Tang *et al*., 2006). The *Kobresia* root mats, however, have very low bulk density (around 0.8 g cm^{-3} for living and dead root mats, 1.1 g cm^{-3} for dead root mat) and with a large pore system so that O_2 diffusion was not hindered in our study.

2.5.5.4 C and N loss from leaching

DOM leaching was highest from dying root mats compared to 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 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 (Fig. SV-2, bottom).

The highest NO_3^- losses were observed from dead root mat (Fig. SV-8). This partly contradicted our first hypothesis about the highest N loss from dying root mat. We suggest that NO_3^- 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_2 fixation by lichen-dominated crusts increased the N transfer into soil (Neff *et al*., 2005). In contrast, leaching of NO_3^- 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_3^- uptake by living plants or immobilization by microorganisms significantly decreased the NO_3^- 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 NH_4^+ (ammonification, Harmsen & Van Schreven, 1955). Then the released NH_4^+ was rapidly taken up by plants and microbes preventing its transformation to NO_3^- (nitrification, Harmsen & Van Schreven, 1955). In fact, no NH_4^+ was leached from the living stage confirming that NH_4^+ uptake likewise lowered 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_{Living}: 9.4), dying (C/N_{Dying}: 7.3) and dead stage (C/N_{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 NH_4^+ and NO_3^-. Although plant N uptake was not present in the dying and dead root mat (no living plants), NH_4^+ leaching did not increase compared to the living stage (dying and dead stages: 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, NH_4^+ will be immediately converted to NO_3^-. Therefore NO_3^- accumulated in the dying and dead stage and consequently higher NO_3^- leaching was observed (NO_3^- leaching: dead > dying).

2.5.6 Conclusion

The dying root mats showed the highest C losses from: decomposition of SOC and roots (CO_2 efflux) and leaching of DOM. The dying of *K. pygmaea* provided more labile C to microorganisms due to 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 NO_3^- losses from dead root mat were mainly caused by long-term 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.

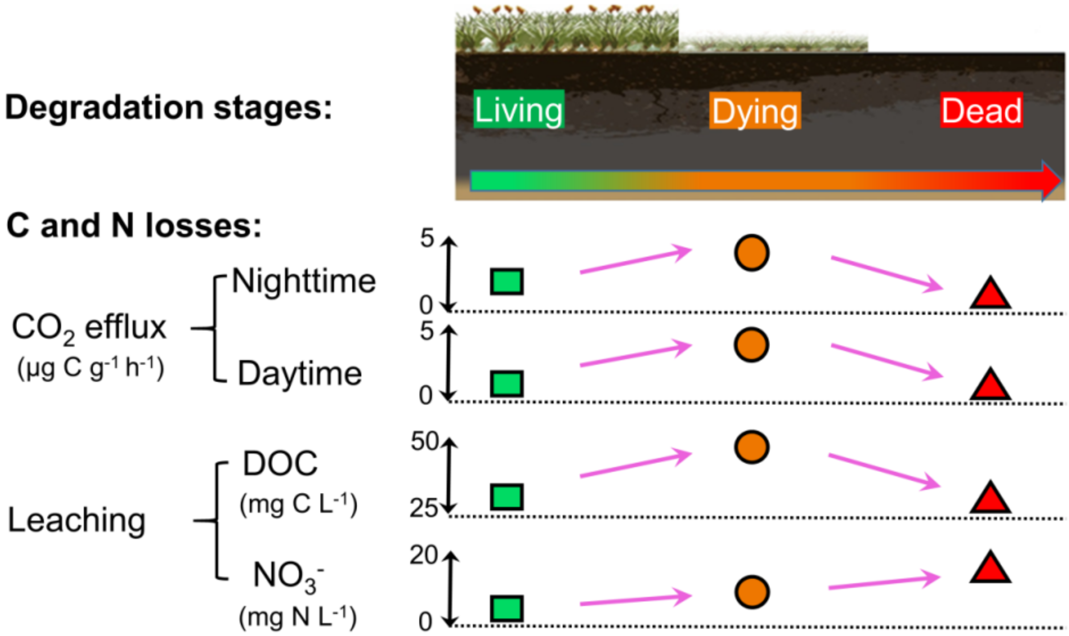

Figure SV-8: Conceptual diagram of C and N losses from K. pygmaea pastures depending on degradation stages. C loss as CO2 emission and leaching was highest in dying root mat. This is mainly caused by the high initial root litter inputs after plant dying and the elimination of competition between plant 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 NO3- 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.

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2.5.8 References

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2.6 Study VI: *Kobresia pygmaea* pasture degradation and its response to increasing N deposition

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2.6.1 Abstract

Kobresia pygmaea pastures occupy around one fifth of the total Tibetan Plateau and provide extensive grazing grounds. In recent decades, *K. pygmaea* pastures have experienced severe degradation because of overgrazing, destruction by small herbivores and climate change. This has induced large nitrogen (N) losses from this ecosystem, which is particularly problematic because it intensifies prevailing N limitation. Simultaneously, atmospheric N deposition has increased across the plateau, but the fate of N input and its impact on variously degraded *K. pygmaea* pastures remain unclear. We investigated the effects of N addition on *K. pygmaea* pastures of three degradation stages: living root mats, dying root mats and dead root mats. ^{15}N was applied as NH_4NO_3 to trace N in the plant-soil system and leaching losses. N addition promoted aboveground biomass and the foliar N content of *K. pygmaea* during the early growth period, indicating an offset of N limitation at least over the short-term. After 7-8 weeks, plant growth and ^{15}N uptake were reduced. This reflected a transition to N limitation because of N consumption and losses from soil. This N limitation was in line with the strongly decreased NO_3^- leaching from living root mats. In contrast, NO_3^- leaching substantially increased in dying and dead root mats (especially for N-fertilized root mats) and accounted for most of the N loss (NO_3^- > DON > NH_4^+). N losses from leaching were up to 32 and 330 times higher than those from N_2O emissions in the dying and dead root mats, respectively. We conclude that increased atmospheric N deposition can facilitate plant growth in intact *K. pygmaea* pastures, whereas in the degraded pastures N deposition directly increased the N leaching. Consequently, the ongoing degradation together with increased N deposition aggravates N losses in *K. pygmaea* pastures. It may also weaken ecosystem recovery, increase NO_3^- loading of adjacent lower landscape parts and pollute the headwater.

2.6.2 Introduction

The *Kobresia* ecosystems of the Tibetan Plateau (TP) occupy about 450,000 km^2 and are the world´s largest alpine pastoral ecosystem. This ecosystem is the source region for the largest rivers in SE Asia and is mainly dominated by *Kobresia pygmaea* C.B.Clarke (*K. pygmaea*) (Miehe et al., 2008a; Zhou et al., 2005; Sa et al., 2012). It stores huge amounts of soil organic carbon (SOC) and nutrients and provides important grazing ground (Unteregelsbacher et al., 2012; Yang et al., 2009). Ongoing pasture degradation in recent decades, however, has initiated high losses of carbon (C) and nitrogen (N) via erosion, soil organic matter mineralization and leaching (Wang et al., 2009b; Wang et al., 2010). Pasture degradation and CO_2 release contribute to climate change globally, export nutrients, and deposit sediments in the basins and rivers. This compromises pasture quality onsite and jeopardizes the clean water supply of a large human population offsite. Moreover, it decreases the coverage of plant communities and species richness as well as soil fertility levels (Wang et al., 2009a). Overall, degradation causes plant death (i.e. reduces vegetation cover and above- and belowground biomass) and strongly reduces grassland recovery (Wang et al., 2013; Zhang et al., 1998). This has put the large human population of the TP at risk regarding their livelihoods and food security (O'Mara, 2012).

Nitrogen is a limited nutrient in most terrestrial ecosystems (Lebauer and Treseder, 2008; Menge et al., 2012). This is particularly true for the degraded *Kobresia* grasslands, where low temperature and precipitation hamper N fixation as well as slow the mineralization of soil organic matter and therefore nutrient release (Shi et al., 2012; Vitousek and Howarth, 1991). This makes N deposition an important N input into this ecosystem. Increasing N input can stimulate plant productivity and potentially facilitate ecosystem recovery (Fu and Shen, 2016; Lee et al., 2010). In contrast, it can also lead to negative consequences, for example, decreases in species richness by excluding less competitive species (competitive exclusion, Roth et al., 2015). Atmospheric N deposition on the Tibetan Plateau has also increased since the mid-20th century (Thompson et al., 2000; Kang et al., 2002). A total N deposition rate of 7.0-7.6 kg N ha^{-1} yr^{-1} on Qinghai-Tibetan plateau has been reported by Lü and Tian (2007). The annual mean ambient N_2O concentration also increased 79%-124% in south Tibet from 1994 to 2003.

To clarify the effects of N deposition, some studies focused on various aspects of *K. pygmaea* pastures. For example, increasing N fertilization decreased the coverage and biomass of *K. pygmaea* because of the competition with other species (Wang et al., 2015). In response to N addition, *K. pygmaea* also germinated quicker (Xi et al., 2015). Increasing N deposition stimulated soil microbial metabolic activity and the utilization of C substrates in the alpine meadow on the Tibetan Plateau (Fang et al., 2014). However, nearly all N studies were conducted on intact *Kobresia* pastures and did not consider the strong effects of degradation on the N cycle. This makes the consequences of deposited N and its fate in degraded *K. pygmaea* pastures unclear. N deposition may have contrasting effects on intact and degraded pastures because of their different physical and biochemical properties (Liu et al., 2016; Yao et al., 2016), in particular plant N uptake. These effects can be directly reflected in N fluxes and N stocks of *K. pygmaea* pastures and are thus important in evaluating the self-restoration capacity of the pastures (Andrade et al., 2015).

We investigated the effects of N deposition using three types of *Kobresia pygmaea* root mats with increasing degradation: (a) living root mats, (b) dying root mats and (c) dead root mats. The dying root mats represent the transition between living and dead root mats: it was alive during sampling but died during transport, reflecting the initial stage of root mat degradation. NH_4NO_3 was added to evaluate the effects of increasing N deposition on *K. pygmaea* growth as well as on N cycling. The ^{15}N labelling technique was applied to quantify N partitioning among different pools (above- and belowground biomass, root litter, microbial biomass, soil). Leaching was simulated to determine losses of dissolved N (NH_4^+ and NO_3^-) and organic C. We hypothesized that N deposition increases *Kobresia* biomass (above- and belowground) and its foliar N stock in the living root mats because the *Kobresia* pastures are N limited (H1). Furthermore, we also hypothesized that degraded root mats (dying and dead root stages) were less capable of retaining N due to the absence of the N uptake by living plants (H2). Finally, total N stocks were hypothesized to be significantly lower in the degraded than in the intact stage due to increasing N losses from leaching and N_2O emission (H3).

2.6.3 Materials and methods

2.6.3.1 Site description

The sampling site was located at the research station "*Kobresia* Ecosystem Monitoring Area" (KEMA) (31°16′45''N 92°59′37''E, 4410 m) close to the village Kema, near Nagqu, Tibetan Autonomous Region (TAR). The detailed description of the area and soils is presented in Babel et al. (2014). The region is described as "Plateau Frigid Monsoon Region with semi-moist climate" (Leber et al., 1995). Mean annual precipitation and temperature are 430 mm and -1.2 °C, respectively. The site is located in the core area of *K. pygmaea* distribution, and *K. pygmaea* is the dominant plant species with an average height of no more than 2 cm (Miehe et al., 2008a). The other species are *Carex* spp., *Festuca* spp., *Kobresia humilis*, *Poa* spp., *Stipa purpurea* and *Trisetum* spp. (Seeber et al., 2015). The growing season of *K. pygmaea* pastures mainly depends on the summer monsoon and ranges from May to October (Miehe et al., 1989).

The soils are *Stagnic Eutric Cambisol* (Humic) (WRB 2014) with a texture of 50% sand, 33% silt and 17% clay. Soils are free of carbonates and have a mean pH (H_2O) of 6.85. The topsoil (0-5 cm) contains large amount of living and dead roots which form a very dense root mat (Miehe et al., 2008b; Schleuss et al., 2015). Large areas on the study sites are degraded. Intact living *Kobresia* root mats cover 65% of the area, while dead *Kobresia* root mats occupy 16% of the area. The remaining part is covered by completely degraded bare soil patches (19%) entirely missing the dense *Kobresia pygmaea* turf (Babel et al., 2014). The bare soil degradation was not considered during this experiment.

2.6.3.2 Experimental set-up, sampling and preparation

Undisturbed soil cores (height: 5.0 cm, diameter: 5.0 cm) were collected from intact living and dead *Kobresia pygmaea* root mats. Shoot biomass was removed from the surface before transport. Sub-samples from each root mat (n=6) were collected to measure the water holding capacity (WHC). All the samples were put in PVC collars (height: 5.0 cm, diameter: 5.0 cm) and transferred to the laboratory.

Before starting the experiment, samples of living and dead root mats were pre-incubated for two months to enable *K. pygmaea* to recover and reach the maximal biomass. In some samples, however, the living *K. pygmaea* did not recover. These samples were considered as an additional treatment “dying root mats”. A total of three root mats were considered: living root mats, dying root mats and dead root mats, which reflect a gradual degradation sequence (Living < Dying < Dead). A detailed explanation for distinguishing the three different root mats is given in Liu et al. (2016).

Six samples were randomly picked out from each root mat type and transferred into incubation boxes (Liu et al., 2016). The experiment was conducted at a constant temperature (20 °C), which is in the range of daily mean temperature during the growing season in Nagqu (9.3-21.3°C, Geng et al., 2012). Samples were illuminated diurnally for 14 h with a photosynthetic photon flux density of 80 µm m^{-2} s^{-1} and were kept in darkness for 10 h.

^{15}N labelling and fertilization were conducted at the beginning of the incubation. ^{15}N-labelled NH_4NO_3 solution (95% ^{15}N enrichment in total) with a total N amount of 0.5 mg was homogeneously injected as a tracer (very low N addition level) into each soil core (multi needle injection technique, Murphy et al., 1997). Three replicates from each ^{15}N labelled root mat were then randomly selected and fertilized with NH_4NO_3 solution (9.5 mg N per soil core). After fertilization, the ^{15}N enrichment of added N (totally 10 mg N) in these three replicates was diluted from 95% to 4.75%. In total, a two-factor design included the three root mats (living, dying and dead) and two fertilization levels (high N fertilization: 50.9 kg N ha^{-1} and low N fertilization: 2.5 kg N ha^{-1}). The low N fertilization was here referred to as “non-fertilized” and the high N fertilization as “N-fertilized”.

One week after labelling and fertilization (Day 7), all shoots from living root mats were harvested (termed “1st generation”) and the ^{15}N recovery in shoots determined. A small proportion of the “new” upcoming shoot biomass in living stage (termed “2nd generation”) was harvested on days 21, 28, 35, 42, 49, 56, 63, 70, 77 and 98. The total dry weight of the upcoming shoot biomass at each sampling event was estimated and ^{15}N recovery was measured.

N_2O emission was measured weekly starting from Day 9. Briefly, the chamber was sealed and an aliquot of 15 ml gas was extracted from the chamber using an evacuated tube. After one day, another aliquot of 15 ml gas was extracted from the chamber.

The leaching experiment was conducted from Day 10 to assess the effect of N addition on dissolved C and N concentration in the leachate. Soil moisture was initially adjusted to 100% WHC (i.e. 84% of dry weight for living and dying root mats; 47% of dry weight for dead root mat). Then, 11 ml distilled water was added onto each sample from the inlet of the incubation box to simulate precipitation events (5 mm week^{-1}). Later, a glass tube was connected to the outlet of the incubation box to collect leachate. Leaching was repeated weekly, i.e. 14 times during the experiment. The leachate was analyzed for dissolved organic carbon (DOC), dissolved organic nitrogen (DON), NH_4^+ and NO_3^- concentration.

Total aboveground biomass (AGB) and belowground biomass (BGB; including living and dead roots) was determined at the end of the incubation by separating roots from soil core, washing with distilled water and drying at 60 ˚C for 24 h. Carbon and N contents in soil and root of each sample were analyzed using an elemental analyzer (Vario Max CN, Hanau, Germany). DOC, DON, NH_4^+ and NO_3^- concentration in the leachate were determined with a multi N/C 2100s analyzer (Analytik Jena Inc., Germany) and Cenco (Dual Tubingpump, Instrumenten B.V., Breda, The Netherlands). Soil microbial biomass C and N were determined using the chloroform fumigation extraction method (Brookes et al., 1985; Vance et al., 1987). The N_2O concentration was measured using a gas chromatograph (GC 6000 Vega series 2, Carlo Erba Instruments, Milan, Italy) equipped with an electron capture detector and an auto-sampler.

Samples of oven-dried soil, shoots (1st and 2nd generations) and root were grounded and analyzed using an isotope ratio mass spectrometer (Delta plus, Conflo III, Thermo Electron Cooperation, Bremen, Germany) to obtain the stable isotope signatures of nitrogen ($\delta^{15}N$). The $\delta^{15}N$ signature was calculated using the isotope ratio of each sample ($R_{sample} = {}^{15}N/{}^{14}N$) and recalculated as ^{15}N atom%. ^{15}N recovery by microbial biomass was determined as the difference in ^{15}N mass between fumigated and non-fumigated soil samples. ^{15}N recovery was then calculated according to the equation presented by Cabrera and Kissel (1989):

$$\text{Recovered N (\%)} = \frac{\mathrm{N_{stock}} \times \dfrac{\mathrm{atom\%^{15}N_{labeled}} - \mathrm{atom\%^{15}N_{NA}}}{\mathrm{atom\%^{15}N_{added}} - \mathrm{atom\%^{15}N_{NA}}}}{\mathrm{N_{added}}}$$

where N_{stock} is the total N (mg), N_{added} is the added N (mg), atom%$^{15}N_{labeled}$ is the content of ^{15}N atoms in the sample, atom% $^{15}N_{NA}$ is the content of ^{15}N atoms in the control sample. Atom% $^{15}N_{added}$ is the content of ^{15}N atoms in the added N pool, which is 4.75% for fertilized samples and 95% for non-fertilized samples.

2.6.3.3 Statistical analysis

Soil and plant characteristics were analyzed and expressed as means with standard errors (mean ± SE). Significance differences of ^{15}N among the three root mats were also tested using two-way ANOVA. Before applying ANOVA, data were checked for normality (Shapiro-Wilk-test, $p>0.05$) and homogeneity of variance (Levene-test, $p>0.05$). After obtaining a significant omnibus test result, a post-hoc test (Tukey's HSD test) was conducted for multiple comparisons. Repeated measures ANOVA was conducted to evaluate the impact of N addition on AGB and its foliar nitrogen content. All analyses were conducted using STATISTICAS 10.0 (StatSoft Inc.).

2.6.4 Results

2.6.4.1 Plant and soil characteristics

The AGB of the 1st generation was similar in fertilized and non-fertilized root mats, whereas in the 2nd generation, N addition increased AGB and its foliar N stock (Fig. SVI-1, top and bottom left; p=0.008).

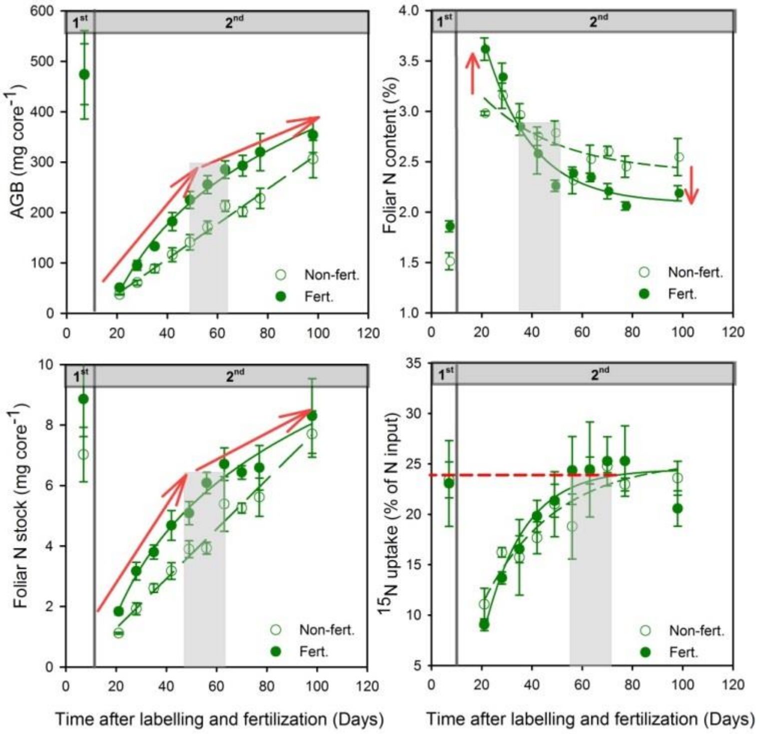


Figure SVI-1: Aboveground biomass (AGB, top left), foliar N content (top right), foliar N stock (bottom left) and 15N uptake (bottom right) by K. pygmaea. "Non-fert.": non-fertilized samples; "Fert.": N-fertilized samples. "1st" and "2nd": first and second generation of K. pygmaea. Error bars are standard error (SE).

Some moss was found growing in dying root mats (ca. 4.3±0.4 mg dry mass cm^{-2}), whereas the dead root mats were free of any vegetation. After the 2nd generation, total BGB of the living stage significantly increased to 4.2 ± 0.02 kg m^{-2}. This was nearly twice that of the dying and dead root mats (Table 1, p<0.05). Soil C content decreased from 70±7g kg^{-1} to 48±2g kg^{-1} along the degradation stages (Table 1).

Table 1: Characteristics of soil, root and microbial biomass

Root mat	pH	Bulk density (g cm^{-3})	BGB (kg m^{-2})	MBC (mg C g^{-1} dry soil)	MBN (mg N g^{-1} dry soil)
Living	6.7 ± 0.04 b	0.66 ± 7.1 b	4.2 ± 0.02 a	1.17 ± 0.1 b	0.12 ± 0.02 b
Dying	6.3 ± 0.06 c	0.68 ± 2.6 b	2.3 ± 0.02 b	1.63 ± 0.1 a	0.22 ± 0.03 a
Dead	7.2 ± 0.03 a	0.92 ± 1.1 a	2.5 ± 0.03 b	0.86 ± 0.1 c	0.18 ± 0.03 a

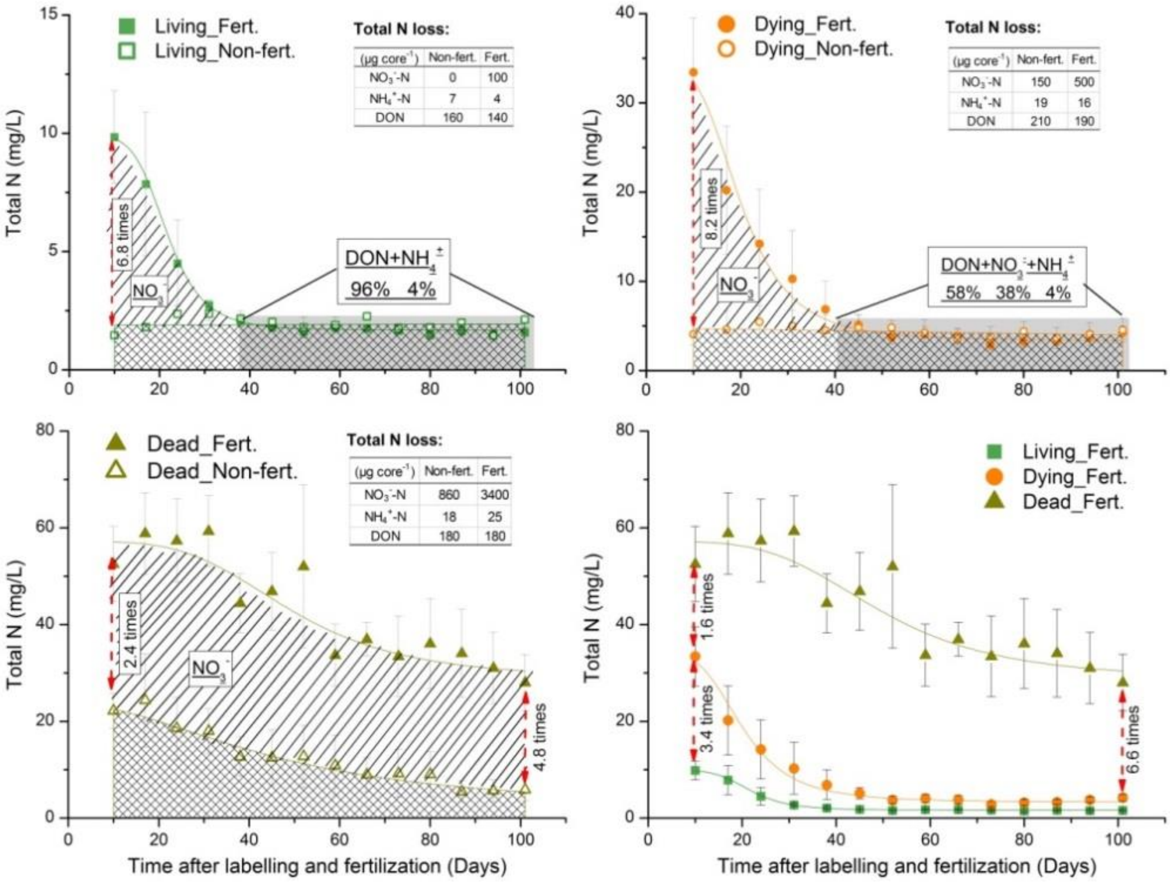
Root mat	Root C (%)	Root N (%)	Root C/N	Soil C (%)	Soil N (%)
Living	46±0.5a	0.6±0.02c	79±3.9a	7±0.7a	0.5±0.04a
Dying	44±1.3ab	0.7±0.03b	63±3.8b	8.5±0.4a	0.6±0.02a
Dead	41±0.9b	0.9±0.04a	45±2.7c	4.8±0.2b	0.4±0.01b

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. MBC and MBN represent microbial biomass C and N.

Soil bulk density increased from 0.66±7.1g cm^{-3} to 0.92 ± 1.1g cm^{-3} with the intensified degradation. Microbial biomass C in dying root mats was 1.4 times higher than in living root mats and 1.9 times that in dead root mats (p<0.05). The microbial biomass C/N ratio decreased from living to dead root mats. Foliar N contents in fertilized living root mats were higher than those in the non-fertilized root mats but then decreased and were lower after 6 weeks (Fig. SVI-1, top right). The foliar N stock increased more strongly, but its increase also slowed down after 7-8 weeks. The ^{15}N recovery of the AGB in the fertilized root mats gradually increased and became stable after 7 weeks, whereas in the non-fertilized root mats this response was delayed (after ca. 10-11 weeks) (Fig. SVI-1, bottom right).

2.6.4.2 Effects of N fertilization on C and N leaching

Nitrogen fertilization increased the NO_3^- concentration in the leachate of all degradation stages (living, dying and dead stages), but had a minor effect on NH_4^+ and DON concentrations. Overall, N fertilization caused higher total N loss from all fertilized compared to non-fertilized root mats (Fig. SVI-2).



Total N loss:

(μg core^{-1})	Non-fert.	Fert.
NO_3^--N	0	100
NH_4^+-N	7	4
DON	160	140

Total N loss:

(μg core^{-1})	Non-fert.	Fert.
NO_3^--N	150	500
NH_4^+-N	19	16
DON	210	190

Total N loss:

(μg core^{-1})	Non-fert.	Fert.
NO_3^--N	860	3400
NH_4^+-N	18	25
DON	180	180

Figure SVI-2: Total N concentration in the leachate of living (top left), dying (top right) and dead (bottom left) root mats and comparison among three fertilized root mats (bottom right). “Living”: living root mats; “Dying”: dying root mats; “Dead”: dead root mats; “Non-fert.”: non-fertilized samples; “Fert.”: N-fertilized samples. Error bars are standard error (SE).

After three weeks, NO_3^- leaching from the living root mats dropped to zero, whereas DON and NH_4^+ remained on the same level (Fig. SVI-2, top left). In contrast, NO_3^- was still present in the leachate of dying root mats after Day 45, when the total N concentration stabilized (Fig. SVI-2, top right). The total N concentration in the leachate of fertilized dead root mats was higher in comparison to non-fertilized throughout the experiment (Fig. SVI-2, bottom left). This increment was mainly caused by the high NO_3^- concentration in dead root mats.

The DOC concentration in the leachate from fertilized root mats was similar to that of non-fertilized root mats (Fig. SVI-3). Living and dying root mats had an average DOC concentration of 29 ± 2.5 and 34 ± 6.9 mg L^{-1}, respectively. However, dead root mats always showed a lower DOC concentration (24 ± 2.7 mg L^{-1}) regardless of fertilization.

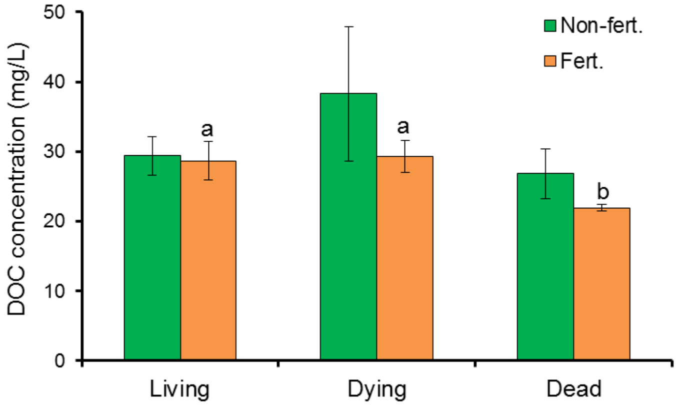


Figure SVI-3: DOC concentrations averaged over 101 days in the leachate of three root mats. Abbreviations as in Figure SVI-2. Different lowercase letters represent significant difference among the three root mats. Error bars are standard error (SE).

2.6.4.3 N recovery in plant, soil and microbial biomass

Total recovered ^{15}N (% of total ^{15}N input) of fertilized root mats was similar to non-fertilized root mats (Fig. SVI-4). ^{15}N recovery in living root mats was the highest (93 ± 2.2 % for non-fertilized, 81 ± 2.4 % for fertilized; $p<0.05$) among the three root mats. In non-fertilized and fertilized dying root mats, 69 ± 9.4 % and 57 ± 4.0 % of ^{15}N was recovered, respectively. Surprisingly, 75 ± 4.5 % and 61 ± 7.7 % of ^{15}N were allocated into root litter, soil and microbes in non-fertilized and fertilized dead root mats.

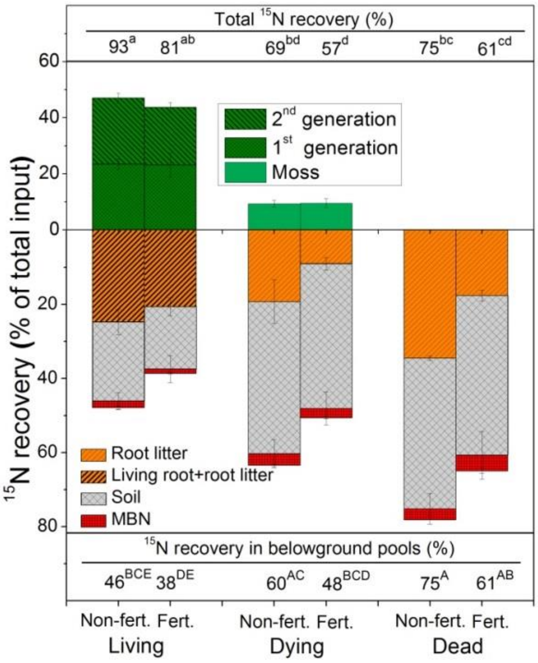


Figure SVI-4: ^{15}N recovery in plant and soil pools of three non-fertilized and fertilized root mats. Abbreviations as in Figure SVI-2. Lowercase and capital letters represent significant difference among the three root mats. Error bars are standard error (SE).

In the living shoots, 45 ± 2.1 % of ^{15}N was recovered, of which 23 ± 1.9 % and 22 ± 1.2 % were contributed by the 1st generation and the 2nd generation, respectively (Fig. SVI-4). Moss in dying root mats recovered approximately 9.4 ± 1.2 % of ^{15}N. ^{15}N recovery in total BGB of fertilized living root mats (21 ± 2.4 %) was similar to that of non-fertilized mats (24 ± 3.4 %). Non-fertilized dying root mats allocated 19 ± 5.9 % of ^{15}N in their root litter, which was twice that of fertilized dying root mats (9.0 ± 1.7 %). Similarly, ^{15}N allocated by the root litter of non-fertilized dead root mats (34 ± 0.6 %) was also around twice that of fertilized dead root mats (17 ± 1.5 %) (Fig. SVI-4, $p<0.001$).

Soil of dying and dead root mats retained 37 ± 2.6 % and 35 ± 3.4 % of ^{15}N, respectively, while only 17 ± 2.0 % was retained in soil of living root mats. Microbial biomass in dead root mats immobilized 6.1± 0.9 % of ^{15}N, which was almost twice that of dying root mats (2.8 ± 0.2 %, $p<0.01$). In contrast, microbes in living root mats immobilized only 1.5 ± 0.3 % of ^{15}N.

2.6.5 Discussion

2.6.5.1 Sensitivity of plants to N fertilization

Nitrogen fertilization increased the AGB of *K. pygmaea* during the second generation, confirming our first hypothesis (H1) for a sensitive response of the AGB to N fertilization. This agreed with data from field experiments, where fertilization with NO_3^- or NH_4^+ increased the shoot biomass of *K. pygmaea* (Seeber, 2016; Xu et al., 2004). This is because fertilization offset the prevailing N limitation at least over the short-term (Xu et al., 2015a). The shoot biomass of the first generation did not increase after N addition because shoots were already full-grown when N was fertilized (Fig. SVI-1, top left).

The increase of AGB (2nd generation) after N fertilization was stronger than in the non-fertilized living root mats during the first 7-8 weeks (Fig. SVI-1, top left). N fertilization over the short-term offset N limitation in living *K. pygmaea*, but after 7-8 weeks it shifted to a N-limited state again. This is because most of the added N was already incorporated in AGB and BGB (Fig. SVI-4), immobilized by microorganisms, fixed by soil organic matter or lost via leaching and gas emissions (i.e. N_2O, N_2).

The transition from a N-unlimited to N-limited state (after 7-8 weeks) was also supported by foliar N content, aboveground N stock and the ^{15}N uptake dynamics (Fig. SVI-1), which also shifted their trend after 5-10 weeks. The constant ^{15}N recovery for both fertilized and non-fertilized root mats after 10-11 weeks demonstrated that no ^{15}N was taken up by plants after this period. We suggest that aboveground N demands were saturated at a recovery rate of about 20-23% of total input. The strategy of *K. pygmaea* to develop dense root mats indicates that the plants mainly invested resources belowground than in AGB (Wang et al., 2015; Ingrisch et al., 2015). The fact that the plants grew to no more than 2-3 cm height during their flowering time also supported this finding (Miehe et al., 2009). This recovery rate greatly matched with field data, which showed that *K. pygmaea* shoots took up 18% of the total added ^{15}N 45 days after labelling (Schleuss et al., 2015).

Nitrogen fertilization did not stimulate belowground root production, which partly contradicted our first hypothesis (H1). This non-significant response of BGB to N addition was also observed by other studies with *K. pygmaea* (i.e. Elke, 2016; Yang et al., 2014). We suggest that living *K. pygmaea* initially allocated more resources (e.g. N) to shoots, as was indicated by the increase of AGB. This reflects a specific strategy of *K. pygmaea* to cover the high belowground C costs by producing photosynthetic-active shoot biomass for CO_2 assimilation (Zong et al., 2012; Schleuss et al., 2015). High belowground investments of C and N in upper root mats (0-5 cm) were also indicated by field ^{15}N and ^{13}C pulse labelling studies showing that about 50 % of labelled ^{15}N and ^{13}C were incorporated in root biomass of the topsoil 45 and 15 days after labeling, respectively (Schleuss et al., 2015; Ingrisch et al., 2015).

2.6.5.2 Sensitivity of microbes to N addition

Microbial biomass was not sensitive to N fertilization for the three root mats but changed with intensified degradation stages (Dying > Living > Dead, Table 1). The ratio of microbial biomass C to N decreased with degradation, suggesting that microbes shift from a N-limited to N-unlimited stage with intensified degradation. In N-limited living root mats, microbes compete with plants for N (Kuzyakov and Xu, 2013). Xu et al. (2011) pointed out that the amount of root biomass strongly controls the competition between plants and microbes: a high root biomass (> 4.2 kg m^{-2}) enables plants to outcompete microbes for N uptake. This was also supported by the low ratio of ^{15}N recovered by microbial biomass to ^{15}N recovered in living plants (ca. $0.03<1.0$). This ratio lower than 1.0 indicates that plants recover more ^{15}N and, thus, outcompete microbes. Dying root mats provided a favorable environment for microbial growth because of abundant easily decomposable organic residues. Furthermore, there was no competition with roots for N. This leads to a weak effect of N deposition on microbial growth in dying root mats. Dead root mats were not N limited for microbial growth. Nonetheless, the lowest root C/N as well as DOC concentration suggested that the availability of labile organic C was a limiting factor for microbial growth in dead root mats.

2.6.5.3 Fate of N in the belowground pools

Total ^{15}N recovery in dying and dead root mats decreased compared with living root mats (Fig. SVI-4). This confirmed our second hypothesis (H2) for the highest N recovery in living root mats. However, the belowground pools (root litter, soil, microbial biomass) in dying and dead root mats retained more ^{15}N than that in the living root mats (Fig. SVI-4).

The higher ^{15}N recovery in the belowground pools of dying and dead root mats was mainly induced by the stronger N affinity of the soil and root litter (Fig. SVI-4). ^{15}N recovery in soil of dying and dead root mats was about twice that of living root mats irrespective of N fertilization. This ^{15}N part can be adhered by soil particles or fixed by soil organic matter as

NH_4^+ (Drury and Beauchamp, 1991; Burge and Broadbent, 1960). ^{15}N can also be released by microbes. The higher turnover rate of microbes induced the release of immobilized ^{15}N in the form of organic N (Schmidt et al., 2007), which was then incorporated into the ^{15}N pool in soil. Moreover, the relatively high soil density (0.92 g cm^{-3}, Table 1) also contributed to the high ^{15}N recovery in the soil of dead root mats.

Roots in dying and dead root mats did not take up ^{15}N as living roots did. Nonetheless, a certain amount of ^{15}N was still retained in their root litter (Figs. SVI-4 and SVI-6). The N immobilization by plant litter was controlled by the size and activity of the microbial biomass (Gallardo et al., 1992). In this process, N is imported to the litter by microbial biomass. This interpretation is also partly supported by Downs et al. (1996). In that study, a substantial proportion of added $^{15}NO_3^-$-N was immobilized by several litter types, indicating that NO_3^- was a viable source of N for microbial immobilization in litter decomposition.

2.6.5.4 Nitrogen loss via leaching and N_2O emission

Nitrogen loss via leaching increased with the degradation (Living < Dying < Dead, Fig. SVI-2). Cumulative DON loss was similar in the three root mats and the loss of NH_4^+ was negligible compared with that of DON and NO_3^-. Therefore, the N loss – increasing from the living to the dead root mats – was mainly explained by the intensified NO_3^- leaching. The much lower N loss (especially NO_3^-) from living root mats indicated that the plants efficiently recaptured N and, thus, reduced the N leaching. This agrees with Xu et al. (2004), who showed that *K. pygmaea* preferred to take up NO_3^-. Moreover, the *K. pygmaea* roots can also intercept and protect the NO_3^- from being leached (Rubio-Asensio et al., 2014). Root litter in dying root mats provided abundant labile organic matter for microbial growth, which caused higher NO_3^- loss from dying versus living root mats. The highest NO_3^- loss from the dead root mats was attributed to the accumulation from long-term decomposition of organic matter (Liu et al., 2016).

The nitrogen loss by N_2O emission was relatively low compared with that from leaching, but also increased with the degree of degradation (Dying > Dead > Living, SVI-5). Our interpretation is that increasing amounts of labile organic matter from root litter in the dying stage has stimulated heterotrophic microbial activity and promoted denitrification (Killham, 1994; Senbayram et al., 2012). By contrast, the lowest N_2O emission from living root mats can be attributed to their more aerobic conditions because of the higher evapotranspiration from living *K. pygmaea* (Hu et al., 2005).

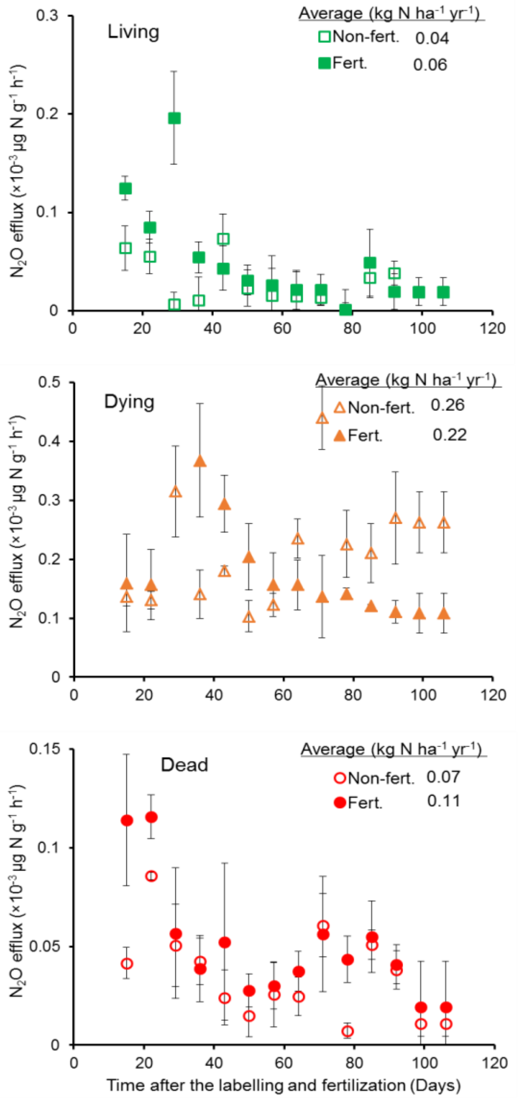


Figure SVI-5: N_2O efflux from living (top), dying (middle) and dead (bottom) root mats during the incubation. “Living”: living root mats; “Dying”: dying mats; “Dead”: dead mats. “Non-fert.”: non-fertilized samples; “Fert.”: N-fertilized samples. Error bars are standard error (SE).

2.6.5.5 Net N loss and N stock along degradation stages

Net N loss from dead root mats was 3.8 times higher than that of the dying and 14.4 times higher than that of the living root mats (Fig. SVI-6). Leaching was the main factor inducing high N loss (mainly as NO_3^-) from dying and dead root mats, while lowest N loss from living root mats can be attributed to the N uptake by *K. pygmaea*.

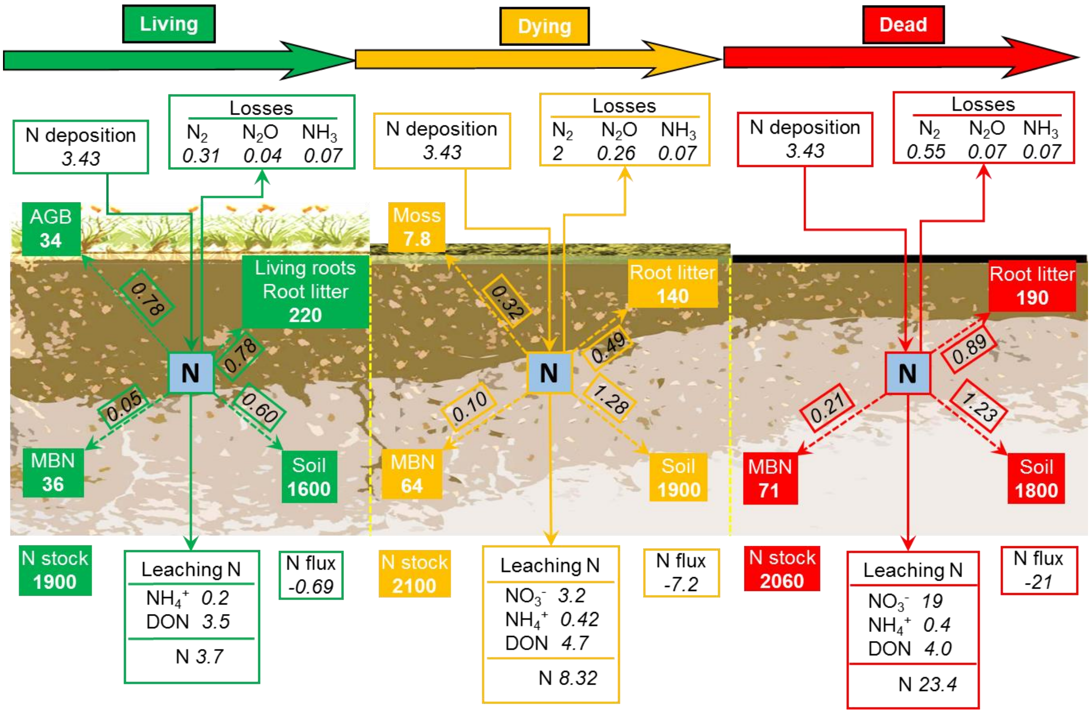


Figure SVI-6: Total N stock and N fluxes in the three root mats during the growing season. Values in **bold**: N stock (kg N ha^{-1} in the upper 5 cm); values in *italics*: N flux (kg N ha^{-1} yr^{-1}). The data along the dash line show the partitioning of deposited N into various pools. We used 3.43 kg N ha^{-1} as total atmospheric N deposition (Xu et al., 2015b). N_2 emission from denitrification was calculated using an average N_2/N_2O ratio of 7.8 for sandy loam soil (Maag and Vinther, 1996). Ammonia emission from volatilization was calculated as 2% of the deposited mineral N (van der Hoek, 1998). Total N loss from leaching during the growing season was predicted based on mean precipitation in growing season in Nagqu (356 mm, Hua et al., 2015). In summary, the greatest differences in the N flux among the three root mats were in N uptake by *living Kobresia* (living root mats) and NO_3^- leaching (dying and dead root mats). The increased soil bulk density as the root mats degraded contributed to the similar N stock in the three root mats.

The total N stock in the three root mats was similar ($p>0.05$) and ranged from 1.8-2.2 Mg N ha^{-1}. This contradicted our third hypothesis for decreasing N stock with degradation stage (H3). Most N was stored in soil, but the soil N content decreased with degradation stage (Table 1), indicating that the similarity in N stock was mainly caused by the increase in soil bulk density (Table 1). As the pasture degraded, roots decomposed and their biomass decreased. This tends to weaken the root reinforcement of the soil (Trükmann et al., 2009). The concurrent livestock trampling on *Kobresia* pasture as well as the higher relative portion of mineral particles then increased soil bulk density (Hiltbrunner et al., 2012).

Overall, the greatest differences in the N fluxes among the three *K. pygmaea* root mats are in the N uptake by living *K. pygmaea* and NO_3^- leaching (Fig. SVI-6). Nonetheless, the N flux increase as the pasture degraded did not alter the N stock in any of the three root mats. This is mainly because soil bulk density increased concurrently.

2.6.6 Conclusion

Aboveground biomass and the foliar N content of *K. pygmaea* were increased by N addition during the early growth period. This indicated that the N limitation common in *Kobresia* pastures on the Tibetan Plateau was alleviated. Nonetheless, plant growth and ^{15}N uptake were not facilitated after around 7-8 weeks. This suggests that living root mats shifted to being N limited again due to N uptake by plants and N leaching. NO_3^- leaching in living root mats strongly decreased and became undetectable after 5-6 weeks. In contrast, NO_3^- leaching markedly increased in dying and dead root mats and accounted for most of the N loss from leaching (NO_3^- > DON > NH_4^+). Leaching N losses from dying and dead mats increased 2.2 and 6.3 times compared to that from living root mats. N losses from leaching were also remarkably higher than N loss from N_2O emissions for dying and dead root mats. We conclude that N addition can facilitate plant growth in intact *K. pygmaea* pastures at least over the short term, and that continuous atmospheric N deposition in the field conditions may prolong this facilitation based on the permanent supply of N from dust deposition and rainfall. In the degraded stages of *K. pygmaea* pastures, N deposition directly increased the N losses from leaching. Thus, degradation together with increased N deposition aggravates N losses in *K. pygmaea* pastures, hampering pasture restoration. This also increases the NO_3^- loading of adjacent lower landscape parts and pollutes the headwater.

2.6.7 Acknowledgements

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2.6.8 References

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3 Abstracts of additional studies

3.1 Abstract I: Effect of overgrazing on C and N dynamics and implications for alpine *Kobresia* pasture degradation on the Tibet Plateau

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Abstract

The *Kobresia* pastures on the Tibetan Plateau provide important grazing ground and sustain the livelihood of the Tibetan herders. These pastures have high organic carbon (C) stocks locking away CO_2 from the atmosphere, and host high portions of the regional biodiversity. However, these ecosystem functions are increasingly threated by large-scale soil degradation with implications from local to global scale. Yet, the main degradation drivers are under debate, but overgrazing has often been stated to be the dominant driver. This is because *Kobresia* pasture degradation extended in the last decades in the same way as the stocking rates intensified. To clarify the effect of grazing a degradation concept was elaborated and tested with field experiments. Therefore, grazing exclosure plots were established in the core area of the *Kobresia* ecosystem on the Kema research sites near Naqu. In a further step soil samples were taken from overgrazing-induced degraded sites across the eastern part of the Tibetan plateau to identify C and N losses.

Overgrazing-induced degradation concept (Fig. 1): The concept postulates that a constant removal of the photosynthetic active shoot biomass via grazing decreases the belowground C allocation (step 1). On the long-term this initiates the death of the root biomass, because the high belowground C demands cannot be maintained (step 2). This lowers the uptake of limited resources such as N, P, H_2O and causes a negative feedback on the aboveground

biomass maintenance (step 3). Overall this leads to a patch-wise dying of the *Kobresia* turf, which encourages the formation of crusts with lichens and algae. These degradation patterns are recurrent across the whole *Kobresia* ecosystem.

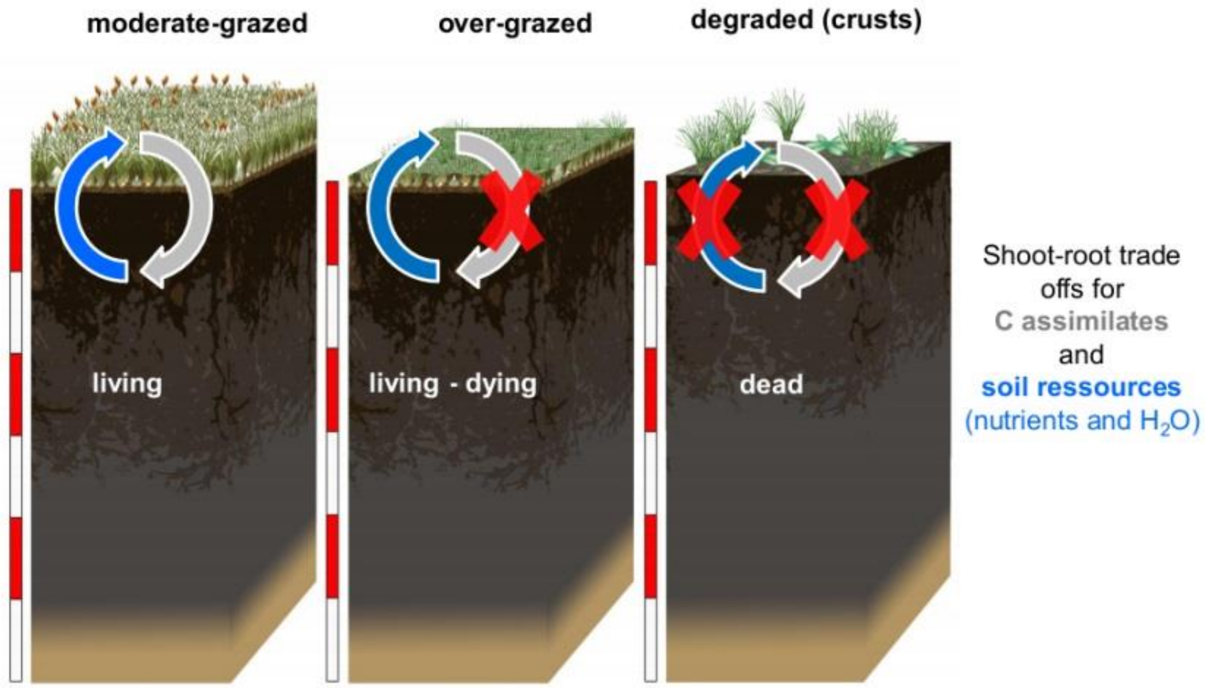

Figure AI-1: A simplified concept to explain overgrazing-induced soil degradation by disrupting above- and belowground plant trade-offs. The 1st and 2nd stages were elaborated by means of ^{13}C and ^{15}N pulse-labeling studies, whereas the 3rd stage was deduced from field observations and the widespread pattern of dead Kobresia turf.

Grazing effects on C and N cycles:

A dual pulse labeling ($^{13}CO_2$ and ^{15}N urea) was used to trace the C and N dynamics over 55 days in the plant-soil system. The ^{13}C incorporation in the root biomass was lower in the grazed compared to the ungrazed sites and indicated that less photosynthetic assimilates were allocated belowground (Figure AI-2). From this it was concluded that overgrazing disrupts the above- belowground trade-off and over a longer period might initiate the dying of the *Kobresia* turf. However, the ^{15}N recovery of the root biomass was similar between both grazing regimes indicating that root N uptake was not affected by grazing. This contrasted the ^{15}N recovery in the shoot biomass, which was lower in grazed sites. Presumably, the permanent removal of the shoot biomass via grazing activities and the decreasing N uptake following imbalanced above-belowground tradeoffs can explain the lower ^{15}N recovery in the shoot biomass.

One day after $^{13}CO_2$ labeling 50% and 46% of assimilated ^{13}C was lost by shoot respiration for grazed and ungrazed sites, respectively. Total belowground fluxes (^{13}C in roots, soil and cumulative CO_2) after 35 days were lower for grazed sites (Grazed: 23% and Ungrazed 32%) and indicated a higher belowground carbon incorporation in the absence of grazing. The higher soil respiration contributed to increasing C loss from grazed sites. It was approximately two times higher than that of the ungrazed sites (Grazed: 10% and Ungrazed 5.5%). To sum up: the larger below-ground C allocation of plants, and less soil organic matter-derived CO_2 efflux create a positive effect for ungrazed sites on C sequestration.

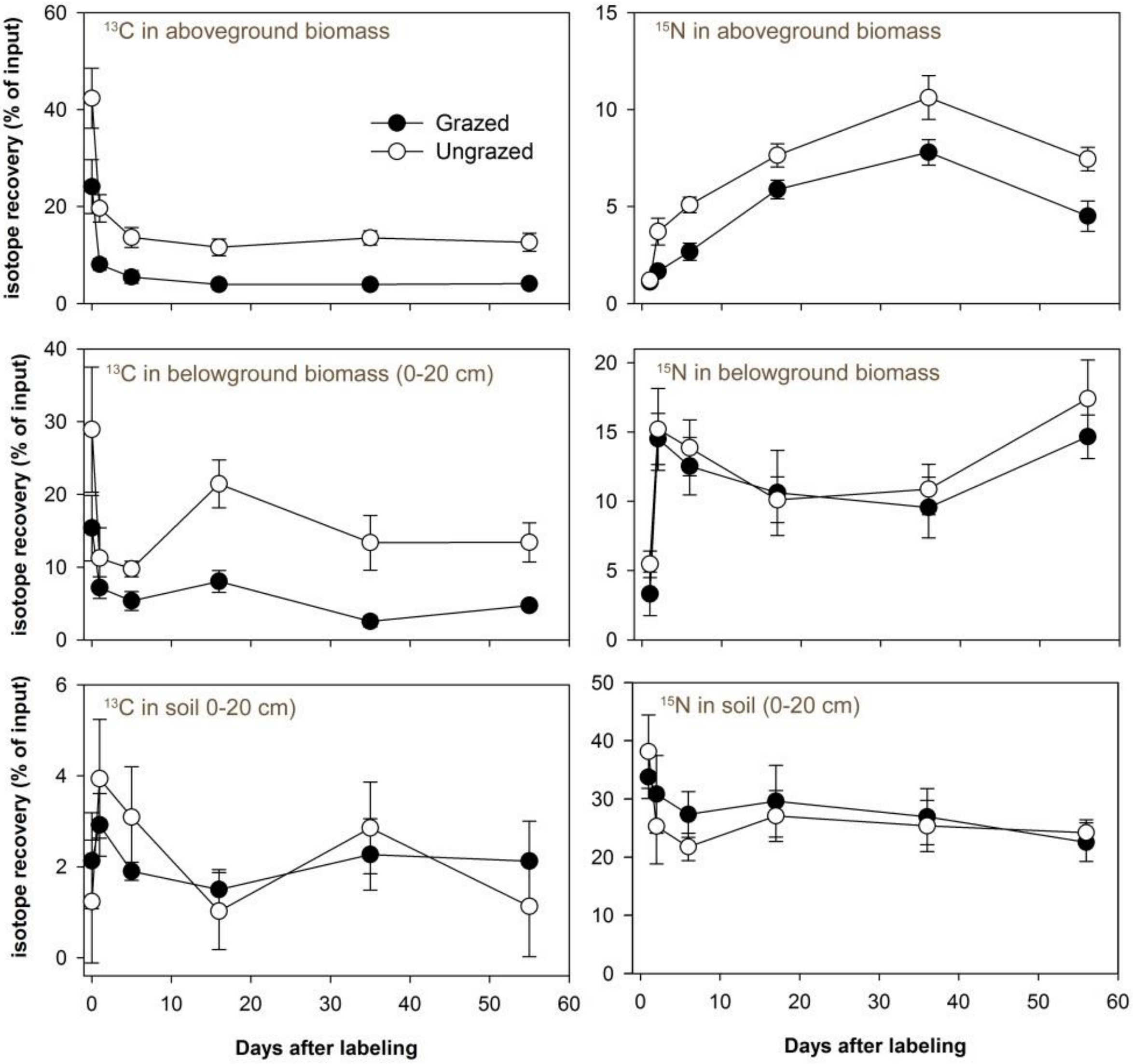

Figure AI-2: ^{13}C and ^{15}N recovery in shoot, root and soil depending on grazing regime (grazed versus ungrazed) within the vegetation period over 55 days in an alpine Kobresia pasture

C and N losses in degraded Kobresia root mats across the eastern Tibetan Plateau

It was assumed that overgrazing-induced degradation causes a dying of the root mats and initiates high C and N losses due to proceeding SOM decomposition and leaching. These site-specific carbon and nutrients dynamics in degraded *K. pygmaea* pastures have been recently studied (see chapter 2.5; 2.6). Less attention, however, was paid on degradation impacts on broader scale. Therefore soil samples (in 0-5 cm; 5-15 cm; 15-25 cm) of crust-covered degraded root mats were taken and compared with adjacent non-degraded plots during a field-excursion in late summer 2015. Overall 17 sites were sampled across the whole *Kobresia* ecosystem with 4 replicates for the intact and degraded plots, respectively (Fig. AI-3). Up to now SOC and N contents as well as ^{13}C of SOC were analyzed for six sites as shown with the red dots (Fig. AI-3).

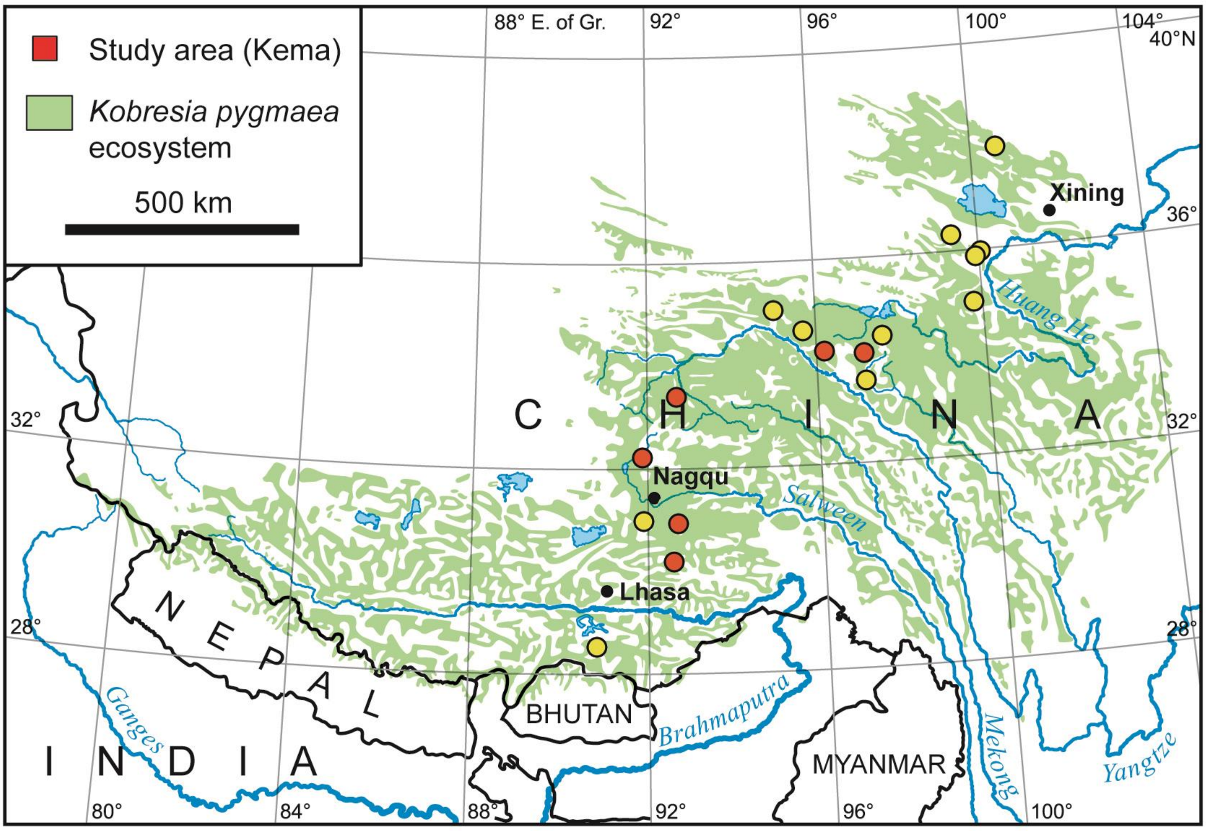

Figure AI-3: Distribution of sampling sites across the *Kobresia* ecosystem on the eastern part of the Tibetan plateau. Red dots are already analyzed, yellow dots are still pending.

Losses were calculated by relating the SOC and N contents of the degraded plots to that of the intact plots. Preliminary results indicated that in the upper topsoil (0-5 cm) SOC and N losses were on average 31% and 20%, respectively. Losses were independed from elevation (Fig AI-4a&b; SOC vs elevation: $R^2 = 0.16$, $p = 0.43$, $n = 6$; N vs elevation: R^2 0.35, $p = 0.21$, $n = 6$) and also annual mean precipitation and temperature turned out to have no significant impact on SOC and N losses. This is mainly attributed to the low sampling size ($n = 6$), which currently does not allow appropriate statistics. It is is expected that the extension of the data set (analysis of missing sites, see yellow dots, Fig. AI-3) will help to identify predominat abiotic factors controlling C and N losses. This includes the mean annual temperature and the mean annual precipitation, which both control mineralization and leaching, and thus are the dominant mechanism for inducing C and N losses from crust-covered degraded root mats. Carbon losses were higher than N losses (Fig. AI-5), because besides to leaching that relativly affects N and C in the same way, C has been lost in from of CO_2 following mineralization. Mineralization was indicated with a correlation between the SOC loss and the changing ^{13}C signature in the soil. It caused an enrichment of ^{13}C in the soil because the lighter ^{12}C isotope was lost in form of CO_2.

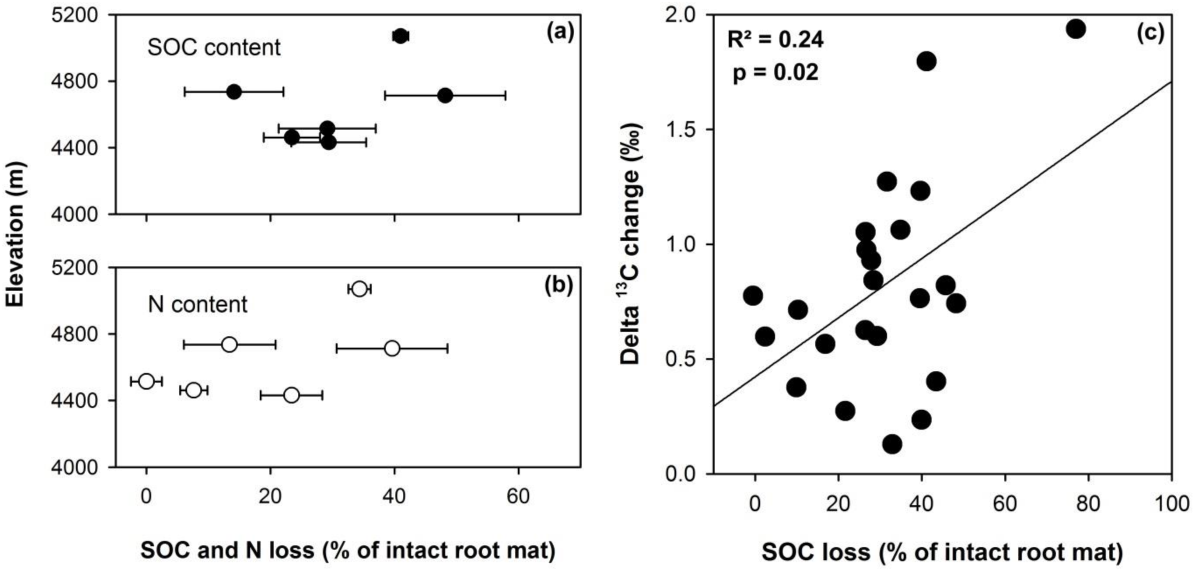

Figure AI-4: **(a)** SOC and N loss for degraded root mats for six sites across the *Kobresia* ecosystems and **(b)** the relationship of SOC loss to changes of the $\delta^{13}C$. SOC and N losses are calculated on the content basis (SOC_{intact} – $SOC_{degraded}$; N_{intact} –$N_{degraded}$). Values are presented as means with standard error. The delta ^{13}C change was calculated as follows: Delta ^{13}C change = $\delta^{13}C_{degraded}$ - $\delta^{13}C_{intact}$.

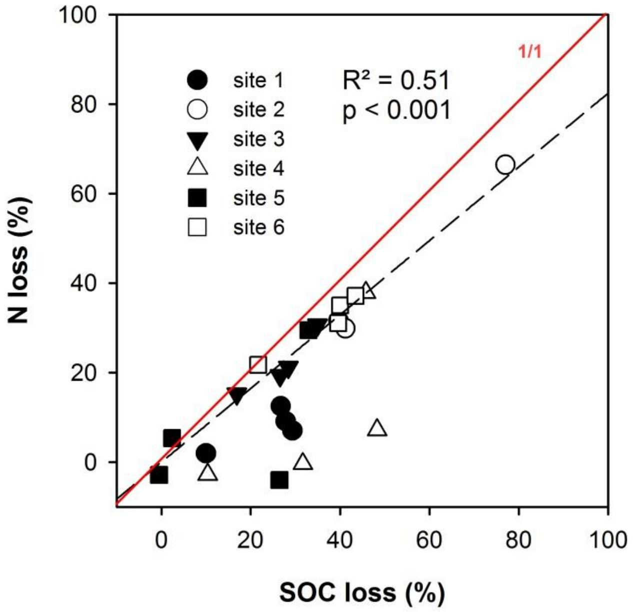

Figure AI-5: Decoupling between SOC and N losses for six sites across the *Kobresia* ecosystem

Distribution of crust-covered degraded Kobresia pastures on the Tibetan plateau:

To analyse the regional patterns of crust-covered degraded root mats, a methodology based on ground samplings and remote sensing data has been developed. Ground truth data has been sampled between 2009 and 2013 between June and September at distinct sites on the Tibetan Plateau. In sum 239 plots have been sampled. In a next step these data were compared to Landsat data (resolution per pixel is 30 m, Fig. AI-6a). The estimated values of the Landsat images have been spatially aggregated so that each aggregated value spatially corresponds to one MODIS pixel (resolution per pixel is 500 m, Fig. AI-6b). Using the averaged Landsat degradation predictions as response variable and the MODIS feature as predictors, a random forest model has been trained and validated. A 10-fold cross-validation with 5 replicates has been applied. This model has finally been used to predict degradation coverage values for all pixels covered by the *Kobresia* ecosystem. Therefore, all available MODIS scenes for the years 2013 to 2015 have been processed. The result shows that on average 8% of the entire *Kobresia* ecosystem are affect by this specific form of degradation (Fig. AI-7). Further, the model reveals that elevation was the most important predictor to explain recurrent degradation patterns, meaning degradation increased with elevation. Most likely the decreasing net primary production in higher elevations has caused an increasing vulnerability towards pasture degradation via overgrazing.

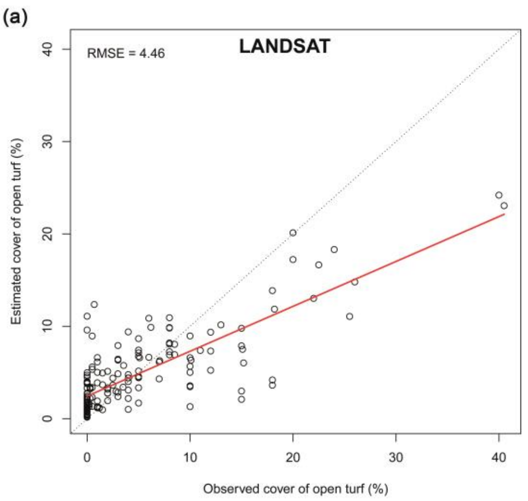

Figure AI-6: Validation of the predicted degraded root mat values at the Landsat scale (a) and the MODIS scale (b). Please note that the observed cover values for the MODIS scale are the predictions from the Landsat scale averaged over all collocated pixel values of the corresponding collocated MODIS pixel. The solid red and dashed black lines show the linear regression lines and the 1:1 lines, respectively.

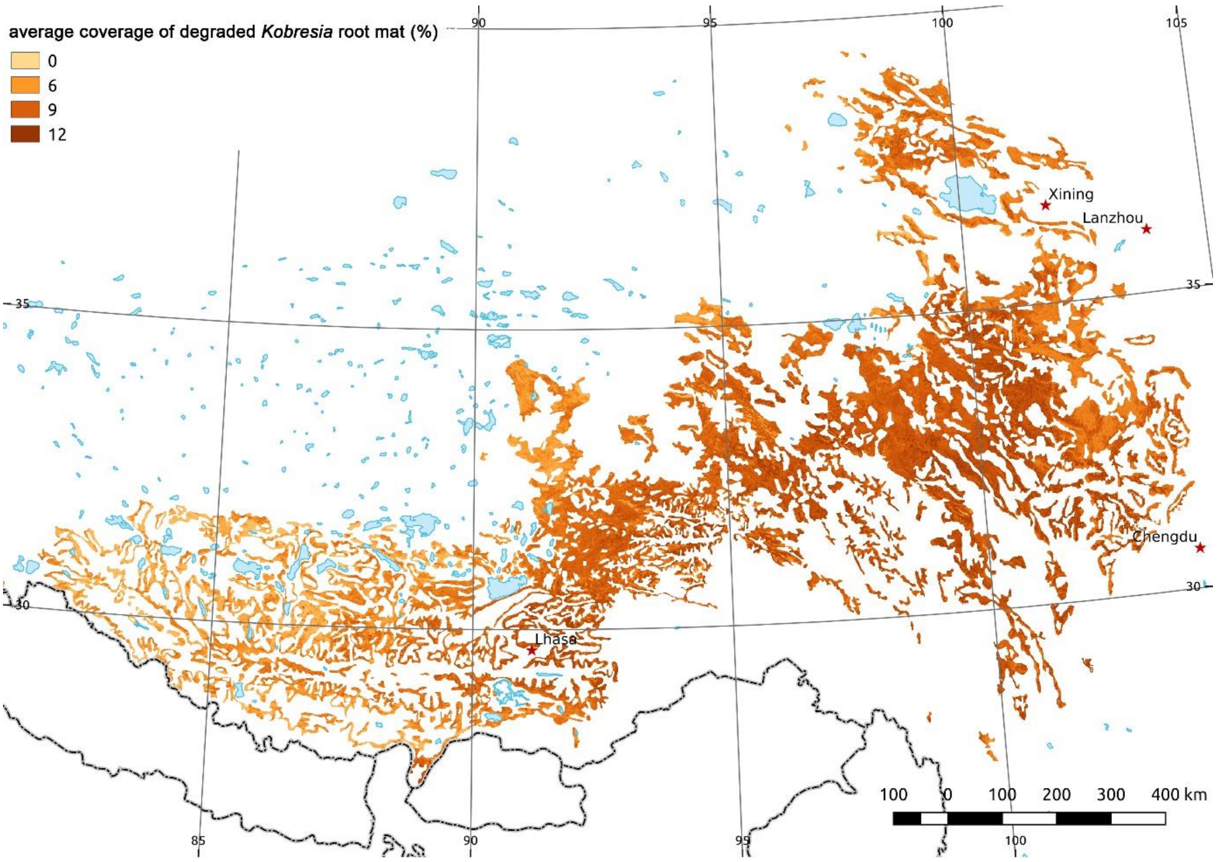

Figure AI-7: Extend of curst-covered degraded root mats within the *Kobresia* ecosystem. Spatial patterns were modeled using MODIS data set (resolution of 500 km). Before data were checked against LANDSAT data set (resolution 30 km, see Figure AI-6).

3.2. Abstract II: Clipping and shading alter NH_4^+ uptake by plants in Tibetan *Kobresia* grasslands

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Abstract

Nitrogen (N) is a limiting nutrient for plant growth in most terrestrial ecosystems and for large parts of the alpine *Kobresia* pastures on the Tibetan Plateau. Nevertheless, N dynamics and availability is strongly affected by grazing activities, i.e. by N removal or redistribution via yak, sheep and goats. Consequently, grazing might aggravate occurring N limitations, decrease grassland productivity and overall promote the degradation of this vulnerable ecosystem.

Plants translocate carbon (C) in form of root exudates to belowground. This C input provides an important energy sources for microorganisms and therefore controls the microbial mobilization of N. This N can be subsequently used for plant uptake. However, the trade-offs between plant C translocation and N uptake, and its response to grazing still remains unknown in *Kobresia* grasslands. A$^{15}NH_4^+$ labeling experiment was implemented for grazed and ungrazed sites to identify the effects of reduced C input on N dynamics in the plant-soil system. In both sites (grazed and ungrazed) plants were clipped and shaded to reduce photosynthetic activity and with this belowground C input. It was hypothesized that decreasing photosynthesis alters plant N uptake and decrease the gross N mineralization.

Grazed versus ungrazed:

Grazing decreased the aboveground biomass (AGB) but increased the belowground biomass (BGB) in 0-10 cm of soil (Fig. AII-1). Twenty-eight days after the labeling, the total ^{15}N recovery of plants (^{15}N in shoot + ^{15}N in root) was similar for both grazing regimes. However, the ^{15}N recovery of the AGB was 0.4 times lower and the ^{15}N recovery of the BGB was 0.1 times higher in grazed plots compared to ungrazed plots (Fig. AII-2). This indicates that grazing changed the plants above-and belowground investments, and led to higher ^{15}N retention in belowground biomass on grazed sites, which presumably improved N uptake to support shoot regrowth.

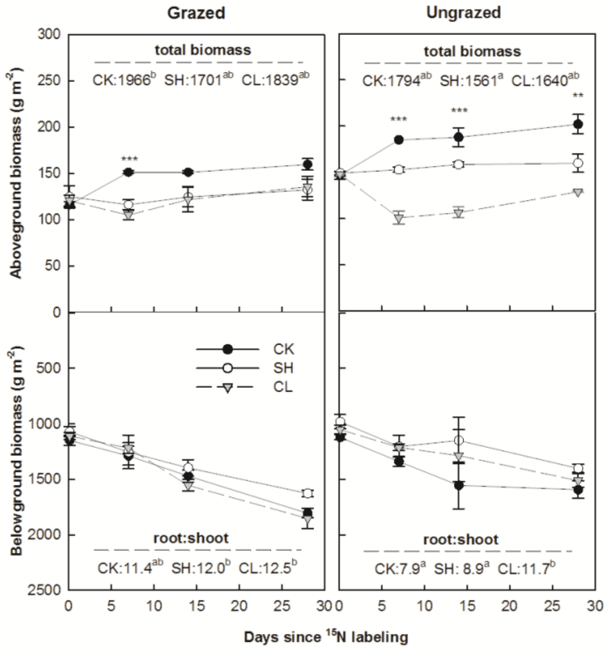

Figure AII-1: Aboveground and belowground plant dry mass (g m-2) in grazed and ungrazed plots 7, 14 and 28 days after clipping or shading. The total plant biomass and ratio of root-to-shoot biomass (root: shoot) 28 days after clipping and shading. The values were mean ± SE of 4 replicates. *** and ** indicates significant differences at p<0.001 and p<0.01 respectively, and lowercase letter (a-b) indicate significant differences at p<0.05 in three treatments (CL, SH, CK).

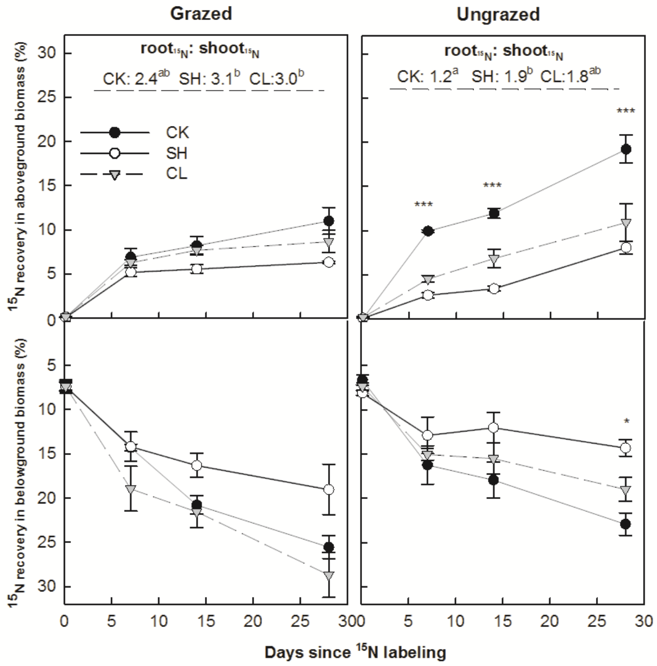

Figure AII-2: The 15N recovery in above- and belowground plant biomass (g m-2) of different treatments (CL, SH, CK) in both grazed and ungrazed plots, 3 hours, 7, 14 and 28 days after labeling. And the ratio of root-to-shoot 15N uptake (root15N: shoot15N), 28 days after labeling. *** and * Indicates significant differences at p<0.001 and p<0.05 respectively in three treatments.

Clipping and shading:

^{15}N recovery in the AGB decreased after clipping for both grazing regimes (Fig. AII-2), whereas it increased in the BGB for the grazed plots but decreased for the ungrazed plots. In contrast shading led to the lowest ^{15}N recovery in AGB and BGB for both grazing regimes. Overall, clipping increased the N uptake (of total plant) in grazed plots while it decreased that in ungrazed plots. Shading decreased the N uptake in both grazing regimes.

Grazing reduced gross N mineralization rates by 24.5% compared with the ungrazed plots, while clipping and shading also decreased gross N mineralization rates. Lowered photosynthesis caused by shading and clipping restrained soil N mineralization. These data suggest that *Kobresia* are highly sensitive towards grazing effects regarding the trade-off between C allocation and N uptake by plants, and soil N mineralization.

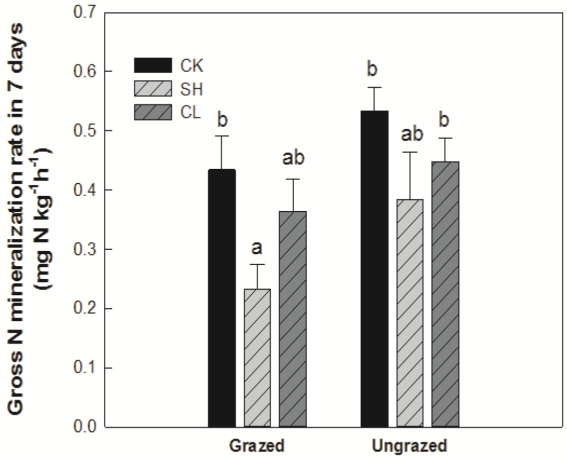

Figure AII-3: Gross N mineralization rate of soil (µg N g^{-1} dw soil) in grazed and ungrazed plots with different treatments (CL, SH, CK) in 7 days after labeling. Lowercase letters (a-b) indicate significant differences between three treatments (p<0.05).

3.3 Abstract III: Pasture management controls SOM stocks, properties, and biochemical functioning in Tibetan grasslands

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Abstract

Given the vital importance of the Tibetan steppes as global OC sinks, we combined data on OC stocks from own studies with an extensive literature review on soils developed under montane and alpine Kobresia pygmaea and Stipa grandis pastures. We calculated soil OC stocks at the Tibetan Plateau within the first 30 cm of the soil profile depending on pasture management and climate. Vertical gradients of $\delta^{13}C$ values, neutral sugar, cutin and suberin contents, lignin phenol contents as well as microbial community composition (t-RFLP analysis, 16S rDNA und IST sequencing) and activities of six extracellular enzymes involved in the C, N, and P cycle were assessed. The depth gradients of these parameters reflected degradation processes from intact Kobresia pastures (stage 0) to pronounced degradation (bare soil; stage 5).

Moderate husbandry is beneficial for the storage of OC, nitrogen (N) and other nutrients (e.g. phosphorus) for the majority of the montane grasslands of the Tibetan Plateau (i.e., *Kobresia pygmaea* pastures). Translocation of topsoil material into the subsoil with advancing degradation (from S1 to S5) was indicated by increasing contributions of cutin to OC in the subsoils. Microbial community composition in the subsoil changed progressively from S1 to S5 with most pronounced changes of the fungal community. These findings were confirmed by the enzyme activities involved in the degradation of more complex OC compounds (e.g. fungal phenoloxidases) that were highest in the subsoil of degradation S4. In contrast, degradation stages 2 and 3 showed low enzyme activities in the subsoil if related to soil OC amount. We conclude that pasture degradation decreases not only the mechanical protection of soil surface by Kobresia root mats, but also changes their biochemical and microbial functions. Moderate grazing improves the pastures, increases OC sequestration and may stop the degradation of soils on Tibetan plateau.

3.4 Abstract IV: A literature review on SOC and nutrient losses with intensified pasture degradation on the Tibetan Plateau

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Abstract

The Tibetan pasture ecosystem covers more than one third of the plateau area. It stores large amount of soil organic carbon (C) and nutrients and provides important grazing ground. Several studies have been implemented on plot scale, which show that proceeding degradation has initiated huge amounts of C and nutrients losses. However, a more quantitative analysis on broader scale for the whole *Kobresia* ecosystem is still missing. This study reviewed the literature for above- and belowground biomass, pH and bulk density as well as for losses of soil C and nutrients (N, P, K) with proceeding degradation stage in this pasture ecosystem. Overall five degradation stages were classified: non-degraded (ND), lightly degraded (LD), moderately degraded (MD), heavily degraded (HD) and severely degraded (SD). The parameters are presented for each degradation stage comparing it to the intact stage (termed as effect size, Fig. AIV-1). The meta-analysis indicated that soil C storage decreased after the degradation from ND to LD (-20%), to MD (-27%), to HD (-47%), to SD (-62%). This trend suggested that degradation strongly reduced soil C storage presumably due combined effects of mineralization, leaching and erosion and decreasing C input.

Similar, soil total N, P and K contents significantly declined along the degradation gradient by 19-60%, 7-23% and 6-29% indicating a decrease in soil fertility. This may have aggravated or shifted nutrient limitations slowing down pasture recovery for alpine *Kobresia* pastures. This was consistent with plant biomass patterns. Degradation from ND to SD caused large losses of aboveground biomass (19-64%) and belowground biomass (2-66%), which indicated that C input via photosynthesis was also negatively affected. Consequently, degradation of *Kobresia* ecosystem strongly decreased soil C and nutrients storage, which may contribute to climate change, decreases pasture quality and overall threatens the livelihood life Tibetan herders.

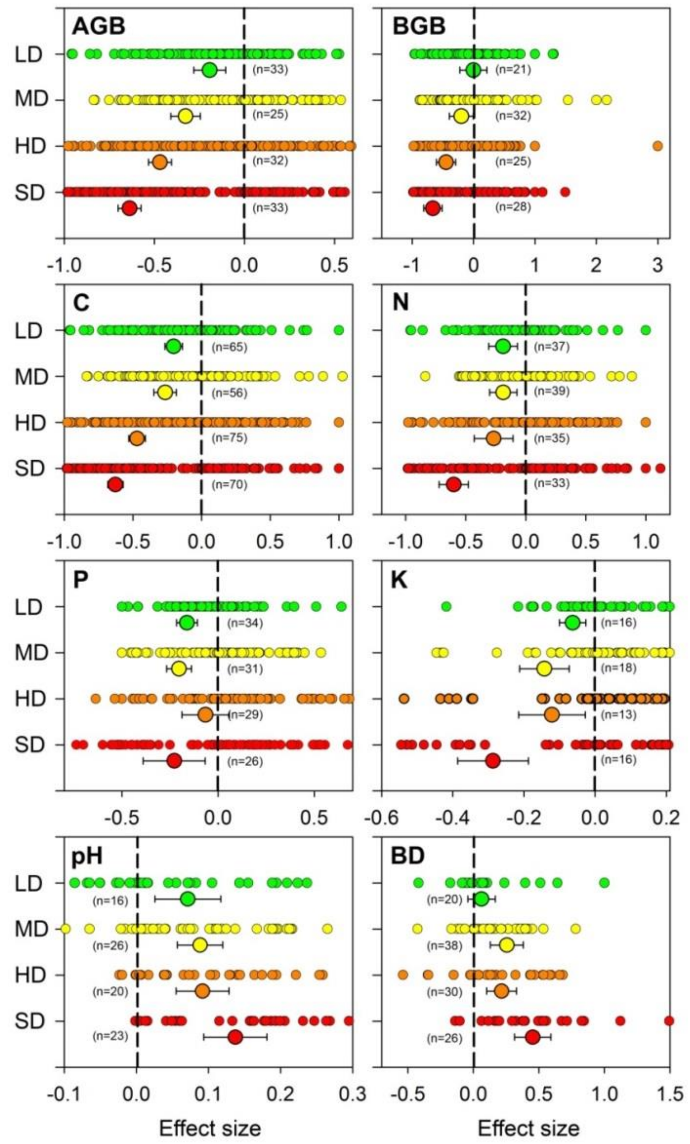

Figure AIV-1: Effect of pasture degradation on soil organic C (SOC), nutrients (TN, TP, TK), plant biomass (AGB, BGB), bulk density and pH. The data point with error bar is the mean value of corresponding degradation stage. The number of observations is shown in the parenthesis. The error bar is the 95% confidence intervals.

3.5 Abstract V: Degradation increases response of priming effects to temperature in Tibetan alpine grasslands

Yue Sun[1,2], Qianru Li[3], **Per Marten Schleuss**[1,2], Xingliang Xu[3], Ouyang Hua[3], Yakov Kuzyakov[1,2]

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Abstract

Kobresia pastures on the Tibet plateau have high soil organic carbon (SOC) stocks, but intensive degradation in recent decades has induced high SOC losses. These losses were recently attributed to erosion and SOC mineralization. In particular, mineralization of SOC is expected to increase as a consequence of elevated temperatures due to climate change.

For this study, it was hypothesized that warmer temperatures may also enhance the productivity of *Kobresia* pastures. For the non-degraded sites this should result in a higher amount of root exudates, which are then released into the soil as labile organic carbon. On the contrary, degradation causes a dying of the *Kobresia* root mats, which leads to depletion of available C due to mineralization and decreasing C inputs from root exudates. Therefore, it was hypothesized that amended C inputs (i.e. as glucose) might activate microorganisms and accelerates SOC mineralization ("priming effects") with a greater response in degraded than in and non-degraded *Kobresia* pastures. We conducted a laboratory incubation experiment to test priming effects within non-degraded and degraded *Kobresia* soil depending on changes in temperature and C input (glucose addition). The non-degraded and degraded stage were both labeled with ^{14}C-glucose in high/low addition and incubated under 0 °C, 10 °C and 20 °C for 80 days.

Cumulative SOC derived CO_2 emission increased significantly with temperature. Degraded soil showed lower SOC derived CO_2 emission at 0 °C, but significant higher CO_2 emission at higher temperature compared to that of non-degraded soil (Fig. AV-1). This clearly shows that increasing temperatures accelerate SOC loss with higher response in degraded *Kobresia* grassland.

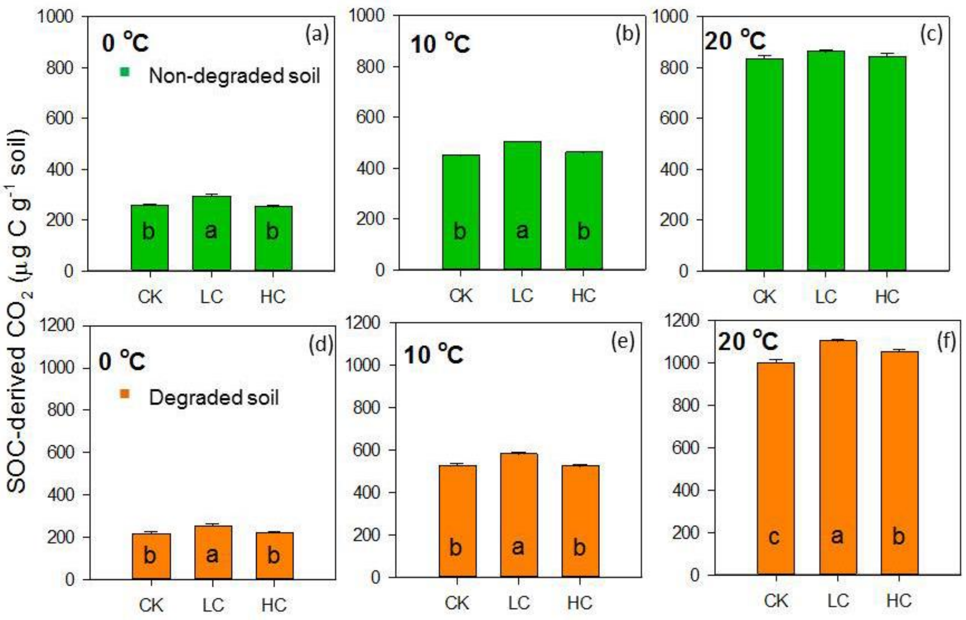

Figure AV-1: Total cumulative CO₂ emissions derived from SOC mineralization of the non-degraded **(a, b, c)** and degraded soil **(d, e, f)**, which were incubated under 0 °C, 10 °C and 20 °C. The values were mean ± SE of 4 replicates, and lowercase letter (a-b) indicate significant differences at *p*<0.05 in three treatments (CK, LC, HC). "CK" = control; "LC" = low glucose-C input; "HC" = high glucose-C input.

Priming effects positively responded to increasing temperature, with about 80 % increment in degraded soil and about 15 % in non-degraded soil. At 20 °C it was significant higher in degraded than non-degraded soil (Fig. AV-2). This implies that degradation increases temperature response of priming effects in the Tibetan *Kobresia* grassland.

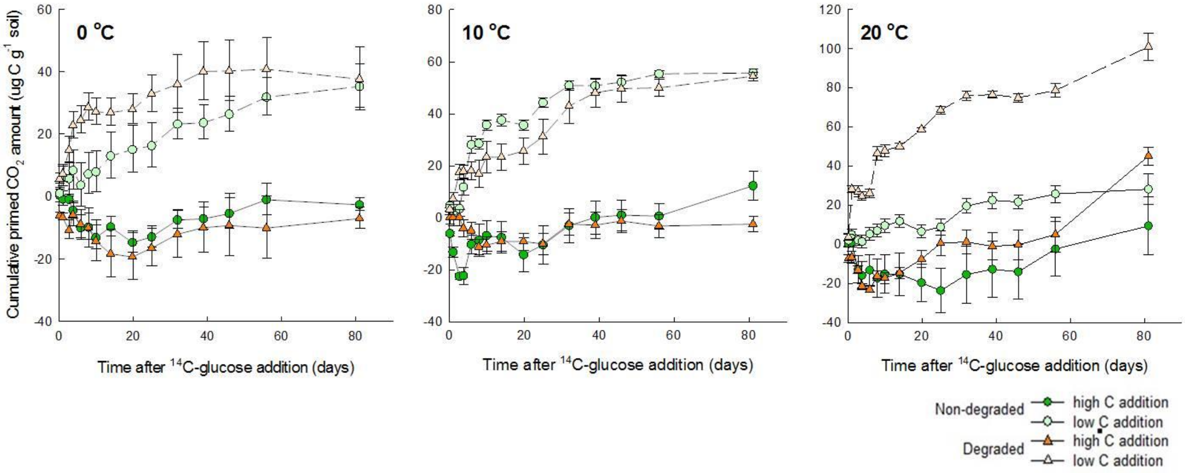

Figure AV-2: Cumulative primed CO₂ emissions from the non-degraded and degraded soil, which were incubated under 0 °C, 10 °C and 20 °C. Relations between cumulative primed CO₂ emissions (in the end of incubation) of high and low glucose-C addition treatments and temperature. The values were mean ± SE of 4 replicates.

The decomposition of SOC is controlled by extracellular enzymes, which are mainly produced by microorganisms. We found that higher temperature increased microbial activity (i.e., qCO_2) (Fig. AV-3) and enzyme activity (i.e., β-glucosidases, chitinase, cellobiohydrolase and Xylosidase) in the degraded and non-degraded stage (Fig. AV-4). Enzyme activity was significantly higher in degraded soil than in non-degraded soil, exhibiting a positive relationship with SOC loss and priming effects. It suggests that rising temperature increased microbial and enzyme activity, and in turn strongly accelerated SOM mineralization and initiated priming effects.

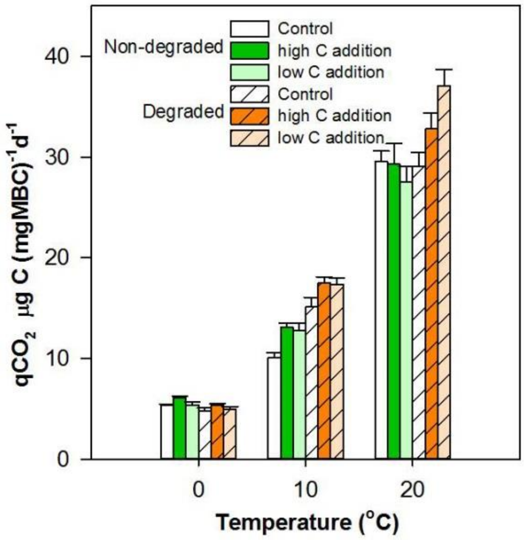

Figure AV-3: Microbial metabolic quotients (qCO2) of non-degraded and degraded soil, which were incubated under 0 °C, 10 °C and 20 °C, with high and low glucose-C addition treatments. The values were mean ± SE of 4 replicates.

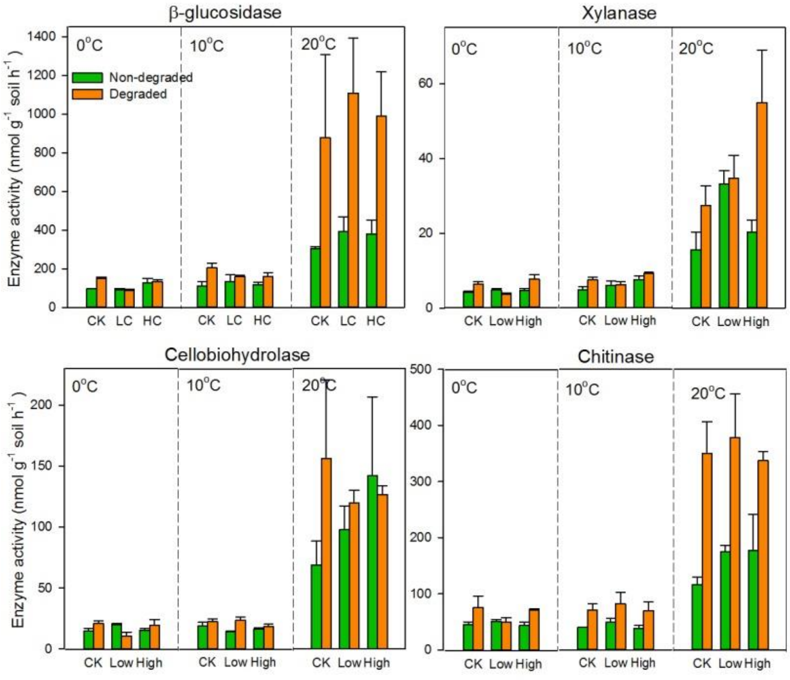

Figure AV-4: Enzyme activities in non-degraded and degraded soil incubated under 0 °C, 10 °C and 20 °C, with high and low glucose-C addition treatments (CK, LC, HC). The values were mean ± SE of 4 replicates.

At 0 and 10°C, low-level glucose input caused an activation of the microorganisms leading to positive priming effects, meaning that the microbial activation induced the mineralization of the stable SOC pool. In contrast high-level glucose additions caused significantly lower priming effects (even negative priming effects for 0°C and 10°C), presumably because microbes preferred to utilize the added glucose rather than the more stable and energy-intensive SOC pool. Nevertheless, at 20°C priming effects were positive in the degraded soil independent of C inputs at the end of incubation (Fig. AV-5).

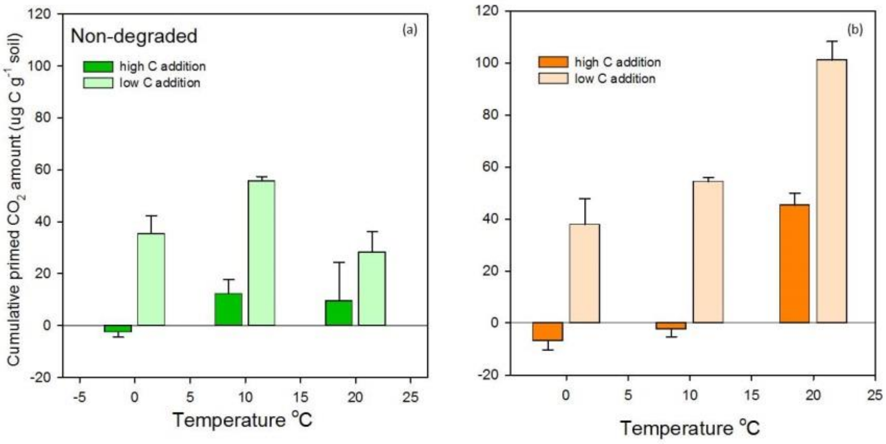

Figure AV-5: Cumulative primed CO_2 emissions from the non-degraded and degraded soil incubated under 0 °C, 10 °C and 20 °C. The values were mean ± SE of 4 replicates.

Overall, the results indicate that labile C input increases SOC turnover, especially under low C input in particular in degraded soil. Due to the higher C deficiency (decreasing C content following mineralization and absence of labile C inputs from root exudates), degradation increases the response of SOC loss to labile C input and increasing temperature. Therefore it was concluded that elevated temperature following climate change may enhance priming effects via higher microbe and enzyme activity.

3.6 Abstract VI: Fate of organic and inorganic nitrogen in crusted and non-crusted Kobresia grasslands

Accepted in *Land Degradation and Development* (2016)

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Abstract

A widespread pattern of the Tibetan plateau is mosaics of grasslands of Cyperaceae and grasses with forbs, interspersed with patches covered by lichen crusts induced by overgrazing (Fig. AVI-1). However, the fate of inorganic and organic N in non-crusted and crusted patches in *Kobresia* grasslands remains unknown.

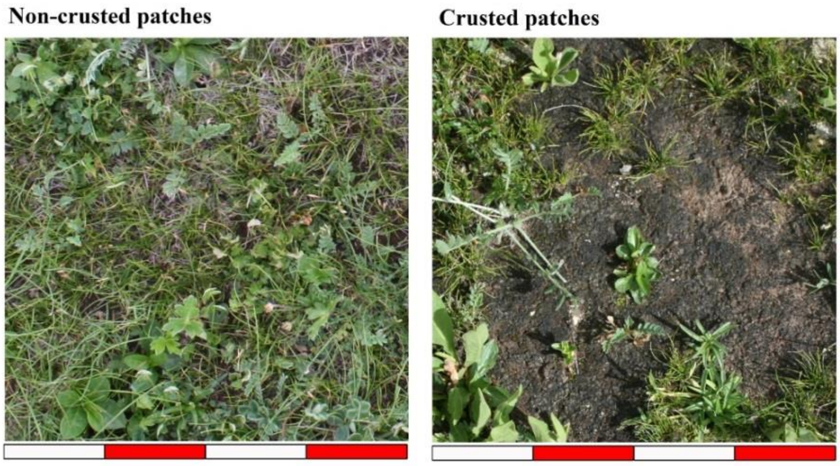

Figure AVI-1: Picture showed our study sites with two contrasting patches of vegetation in 07.2009. Left: Vegetation cover approximately 100% with predominant *Kobresia* and *Stipa* species (referred to as non-crusted patches). Right: With the same species, cover less than 30%, more than 70% of the surface is covered by blue-green algae and crustose-lichens (referred to as crusted patches). The bars on the scale are 10 cm.

We reported on a field ^{15}N-labeling experiment in two contrasting patches to compare retention of organic and in-organic N over a period of 29days. ^{15}N as KNO_3, $(NH_4)_2SO4$ or glycine was sprayed onto soil surface. Crusted patches decreased plant and soil N stocks. More ^{15}N from three N forms was recovered in soil than plants in both patches 29 days after the labeling. In non-crusted patches, ^{15}N recovery by the living roots was about two times higher than in crusted ones, mainly because of higher root biomass. Microorganisms in non-crusted patches were N-limited because of more living roots and competed strongly for N with roots. Inorganic N input to non-crusted patches could alleviate N limitation to plants and microorganisms, and leads to higher total ^{15}N recovery (plant + soil) for in organic N forms (Fig. AVI-2). Compared to non-crusted patches, microorganisms in crusted patches were more C-limited because of depletion of available C caused by less root exudation. Added glycine could activate microorganisms, together with the hydrophobicity of glycine and crusts, leading to higher ^{15}N-glycine than inorganic N. We conclude that overgrazing-induced crusts in *Kobresia* grasslands changed the fate of inorganic and organic N, and lead to lower total recovery from inorganic N but higher from organic N.

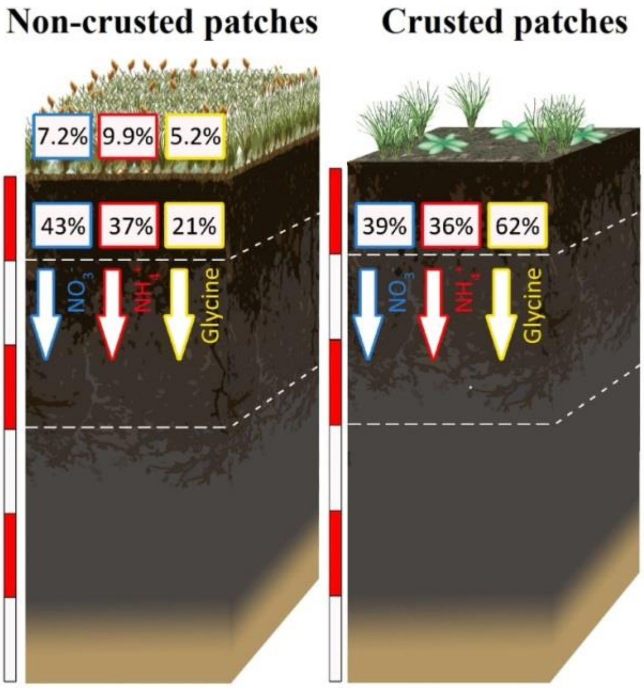

Figure AVI-2: A summary for the fate of inorganic and organic nitrogen in both non-crusted and crusted patches in a *Kobresia* grassland.

3.7 Abstract VII: Pasture degradation modifies the water and carbon cycles of the Tibetan highlands

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Corresponding author: Thomas Foken

Abstract

The Tibetan Plateau has a significant role with regard to atmospheric circulation and the monsoon in particular. Changes between a closed plant cover and open bare soil are one of the striking effects of land use degradation observed with unsustainable range management or climate change, but experiments investigating changes of surface properties and processes together with atmospheric feedbacks are rare and have not been undertaken in the world's two largest alpine ecosystems, the alpine steppe and the *Kobresia pygmaea* pastures of the Tibetan Plateau. We connected measurements of micro-lysimeter, chamber, ^{13}C labelling, and eddy covariance and combined the observations with land surface and atmospheric models, adapted to the highland conditions. This allowed us to analyse how three degradation stages affect the water and carbon cycle of pastures on the landscape scale within the core region of the *Kobresia pygmaea* ecosystem.

The study revealed that increasing degradation of the *Kobresia* turf affects carbon allocation and strongly reduces the carbon uptake, compromising the function of *Kobresia* pastures as a carbon sink (Figure AVII-1, AVII-2).

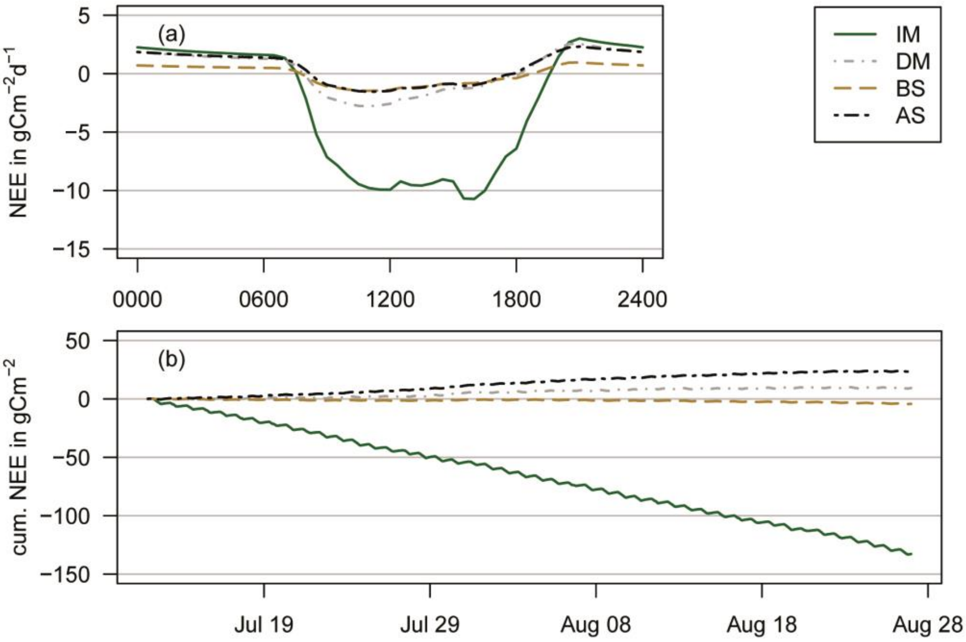

Figure AVII-1: Model results of net ecosystem exchange (NEE) over 46 days of July and August 2012 at Kema. (a): mean diurnal cycle, and (b): cumulative NEE. The four lines represent different stages of vegetation degradation (IM, DM, BS, and AS)

Pasture degradation leads to a shift from transpiration to evaporation while a change in the sum of evapotranspiration over a longer period cannot be confirmed. The results show an earlier onset of convection and cloud generation, likely triggered by a shift in evapotranspiration timing when dominated by evaporation (Figure 3). Consequently, precipitation starts earlier and clouds decrease the incoming solar radiation. In summary, the changes in surface properties by pasture degradation found on the highland have a significant influence on larger scales.

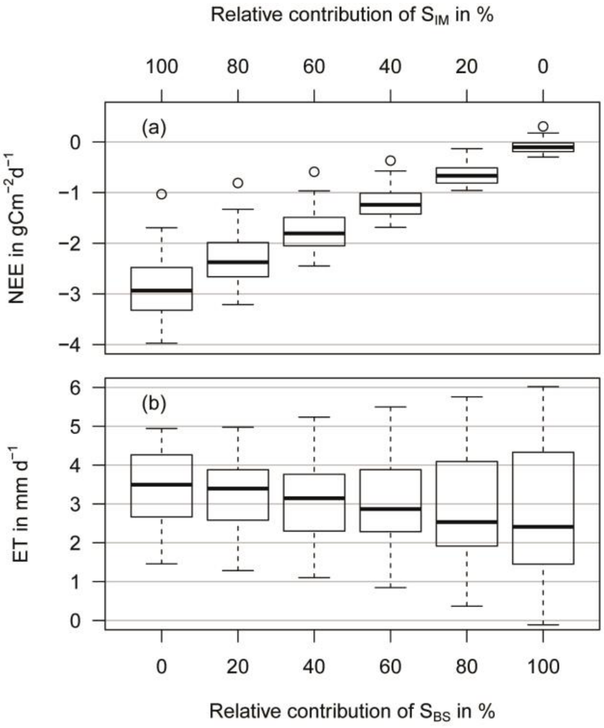

Figure AVII-2: Modelled daily net ecosystem exchange (top, NEE) and modelled daily evapotranspiration (bottom, ET) for 46 days (12 July to 26 August 2012) at Kema (varying combination of SIM and S BS): box plot with median, 25 % and 75 % quartiles; bars represent quar-tiles 1.5 times interquartile range.

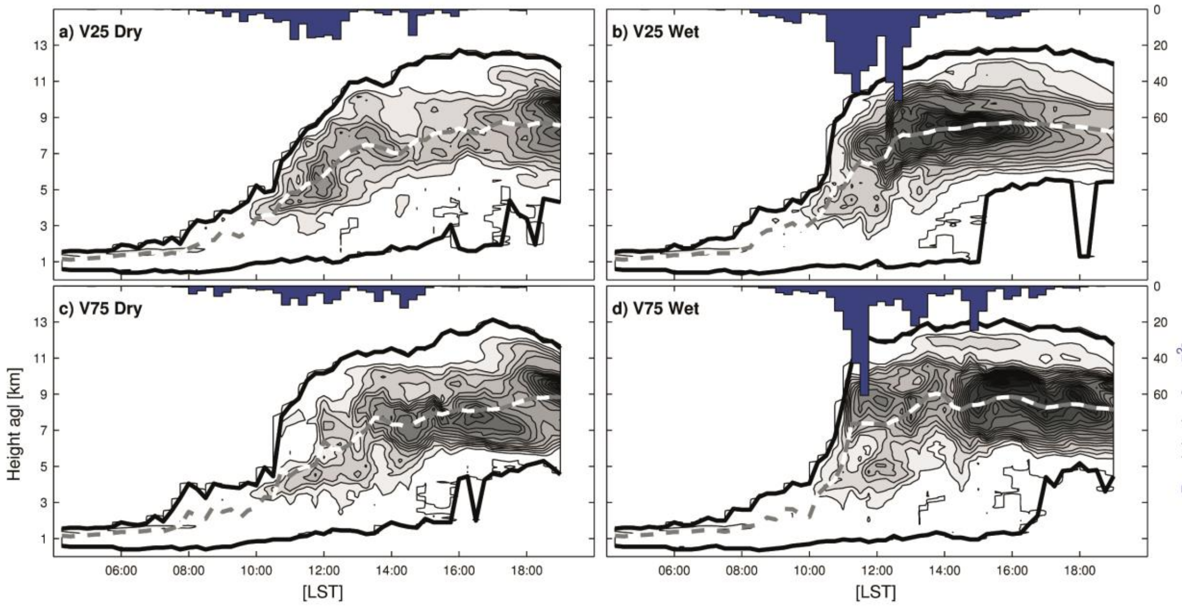

Figure AVII-3: Simulated convection development and deposited precipitation (blue bars) for a symmetric Tibetan Valley with 150 km width. The black lines indicate cloud base and cloud top in kilometres above ground level; the dashed line shows the centre of the cloud mass and the contours give the mean cloud water and ice concentration integrated over the model domain. V25 and V75 refer to 25% and 75% vegetation cover, while wet and dry indicate initial soil moisture corresponding to 1.0 and 0:5field capacity, respectively. Times are given in local mean time (LMT), which is two hours before Beijing standard time (CST).

Appendix

Contributions on the studies

Study 1: (manuscript) The *Kobresia pygmaea* ecosystem of the Tibetan highlands – origin, functioning and degradation of the world's largest pastoral alpine ecosystem

Review concept: Georg Miehe

Manuscript writing: Georg Miehe, Karsten Wesche **Per-Marten Schleuss**, Elke Seeber, Tobias Biermann

Comments on the manuscript: (all co-authors)

Per-Marten Schleuss: ***medium contribution***

Study 2: (publication) Nitrogen uptake in an alpine *Kobresia* pasture on the Tibetan Plateau: localization by ^{15}N labelling and implications for a vulnerable ecosystem

Study design: **Per-Marten Schleuss**, Yakov Kuzyakov

Field work: **Per-Marten Schleuss**

Laboratory work: **Per Marten Schleuss**

Data analysis: **Per Marten Schleuss**

Data interpretation: **Per Marten Schleuss**, Felix Heitkamp

Manuscript writing: **Per Marten Schleuss**

Comments on the manuscript: (all coauthors)

Per-Marten Schleuss: ***high contribution***

Study 3: (mansuscript) Mechanisms and consequences of Tibetan grassland degradation

Study design: **Per-Marten Schleuss**, Yakov Kuzyakov, Georg Guggenberger

Field work: **Per-Marten Schleuss,** Laura Steingräber

Laboratory work: **Per Marten Schleuss,** Sandra Spielvogel + student laboratory assistants

Data analysis: **Per Marten Schleuss**

Data interpretation: **Per Marten Schleuss**, Felix Heitkamp, Yakov Kuzyakov

Manuscript writing: **Per Marten Schleuss**

Comments on the manuscript: (all coauthors)

Per-Marten Schleuss: ***high contribution***

Study 4: (manuscript) Degradation-driven nutrient losses of the Tibetan *Kobresia* pastures

Study design: **Per-Marten Schleuss**, Yakov Kuzyakov, Georg Guggenberger
Field work: **Per-Marten Schleuss,** Laura Steingräber
Laboratory work: **Per Marten Schleuss** + student laboratory assistants
Data analysis: **Per Marten Schleuss**
Data interpretation: **Per Marten Schleuss**, Kyle Mason Jones, Yakov Kuzyakov
Manuscript writing: **Per Marten Schleuss**
Comments on the manuscript: (all coauthors)
Per-Marten Schleuss: ***high contribution***

Study 5: (publication) Carbon and nitrogen losses from soil depend on degradation of Tibetan Kobresia pastures

Study design: Shibin Liu, **Per-Marten Schleuss**,
Field work: **Per-Marten Schleuss**
Laboratory work: Shibin Liu
Data analysis: Shibin Liu
Data interpretation: Shbin Liu, **Per Marten Schleuss**, Yakov Kuzyakov
Manuscript writing: Shibin Liu, **Per Marten Schleuss**
Comments on the manuscript: (all coauthors)
Per-Marten Schleuss: ***medium - high contribution***

Study 6: (manuscript) *Kobresia pygmaea* pasture degradation and its response to increasing N deposition

Study design: Shibin Liu, **Per-Marten Schleuss**,
Field work: **Per-Marten Schleuss**
Laboratory work: Shibin Liu
Data analysis: Shibin Liu
Data interpretation: Shbin Liu, **Per Marten Schleuss,** Yakov Kuzyakov
Manuscript writing: Shibin Liu, **Per Marten Schleuss**
Comments on the manuscript: (all coauthors)
Per-Marten Schleuss: ***medium - high contribution***

Abstract 1: Effect of overgrazing on carbon and nitrogen dynamics and its implication for alpine pasture degradation on the Tibetan Plateau

Study design: **Per-Marten Schleuss**, Elke Seeber, Kartsen Wesche, Georg Miehe, Yakov Kuzyakov
Field work: **Per-Marten Schleuss,** Elke Seeber
Laboratory work: **Per Marten Schleuss,** Elke Seeber, Shibin Liu, Lukas Lehnert
Data analysis: **Per Marten Schleuss,** Elke Seeber
Data interpretation: **Per Marten Schleuss**, Elke Seeber
Manuscript writing: in preparation
Comments on the manuscript: in preparation
Per-Marten Schleuss: ***high contribution***

Abstract 2: Clipping and shading alter NH4+ uptake by plants in Tibetan Kobresia grasslands

Study design: Xingliang Xu, Sun Yue
Field work: Sun Yue, **Per-Marten Schleuss**
Laboratory work: Sun Yue
Data analysis: Sun Yue
Data interpretation: Sun Yue, Xingliang Xu, **Per-Marten Schleuss**
Manuscript writing: in preparation
Comments on the manuscript: in preparation
Per-Marten Schleuss: ***low - medium contribution***

Abstract 3: Pasture management controls soil organic matter stocks, properties, and biochemical functioning in Tibetan grasslands

Study design: Sandra Spielvogel, **Per-Marten Schleuss**, Yakov Kuzyakov, Georg Miehe
Field work: Sandra Spielvogel, **Per-Marten Schleuss**, Laura Steingräber
Laboratory work: Andreas Breidenbach, Tilman de la Haye, **Per-Marten Schleuss**, Sandra Spielvogel
Data analysis: Andreas Breidenbach, Tilman de la Haye, **Per-Marten Schleuss**
Data interpretation: Sandra Spielvogel
Comments on the manuscript: in preparation
Per-Marten Schleuss: ***low - medium contribution***

Abstract 4: A literature review on SOC and nutrient losses with intensified pasture degradation on the Tibetan Plateau

Review concept: Per-Marten Schleuss, Shibin Liu
Data analysis: Shibin Liu
Data interpretation: Shibin Liu, Per- Marten Schleuss
Manuscript writing: in preparation
Comments on the manuscript: in preparation
Per-Marten Schleuss: ***medium to high contribution***

Abstract 5: Degradation increase response of priming effects to temperature in Tibetan alpine grasslands

Study design: Sun Yue, Qianru Li, **Per-Marten Schleuss,** Yakov Kuzyakov, Xingliang Xu
Field work: **Per-Marten Schleuss**
Laboratory work: Sun Yue, Qianru Li
Data analysis: Sun Yue, Qianru Li
Data interpretation: Sun Yue, Qianru Li, **Per-Marten Schleuss**
Manuscript writing: in preparation
Comments on the manuscript: in preparation
Per-Marten Schleuss: ***low - medium contribution***

Abstract 6: Fate of organic and inorganic nitrogen in crusted and non-crusted Kobresia grasslands

Study design: Sebastian Unteregelsbacher, Silke Hafner, Yakov Kuzyakov
Field work: Sebastian Unteregelsbacher, Silke Hafner
Laboratory work: Sebastian Unteregelsbacher
Data analysis: Li Zhang
Data interpretation: Li Zhang, Xingliang Xu
Manuscript writing: Li Zhang, Xingliang Xu, **Per-Marten Schleuss**
Comments on the manuscript: Xingliang Xu, **Per-Marten Schleuss**, Yakov Kuzyakov
Per-Marten Schleuss: ***low contribution***

Abstract 7: Pasture degradation modifies the water and carbon cycles of the Tibetan highlands

Study design: Wolfgang Babel, Tobias Biermann, Thomas Foken
Field work: PhD and Master students of the *Kobresia* Cluster
Laboratory work: PhD and Master students of the *Kobresia* Cluster
Data analysis: Wolfgang Babel, Tobias Biermann, Heinz Coners, Eva Falge Johannes Ingrisch
Data interpretation: Wolfgang Babel, Tobias Biermann, Thomas Foken
Manuscript writing: Wolfgang Babel, Tobias Biermann, Thomas Foken
Comments on the manuscript: (all coauthors)
Per-Marten Schleuss: ***low contribution***

Curriculum Vitae

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EXPERTISE

land use changes
plant-soil-system
grassland ecosystems
alpine environments
carbon and nutrient cycling
forest ecosystems
grassland degradation
stable isotopes

PROFESSIONAL EXPERIENCE

May 2013 - up to now	PhD Student (GAUSS Programme) Faculty of Biology and Psychology University of Göttingen
Jan. 2013 – Jan. 2016	Research Associate Dept. of Soil Science of Temperate Ecosystems University of Göttingen
Jun. 2012 – Sep. 2012	Student Research Assistant Dept. of Soil Science of Temperate Ecosystems University of Göttingen
Aug. 2008 – Aug. 2009	Student Research Assistant Dept. of Landscape Ecology University of Göttingen

Education

May 2013 - up to now	PhD Student (GAUSS Programme) Faculty of Biology and Psychology University of Göttingen
Oct. 2005 – Jan. 2013	Geography studies (Diploma) University of Göttingen
(Sep. 2004 – Jun. 2005)	Community Service (Kappelner Werkstätten)
Aug. 1995 – Jun. 2004	High School Klaus-Harms Schule Kappeln (Gymnasium)

Per

Per-Marten Schleuss Göttingen, 15.01.2016

SCIENTIFIC CONTRIBUTIONS

Peer reviewed publications:

Schleuss P.-M., Heitkamp F., Leuschner C., Fender A.-C., Jungkunst H.F. (2014): Higher subsoil carbon storage in species-rich than species-poor temperate forests. *Environmental Research Letters* 9: 014007 (Open Access)

Babel W., Biermann T., Coners H., Falge E., Seeber E., Ingrisch J., **Schleuss P.-M**., Gerken T., Leonbacher J., Leipold T., Willinghöfer S., Spielvogel S., Li X., Xu X., Sun Y., Zhang L., Yang Y., Ma Y., Wesche K., Graf H.-F., Leuschner C., Guggenberger G., Kuzyakov Y., Miehe G., and Foken T. (2014). Pasture degradation modifies the water and carbon cycles of the Tibetan highlands. *Biogeosciences* 11: 6633-6656.

Schleuss P.-M., Heitkamp F., Sun Y., Miehe G., Xu X., Kuzyakov Y. (2015). Nitrogen uptake in an alpine Kobresia pasture on the Tibetan plateau: Localization by ^{15}N labeling and implications for a vulnerable ecosystem. *Ecosystems*, 18: 946-957.

Liu S., **Schleuss P.M.**, Kuzyakov Y. 2016. Carbon and nitrogen losses from soil depend on degradation of Tibetan *Kobresia* pastures. *Land Degradation & Development* (online version). DOI: 10.1002/ldr.2522.

Zhang L., Unteregelsbacher S., Hafner S., Xu X., **Schleuss P-M.**, Miehe G., Kuzyakov Y. 2016 Different fate of organic and inorganic nitrogen in degraded and non degraded patches of Kobresia grasslands. *Land Degradation and Development* (accepted)

Submitted publications:

Liu S., **Schleuss P.M.**, Kuzyakov Y. (submitted) *Kobresia pygmaea* pasture degradation and its response to N deposition. *Land Degradation and Development*

Non-peer reviewed publications:

Biermann T., Seeber E., **Schleuss P-M.**, Willinghöfer S., Leonbacher J., Schützenmeister K., Steingräber L., Babel W., Coners H., Foken T., Guggenberger G., Kuzyakov Y.,Leuschner C., Miehe G., Wesche K. (2013) Tibet Plateau At-mosphere–Ecology–Glaciology Cluster Joint *Kobresia* Ecosys-tem Experiment: Documentation of the second Intensive Observation Period, Summer 2012 in KEMA, Tibet, Arbeitsergebn.,Univ. Bayreuth, Abt. Mikrometeorol., ISSN 1614-8916, 54, 52 pp

Publications in preparation:

Schleuss P.-M., Miehe G., Lukas Lehnert, Heitkamp H., Seeber S., Yun Wang, Spielvogel S., Xu X., Guggenberger G., Kuzyakov Y. Mechanisms and consequences of Tibetan grassland degradation. (in prep. for *Nature Geoscience)*

Schleuss P.-M., Manson-Jones K., Heitkamp H., Miehe G., Coners H., Seeber S., Willinghöfer S., Spielvogel S., Xu X., Kühn P., Scholten T., Wesche K., Leuschner C., Guggenberger G., Kuzyakov Y. Degradation-driven nutrient losses of the Tibetan *Kobresia* pastures (in prep. for *Global Change Biology)*

Schleuss P-M., Seeber E., Shibin Liu, Lukas Lehnert, Jungkunst H., Miehe G., Guggenberger G., Wesche K., Kuzyakov Y. Effect of overgrazing on carbon and nitrogen dynamics and its implication for alpine pasture degradation on the Tibetan Plateau (in prep.)

Miehe M., **Schleuss P-M.**, Seeber S., Lehnert L., Biermann T., Babel W., Ingrisch J., Wang Y., Willinghöfer S., Hafner S., Unteregelsbacher S., Liu S., Coners H., Leuschner L., Guggenberger G., Kuzyakov Y., Xu X., Spielvogel S., Foken T., Graf H-F., Ma Y., Yang Y., Zhang S., Noltie H. J., Opgenoorth L., Schmidt J., Lai Z., Mosbrugger V., Chen F., Liu J., Wesche K. The dwarfs of the world's largest alpine ecosystem: Kobresia pastures of the Tibetan highlands. (in prep. for *Ecological Monographs)*

Liu Shibin, **Schleuss P-M.,** Kuzyakov Y. A literature review on SOC and nutrient losses with intensified pasture degradation on the Tibetan Plateau (in prep.)

Spielvogel S., de la Haye T., Hüllen J., Deggelmann A., Bange U., **Schleuss P-M.**, Xu X., Kuzyakov Y., Guggenberger G. Physical and chemical protection of grassland soil carbon: Tibetan pasture degradation and soil carbon sequestration capacity in a global context (in prep.)

Spielvogel S., Breidenbach A., de la Haye T., **Schleuss P-M.**, Kuzyakov Y., Guggenberger G. Pasture management controls soil organic matter stocks, properties, and biochemical functioning in Tibetan grasslands (in prep.)

Sun Y., **Schleuss P-M.**, Li Q., Yang, B., Xu X., Kuzyakov Y. Clipping and shading alter NH_4 uptake by plants in Tibeatn *Kobresia* grasslands (in prep.)

Sun Y., Li Q., Xu X., **Schleuss P-M.**, Hua O., Kuzyakov Y., Degradation increase response of priming effects to temperature in Tibeatan alpine grasslands (in prep.)

Talks and posters (first author only):

Schleuss P.M., Manson-Jones K., Heitkamp H., Miehe G., Coners H., Seeber S., Willinghöfer S., Spielvogel S., Xu X., Kühn P., Scholten T., Wesche K., Leuschner C., Guggenberger G., Kuzyakov Y. (2016) Degradation mechanisms and consequences for soil organic carbon stocks in the world´s largest alpine pastoral ecosystem, 05-07.09.2016. 46th Annual meeting of the Ecological Society of Germany, Austria and Switzerland, Marburg, Germany (talk)

Schleuss P.M., (2016) The fate of the world´s largest alpine pastoral ecosystem. Department of Soil Ecology at University of Bayreuth (seminar talk)

Schleuss P.-M., Miehe G., Heitkamp H., Seeber S., Spielvogel S., Xu X., Guggenberger G., Kuzyakov Y. (2015) Intensive SOC loss by degradation of an alpine *Kobresia* pasture on the Tibetan Plateau. European Geoscience Union, 12.04-17.04.2015 – Vienna, Austria (talk)

Schleuss P.-M., Heitkamp H., Sun Y., Xu X., Miehe G., Kuzyakov Y. (2015): Nitrogen uptake in an alpine *Kobresia* pasture on the Tibetan Plateau. Annual meeting of the German Soil Science

Society (DBG), 07.09-09.09.2016 – Munich, Germany (talk)

Schleuss, P-M., Heitkamp F., Jungkunst H-F. (2013) Doest tree species diversity affect mineral SOC storage in a near-natural beech forest of the Hainich National Park? Annual meeting of the German Soil Science Society (DBG), 07.09-12.09.2013 – Rostock, Germany (poster)

Schleuss P-M., and Kuzyakov Y. (2014) Localization of nitrogen uptake in a Tibetan alpine *Kobresia* pasture. Biogeomon, 13.07-17.07.2014 – Bayreuth, Germany (poster)

Schleuss P.-M., Miehe G., Heitkamp H., Seeber S., Spielvogel S., Xu X., Guggenberger G., Kuzyakov Y. (2014) Mechanisms and consequences of tibetan grassland degradation. Third Pole Environment (TPE), 08.12-09-12.2014 – Berlin, Germany (poster)

Schleuss P.-M., Miehe G., Heitkamp H., Seeber S., Spielvogel S., Xu X., Guggenberger G., Kuzyakov Y. (2015) Mechanisms od soi degradation and ist consequences for SOC storage on alpine grasslands of the Tibetan Plateau. 5th symposium on Soil Organic Matter, 20.09-24.09.2015 – Göttingen, Germany (poster)

Workshops:

TiP Kobresia Workshop I. 19.03-21.03.2012 – Marburg, Germany Workshop on Stable Isotops in Soil Science. German Soil Science Society (DBG). 18.04-21.04.2012 – Göttingen, Germany

TiP&BMBF PhD meeting. 14.01-18.01.2013 – Oberjoch, Germany

TiP Kobresia Workshop II. 27.03-28.03.2013 – Göttingen, Germany

Joint Kobresia Excursion. 11.07-04.08.2015. From Xining to Lhasa crossing the whole Kobresia ecosystem.

Declarations

1. I, hereby, declare that this Ph.D. dissertation has not been presented to any other examining body either in its present or a similar form.

Furthermore, I also affirm that I have not applied for a Ph.D. at any other higher school of education.

Göttingen,

....

(Signature)

2. I, hereby, solemnly declare that this dissertation was undertaken independently and without any unauthorized aid.

Göttingen,

....

(Signature)