# An investigation into the *Kobresia pygmaea* ecotone of the Tibetan Plateau

# - From species to community ecology -

## Dissertation (kumulativ)

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Tso Ngonpo (Lake Kokonor)

The northern grasslands abound in sheep,
Cattle and sheep thrive on green pastures.

And their fat and sheen improve
Because of the pastures.

*Second verse, Unknown artist*

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## SUMMARY

Alpine ecosystems have attracted increasing attention in recent years due to their potential importance to global carbon cycles as well as their vulnerability to changes in land-use and global climate. The Tibetan Plateau hosts the largest and highest alpine range in the world. The humid south-eastern section is mainly covered by *Kobresia pygmaea* C.B.Clarke ex Hook.f. dominated pastures, which extend over 450,000 $km^2$. The pastures are most notable for three reasons: (1) they extend across an elevational range of approximately 3000 m, (2) a single sedge, *K. pygmaea*, constitutes up to 98% of the total plant cover, and (3) they built up a root turf that preserves the underlying soil from erosion and which sequestrates huge amounts of carbon. However, due to the remote location and logistical constraints, only a few studies are available from the truly alpine *K. pygmaea* populations situated far above 4000 m a.s.l. This thesis aims to close the knowledge gap and provide new insights into the ecology of the dominant species *K. pygmaea* within its alpine core habitat. The abiotic and biotic factors influencing the ecosystem are also explored through the various studies presented in the thesis. The investigations were mainly conducted at the alpine site in Kema in the Nagqu prefecture of Xizang, and on a gravel terrace of the Huang He near Xinghai in Qinghai province, which is located within the montane belt. Where possible, comparisons of the alpine and montane sites are presented along with a host of other detailed findings developed through a total of six manuscripts prepared for publication in international journals.

The first supporting study laid the genetic foundations for subsequent manuscripts and assessed the basic chromosome numbers and the role of polyploidy in the genus *Kobresia*. Therefore, chromosome counts were conducted and results combined with data from available literature. New genetic tools were established, including microsatellite markers for the key species *K. pygmaea* as well as protocols for DNA analysis and flow cytometry that account for the low amount of plant tissue typically available for analyses (~3-8 mg). *Kobresia pygmaea* has $2n = 4x = 64$ chromosomes and is tetraploid. Ploidy of congeners ranged from di- to hexa- or even heptaploidy. The study therefore provided basic knowledge on cytological and genetic features of the genus *Kobresia* and negotiated the methodological constraints attributed to small alpine individuals.

The objective of the second main study was to investigate the reproductive and cytological characteristics of *K. pygmaea* at the alpine key site in Kema. In accordance with expectations derived from sedges in the Alps, a molecular approach revealed large clones as well as overall high genetic diversity introduced by consecutive events of sexual reproduction under favourable conditions, and probably over several centuries of the populations' persistence. *Kobresia pygmaea* produced high numbers of inflorescences and viable seeds but germination rates were low. To

obtain dominance in the plant communities, *K. pygmaea* benefited from its longevity, mixed reproduction strategy, long-term seed bank and polyploidy.

The aim of the third study was to test whether the reproductive characteristics of *K. pygmaea* were only attributable to a limited elevational range or to the species' distribution range. The experiment along an elevational gradient in Qinghai revealed higher genetic and clonal diversity, and thus sexual reproduction, at the lower and upper limits, which were mainly influenced by enhanced availability of water, open substrate for germination and, probably, lower grazing intensities. In addition, the mode of reproduction (clonal *versus* sexual) in *K. pygmaea* shaped species' abundance and thereby community composition, with extensive clonal reproduction at intermediate altitudes leading to overall species-poor communities.

The forth study was conducted to assess the impacts of water and nutrient availability as well as grazing on pastoral characteristics and plant performance, including soil nutrient contents, above- and below-ground biomass, tissue nutrient contents and reproduction of *K. pygmaea* by way of a nutrient addition experiment, which was conducted over three consecutive years and under two grazing treatments. Productivity of *K. pygmaea* and herbs was mainly limited by nitrogen and co-limited by phosphorus. Inter-annual variability in climate was high but only affected above-ground biomass production in fertilized plots. Fertilization enhanced nutrient availability in the soil but did not affect the large below-ground biomass pools. Tissue nutrient contents of *K. pygmaea* and herbs, but not of other plant functional groups, increased after nutrient addition. The study proved that nutrient availability, rather than climate mainly restricts ecosystem productivity.

The last two studies aimed to investigate carbon fluxes and cycles of *Kobresia* pastures in relation to grazing cessation. $^{13}CO_2$ pulse labeling and coupling with eddy covariance measurements revealed no effects of grazing cessation within one growing season at the alpine pasture in Kema. Long-term grazing exclusion shifted assimilate allocation from below- to above-ground pools and fostered turf degradation in the montane pasture in Xinghai. In the alpine *Kobresia* pasture, roots and soil were of equal importance to carbon storage and cycling, while in montane pastures it was mainly just soil. In any case, degradation of *Kobresia* pastures can affect carbon cycles, and probably at the global scale.

This thesis emphasizes the importance of the species *K. pygmaea* for the *Kobresia* ecosystem over a wide altitudinal range, but it also proves that results on species and ecosystem properties are not transferable between elevational belts without further investigation. Moreover, the findings partly support concerns about the degradation of the *Kobresia* ecosystem, as this will have severe consequences on regional, and probably global, climate and carbon cycles.

# ZUSAMMENFASSUNG

Alpine Ökosysteme rücken zunehmend in den Focus der Öffentlichkeit, einerseits aufgrund ihrer potentiellen Bedeutung für den globalen Kohlenstoffkreislauf, aber auch aufgrund ihrer Anfälligkeit gegenüber Änderungen in der Landnutzung und des globalen Klimas. Das Hochland von Tibet ist das größte und höchste alpine Plateau der Welt. Der humide Südosten wird vorrangig durch von *Kobresia pygmaea* C.B.Clarke ex Hook.f. dominierten Weiden bedeckt, die sich über 450.000 $km^2$ erstrecken. Diese zeichnen sich durch drei Merkmale aus: (1) sie erstrecken sich über einen Höhengradienten von ca. 3000 m, (2) eine einzelne Segge, *K. pygmaea*, stellt bis zu 98% der gesamten Pflanzendecke und (3) sie bilden einen dichten Wurzelhorizont, welcher den mineralischen Unterboden vor Erosion schützt und große Mengen Kohlenstoff bindet und speichert. Trotz der großen Bedeutung dieses Ökosystems gibt es aufgrund der abgelegenen Lage und logistischen Herausforderungen nur wenige Studien, die in alpinen Höhenlagen weit über 4000 m ü.M. durchgeführt wurden. Die vorliegende Dissertation versucht diese Lücke zu schließen und neue Informationen über die Ökologie der dominanten Art *K. pygmaea* in ihrem alpinen Kernhabitat zu erlangen. Des Weiteren wurden abiotische und biotische Faktoren untersucht, die dieses Ökosystem beeinflussen. Die Untersuchungen unter alpinen Bedingungen wurden in Kema in der Nagqu Präfektur (Autonome Region Tibet) vorgenommen, während Studien in der montanen Stufe vorrangig auf einer Schotterterrasse des Huang He in der Nähe von Xinghai in der Provinz Qinghai durchgeführt wurden. Soweit möglich, wurden Vergleiche der alpinen und montanen Stufe unternommen. Weitere Einzelheiten sind in sechs Manuskripten zusammengefasst, die für die Publikation in internationalen Zeitschriften vorgesehen sind.

Die erste Studie legt die genetischen und methodischen Grundlagen für alle weiteren Studien und untersucht die Basischromosomenzahlen und die Bedeutung von Polyploidie in der Gattung *Kobresia*. Dafür wurden Chromosomenzählungen durchgeführt und die Ergebnisse mit Literaturdaten kombiniert. Weiterhin wurden für die wichtigste Art, *K. pygmaea*, neue Mikrosatelliten-Marker etabliert, sowie Protokolle entwickelt, die die DNA-Analyse und Durchflusscytometrie dieser sehr kleinen Art (~3-8 mg pro Individuum) ermöglichen. *Kobresia pygmaea* hat einen Chromosomensatz von $2n = 4x = 64$ und ist vorrangig tetraploid. Die Ploidiestufen innerhalb der Gattung *Kobresia* reichten von di- bis hexa- oder sogar heptaploid. Diese Studie lieferte Erkenntnisse über cytologische und genetische Merkmale von *K. pygmaea* und weiteren Arten der Gattung. Weiterhin konnten methodische Schwierigkeiten aufgrund der geringen Mengen an verfügbaren Pflanzenmaterials ausgeräumt und angepasste Methoden für weiterführende Untersuchungen etabliert werden.

Das Ziel der zweiten Studie war die Erfassung der reproduktiven und cytologischen Eigenschaften von *K. pygmaea* im alpinen Kernhabitat in Kema. Übereinstimmend mit früheren Studien an

Seggen aus den Alpen, zeigte ein molekularer Ansatz nicht nur große und ineinander verwachsenen Klone, sondern auch eine insgesamt hohe genetische Vielfalt. Diese ergab sich vermutlich durch aufeinander folgende sexuelle Reproduktion unter günstigen Bedingungen über die langen Zeiträume, vermutlich Jahrhunderte, seit der Etablierung der Population. *Kobresia pygmaea* produzierte eine hohe Anzahl an Infloreszenzen und keimfähigen Diasporen, wohingegen die Keimraten niedrig waren. Dominanz innerhalb der Pflanzengesellschaft erlangte *K. pygmaea* vermutlich durch ihre Langlebigkeit, die gemischte Reproduktionsstrategie, eine dauerhafte Diasporenbank und Polyploidie.

Die dritte Studie untersuchte, ob diese reproduktiven Eigenschaften nur für einen begrenzten Höhenbereich oder aber für das gesamte Höhenareal der Verbreitung gelten. Die Experimente entlang eines Höhengradienten in Qinghai bewiesen höhere genetische und klonale Diversität und damit sexuelle Reproduktion an den Rändern der Höhenausdehnung, was vor allem auf veränderte Umwelteinflüsse wie Wasser- und Substratverfügbarkeit für die erfolgreiche Keimung, sowie vermutlich geringere Beweidungsintensitäten zurückzuführen war. Des Weiteren bestimmte die Art der Reproduktion (klonal *versus* sexuell) die Häufigkeit von *K. pygmaea* und beeinflusste somit die Zusammensetzung der gesamten Pflanzengesellschaft, wobei ein hoher Anteil an klonalem Wachstum zu insgesamt artenarmen Gesellschaften führte.

Die vierte Studie wurde durchgeführt um den Einfluss von Wasser- und Nährstoffverfügbarkeit sowie Beweidung auf die Nährstoffgehalte im Boden, die Produktion von unter- und oberirdischer Biomasse, den Nährstoffgehalt der Biomasse und die Reproduktion von *K. pygmaea* abzuschätzen. Dafür wurde ein kombiniertes Dünge- und Beweidungsexperiment über drei aufeinander folgende Jahre hinweg durchgeführt. Die Produktivität von *K. pygmaea* und dikotylen Kräutern wurde vor allem von Stickstoff begrenzt und war co-limitiert durch Phosphor. Die Variabilität der klimatischen Faktoren zwischen den Untersuchungsjahren war hoch aber beeinflusste die Produktion von oberirdischer Biomasse nur in gedüngten Plots. Düngung erhöhte die Nährstoffverfügbarkeit des Bodens, hatte aber keinen Einfluss auf die unterirdische Biomasse. Der Nährstoffgehalt der Biomasse stieg bei *K. pygmaea* und Kräutern nach der Düngung an, nicht aber bei den anderen funktionellen Pflanzengruppen. Diese Studie bewies, dass nicht die klimatischen Bedingungen sondern Nährstoffmangel die Produktivität der *Kobresia*-Weiden begrenzt.

Ziel der letzten beiden Studien war es die Kohlenstoffkreisläufe und -flüsse in beweideten und unbeweideten *Kobresia*-Matten zu bestimmen und zu vergleichen. Eine Kombination aus $^{13}CO_2$ Puls-Markierungen und Eddy-Kovarianz-Messungen konnte keine Effekte des Beweidungsausschlusses innerhalb einer Vegetationsperiode in alpinen *Kobresia*-Matten in Kema nachweisen. Auszäunung über längere Zeiträume in der montanen Stufe bei Xinghai verschob die Kohlenstoffspeicherung hin zur oberirdischen Biomasse, während sich die Wurzelbiomasse des wichtigen Wurzelhorizontes verringerte. Des Weiteren sind in der alpinen Stufe die Wurzeln und der Mineralboden von etwa gleicher Bedeutung für die Kohlenstoffzyklen und -speicherung, während es in der montanen Stufe hauptsächlich der Mineralboden ist. Eine Zerstörung der *Kobresia*-Weiden und damit des Wurzelfilzes könnte die globalen Kohlenstoffkreisläufe beeinflussen.

Diese Arbeit hebt die Bedeutung von *K. pygmaea* für die *Kobresia*-Weiden hervor, belegt aber auch, dass die Ergebnisse von unterschiedlichen Höhenstufen nicht uneingeschränkt übertragbar sind. Die Studie belegt, dass die zunehmende Besorgnis über die Zerstörung dieses Ökosystems gerechtfertigt ist, da bei Verlust des Wurzelfilzes mit weitreichenden Folgen sowohl für regionale, als auch globale Kohlenstoffzyklen, sowie das Klima zu rechnen ist.

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# 摘要

由于在全球碳循环过程的重要性和对土地利用变化和全球气候变化的敏感性，高寒生态系统在近年的研究中受到越来越多的关注。青藏高原拥有世界上最大和最高的高寒生态系统，而东南部地区广泛分布的高山嵩草 (*Kobresia pygmaea* C.B.Clarke ex Hook.f.) 草场面积超过 450,000 $km^2$。高山嵩草草场具有以下三个特点：1）海拔分布范围在 3000 m 以上；2）以单一的莎草科物种，高山嵩草为优势物种，其覆盖度可高达 98 %；3）根系联接形成的草皮层能够防止土壤侵蚀，吸附并储存大量的碳。然而，由于地理位置的偏僻和各种野外工作的困难性，对海拔在 4000 m 以上的高山嵩草居群的研究却很少。该论文的主要目标是填补这一研究领域的空白，为高山嵩草在其核心分布区的生态学特征提供新的见解，并进一步分析生物及非生物因子对高山嵩草生态系统的影响。研究地点包括西藏自治区那曲县的克玛村，青海省兴海县黄河的堆积台地，并对高海拔和低海拔的居群进行了比较。具体研究结果通过六篇文章分别发表或准备发表在国际期刊中。

第一篇文章研究了嵩草属植物的染色体数目和多倍性特点，为后期研究提供遗传学基础。染色体数目综合了本人实验和其他已发表的研究结果。进一步的遗传学研究包括为关键物种高山嵩草建立微卫星标记，为其 DNA 分析，以及用少量植物材料（约 3-8 mg）进行流式细胞仪分析提供经验性研究方法。高山嵩草的染色体数量为 $2n = 4x = 64$，为四倍体。同源多倍体包括二倍体，六倍体和七倍体。该研究揭示了嵩草属植物的细胞学及遗传学特性，并进一步讨论了导致高海拔植株小型化的限制因子。

第二篇研究的重点是那曲县克玛村高海拔高山嵩草居群的繁殖和细胞学特性。结果与阿尔卑斯山区分布的莎草相似，高山嵩草保持较大的克隆，但总体仍保留较高的遗传多样性。这是由于在可能的几个世纪的居群发展中，有利环境条件下发生的连续的有性繁殖事件保持了居群的遗传多样性。高山嵩草能产生大量的花序和有活性的种子，但种子的萌发率很低。较长的寿命，混合型繁殖策略，长期的种子库以及丰富的多倍性为其居群在植物群落中成为优势提供了有利条件。

第三篇研究讨论了高山嵩草的繁殖策略是否受海拔分布的限制，或是在整个分布区都具有一致规律。在青海省沿海拔梯度取样和实验的结果证明，较高的遗传和克隆多样性（即有性繁殖）在较低和较高海拔存在，主要原因为嵩草种子萌发所需的水分和立地条件在低海拔和高海拔较为优越，而较低的放牧压力也可能是原因之一。同时，对

克隆和有性繁殖权衡的结果导致群落中高山嵩草大量进行克隆繁殖，也塑造了该植物群落由单一物种占优势，而植物群落多样性较低的特性。

第四篇研究通过连续三年，两种放牧处理对水分和养分有效性，以及放牧对嵩草草场土壤养分，地上和地下生物量，植物养分以及高山嵩草繁殖特性的影响进行了探讨。连续施肥实验结果表明，高山嵩草及其他草本物种的生物量主要受氮的限制，同时也受磷的限制。而气候的年际变化较大也导致较高的地上生物量的年际变化。施肥能够增加土壤的养分有效性，但对地下生物量并无影响。高山嵩草和草本的植物养分在施肥后增加，但其他植物功能群并未产生变化。该研究证实养分而并非水分有效性是限制生态系统生产力的主要因素。

最后两篇研究关注禁牧对嵩草草场碳循环的影响。$^{13}CO_2$ 脉冲标记与涡度相关研究表明在海拔较高的高寒草甸样地 Kema，一个生长季的禁牧对碳循环没有影响。而在海拔相对较低的山地草场兴海，长期的禁牧则促使碳 同化物从地下向地上转移，并导致草皮层的退化。在高寒嵩草草场，根系和土壤对碳储存和碳循环具有同等的重要性，而土壤则在山地草地中发挥主要作用。无论如 何，嵩草草场的退化影响碳循环过程，影响甚至可能在全球尺度上发挥作用。

这篇论文强调了高山嵩草这一物种对嵩草草地生态系统的重要性，通过对比不同海拔的居群，证明物种和生态系统特性都不具有统一的规律，而是受海拔的限制。此外，研究还揭示嵩草生态系统的退化将对部分区域或全球气候及碳循环产生严重的影响。

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# CHAPTER 1

General introduction

# GENERAL INTRODUCTION

## Grassland ecosystems

Grassland ecosystems cover between 30 and 40% of the Earth's non-ice-covered terrestrial surface (Suttie *et al.* 2005; Dixon *et al.* 2014). Their high biodiversity status is underlined as they represent a quarter of the terrestrial eco-regions identified as being *outstandingly diverse* (White *et al.* 2000). Almost all grasslands are subject to some form of management and land-use, as they provide forage for livestock and support animal husbandry in the production of e.g. meat, milk and wool. Around 800 million people live and rely on rangelands worldwide (White *et al.* 2000). Grassland productivity is, however, generally assumed to be water and nutrient limited (Sala *et al.* 1988; Sundriyal & Joshi 1992; LeBauer & Treseder 2008).

Grasslands are almost as important as forests with respect to the greenhouse gas and carbon cycling at the global scale (Minami *et al.* 1993; Jackson *et al.* 2002). In this context, it is alarming that about half of the global grasslands are identified as being lightly to moderately degraded, with at least 5% considered to be strongly degraded (White *et al.* 2000). However, spatial variability in degradation pattern is high. Human impact (e.g. fire, fragmentation, introduction of non-native species), land-use changes (e.g. grazing intensification, land cultivation) and climate change (e.g. desertification, warming) are the most important factors affecting the capacity of grasslands to continue providing vital ecosystem services (White *et al.* 2000).

Sub-Saharan Africa and Asia host the largest grassland areas with 14.5 and 8.9 million $km^2$, respectively, while China alone has nearly 4 million $km^2$, of which more than 40% are located on the Tibetan Plateau (White *et al.* 2000).

## Alpine grasslands of the Tibetan Plateau

About half of the Tibetan highlands are located above 4500 m a.s.l., where the two largest alpine ecosystems in the world predominate: the alpine steppes of the arid south-western plateau, covering some 800,000 $km^2$, and the *Kobresia pygmaea* C.B.Clarke ex Hook.f. dominated pastures (hereafter referred to as *Kobresia* pastures) of the more humid eastern plateau, which extend across 450,000 $km^2$ (Miehe *et al.* 2011). Given the short growing season of the region and the associated lack of profitable crop farming, the livelihoods of around five million pastoralists are dependent on forage supply from the grasslands, which sustain around 12 million yaks and 30 million goats and sheep (Suttie *et al.* 2005).

*Stipa* species dominate the alpine steppes, but total plant cover rarely exceeds 10 to 30% and productivity is low (Suttie *et al.* 2005). In contrast, *Kobresia* pastures have a closed vegetation cover and provide high quality forage (Long *et al.* 1999; Holzner & Kriechbaum 2000). Stocking rates at *Kobresia* pastures in the Qinghai region range from 28 to 70 animals per $km^2$, while alpine steppes host 8 to 9 animals per $km^2$ only (Schaller 1998).

*Kobresia* pastures are of particular importance due to their production of root turf (Rhizomull; Kaiser *et al.* 2008), which mainly consists of roots and rhizomes of *Kobresia pygmaea* mixed with amorphous humus and minerogenic matter (Kaiser 2007). The turf is particularly resistant to trampling and it protects vast areas of the Tibetan Plateau from soil erosion, including the headwater regions of the major Asian river systems such as the Huang He, Yangtze, Mekong, Salween and Brahmaputra (Miehe *et al.* 2008b). As a consequence of this turf formation, they have a high potential for carbon sequestration: Ni (2002) estimated that a quarter of the organic carbon stored in China's grasslands is fixed within alpine *Kobresia* pastures. As such, they influence the carbon cycle, and potentially climate, at a global level (Ni 2002; Zhang *et al.* 2009; Babel *et al.* 2014).

However, pasture health and the ability to maintain ecosystem services is vulnerable and was negatively affected by intensification of land-use, anthropogenic impact and global change, especially within the last ~50 years (Miehe *et al.* 2008b). The traditional land-use of transhumant herding has shifted in recent decades toward sedentarization of herdsman and the privatization of local pastures, with an attendant increase in stocking rates (Suttie *et al.* 2005; Miehe *et al.* 2008b). When coupled with global change, such shifts in land-use practise have resulted in serious levels of rangeland degradation (Niu 1999; Wei *et al.* 2005; Zhou *et al.* 2005; Harris 2010; Babel *et al.* 2014). With respect to *Kobresia* dominated pastures, the total area in the headwater regions of the Yangtze and Yellow Rivers decreased considerably between 1967 and 2000 (Zhou *et al.* 2005; Cui & Graf 2009; Wang *et al.* 2011). To counter such degradation, national authorities together with scientists have implemented measures such as fencing, pasture privatization or reseeding with indigenous grasses, each of which has had variable success (Li *et al.* 1996; Wu & Du 2007; Wang *et al.* 2008).

Perhaps not the most obvious consequences of land use, but certainly one of the most lasting effects, are changes in soil conditions. Over the centuries, the pastoral use of Tibetan grasslands and associated removal of above-ground biomass by wild herbivores (larger ungulates, small mammals) and livestock (mainly yak, goat, sheep), has led to a translocation of nutrients (Gao *et al.* 2008; Bagchi & Ritchie 2010). A lack of alternative fuel for cooking and heating resulted in the widespread collection of animal droppings, especially of yak dung from the range, but also sheep and goat dung from night and winter shelters (Rhode *et al.* 2007). Such long term practice has raised concerns over increasing nutrient limitation for reproductive traits of grassland species and ecosystem productivity. In alpine ecosystems, nitrogen is assumed to be particularly limiting to plant growth, while phosphorus and potassium are more widely available due to rock weathering (Walker & Syers 1976; Körner 2003; Gao *et al.* 2004). However, studies including single and combined application of nutrients, which allows for the assessment of co-limitations, are scarce. Additionally, on the Tibetan Plateau and in alpine habitats in general, productivity is restricted by climatic constraints such as low temperatures and high solar irradiation (Piao *et al.* 2006; Wang *et al.* 2008; Li *et al.* 2011).

Compared to soil conditions, direct effects of grazing on vegetation have received much more attention in the recent literature. The species composition of *Kobresia* pastures ranges from almost pure stands of *K. pygmaea* in well maintained pastures to cushion- and herb-dominated communities or, under heavy degradation, lichen and Cyanophyceae covered turf (Miehe *et al.* 2008b). Depending on the topography, *Kobresia* pastures are assumed to be the natural vegetation at altitudes above 4200 to 4700 m above sea level (a.s.l.) (Kaiser 2007), while stands at lower elevations are presumably secondary in the sense that they replace different grasslands, shrubs and occasionally forests, as a consequence of increasing grazing pressure, human impact and perhaps climatic oscillations (Kaiser 2007; Miehe *et al.* 2008b, 2014).

Most experimental studies on the abiotic and biotic actors affecting the *Kobresia* pasture ecosystem have been conducted at sites <4000 m a.s.l. and thus below the assumed natural range, where species diversity and the evenness of replacement communities is high, resulting in an ecosystem response that is the sum of responses by different plant functional groups (e.g. Chen *et al.* 2008; Gao *et al.* 2008; Wang *et al.* 2010; Wang *et al.* 2012; Zhang *et al.* 2013; see exceptions Wei *et al.* 2005; Wang *et al.* 2006). In contrast, within alpine pastures in the natural range, *K. pygmaea* dominance can reach 98% of the total plant cover (Miehe *et al.* 2008b), and species responses are expected to resemble that of ecosystem responses. As such, a major objective of this thesis was to investigate the biology and ecology of *K. pygmaea* within its core alpine range.

**Biology of alpine plants**

Alpine vegetation often comprises perennial species that can become very long-lived, as shown for *Carex curvula* All., and can age up to 2000 years (Steinger *et al.* 1996). Such species are mostly capable of clonal reproduction, which further increases longevity of well-adapted genets, thereby enhancing population stability (Billings & Mooney 1968; Bliss 1971; Körner 2003).

The role of sexual reproduction in clonal species is controversial, with statements ranging from a generally minor role (Widén *et al.* 1994; Körner 2003) to reports of frequent sexual reproduction (McClintock & Waterway 1993; Jacquemyn *et al.* 2006) in clonal plants in general, and especially in alpine species. Nonetheless, sexual reproduction at all stages is undoubtedly limited under harsh alpine conditions, and it is mainly restricted to favourable years. Still, long-distance dispersal for most alpine plant species is by sexual propagules (Totland 1997; Cain *et al.* 2000; Austrheim & Eriksson 2001; Pluess & Stöcklin 2004; Weppler *et al.* 2006), but the specific environmental factors that foster germination and survival are unclear for the majority of species, and particularly those in remote areas or rare species.

Abiotic factors aside, for most plant species, inflorescence and flower production are largely dependent on the prevailing land-use (Kleijn & Steinger 2002; Bläß *et al.* 2008). Most alpine species, such as those of the common genera *Campanula* or *Gentiana,* are insect-pollinated (Körner 2003), but pollination success is often limited by pollinator availability (Totland & Sottocornola 2001). Grasses and sedges mainly use wind as a pollen vector, which is generally assumed to be less effective than other means due to the often limited height of individuals and for stochastical reasons, but it may favour species that occur in high abundance. On the Tibetan Plateau, the most frequent species of all the major vegetation communities share the common feature of wind-pollination (Liu *et al*. 2014). Some species are ambophile, meaning they use a combination of insect and wind pollination (Sun *et al.* 2014). Many mountain species, including mono- and dicotyledons, further have evolved mechanisms to promote outcrossing, such as the temporal or spatial separation of mature pistils and stamens (dichogamy, heterostyly) or incompatibility systems (Lande & Schemske 1985; Ægisdóttir *et al.* 2007), while they retain the capacity to self-pollinate in the absence of mates or pollen vectors (Körner 2003; Duan *et al.* 2007). For instance, all of the 36 species investigated in a study from the subnival belt of the Hengduan Mountains were shown to be dichogamous (Peng *et al.* 2014).

The rate of seed abortion under alpine conditions is often higher than that recorded for sub-alpine habitats (Stenström & Molau 1992; Kudo & Molau 1999). However, colder climate can also improve longevity of mature diaspores (Funes *et al.* 2003), which can promote the development of long-term seed banks and facilitate species resilience. An investigation into seed bank densities in a montane *Kobresia* pasture recorded more than 130,000 seeds per $m^3$ from a total of 24 species (Deng *et al.* 2003), but no data are available on seed longevity. The proportion of seedlings that emerge from seed banks in alpine sites varies strongly, with seed banks in two Austrian alpine plant communities reaching densities of between 1,350 and 1,521 seedlings per $m^2$, while in a Swedish subarctic alpine mountain side, seed banks only gave rise to 37 ± 19 seedling per $m^2$ (Diemer & Prock 1993). Elsewhere, in a *Kobresia humilis* pasture on the Tibetan Plateau, the dominant sedge *K. humilis* (C.A.Mey. ex Trautv.) Serg. only attained 3-4 seedlings per $m^2$ (Deng *et al.* 2001). Once established, saplings commonly persist for decades before becoming reproductive (Morris & Doak 1998). As such, desiccation, low soil moisture, frost damage and needle ice formation are among the most limiting factors for their survival (Billings & Mooney 1968; Forbis 2003).

The clonal and genetic diversity of alpine plants has gained particular importance in conservation science, as responsive and effective adaption is considered essential to ensure stability and resilience in populations' exposed to environmental and climatic changes (Booy *et al.* 2000; Theurillat & Guisan 2001; De Witte & Stöcklin 2010). The often restricted gene flow between distant populations together with strong selection pressures leads to high differentiation between populations, while clonal growth and the often small effective population size are assumed to result in declining within-population diversity in alpine habitats (e.g. Bauert *et al*. 1998). While information on the genetic diversity of species from the largest alpine plateau, the Tibetan plateau, is scarce (see exceptions e.g. Liu *et al.* 2006; Liu *et al.* 2009), recent studies have shown that genetic diversity in alpine species can be comparable to that of lowlands species (Gugerli *et al.* 1999; Pluess & Stöcklin 2004; Zhao *et al.* 2006), and Kuss *et al.* (2008) demonstrated that even populations of less than 50 reproductive individuals can maintain high levels of molecular diversity. Allelic diversity and differentiation patterns can also be influenced by several other factors, such as pollen and seed dispersal ability, species' clonality and associated longevity, time since colonization, life history traits and/or breeding system (e.g. Nybom 2004, Crispo & Hendry 2005; Kuss *et al.* 2008; De Witte & Stöcklin 2010).

A further factor influencing genetic variability is polyploidy, which leads to high levels of heterozygosity and allelic diversity by polysomic inheritance (Soltis & Rieseberg 1986; Soltis & Soltis 1995; Gauthier *et al.* 1998). During the polyploidization process, genetic diversity may result from multiple incorporations of diploid progenitor populations or species (Soltis & Soltis 1999). An increase in allele numbers can lead to changes in gene expression, promoting novel phenotypes that may have a higher tolerance to harsh conditions and are capable of colonizing new environmental niches (Stebbins 1950; Senock *et al.* 1991; Osborn *et al.* 2003). Thus, alpine floras are often dominated by polyploids, which can constitute up to 85% of vascular plant species (Hanelt 1966; Löve & Löve 1967; Petit & Thompson 1999). In contrast, Tibetan highland species are largely described as being diploid, with polyploids occurring in a limited number of genera (e.g. Liu *et al.* 2001; Liu 2004; Nie *et al.* 2005), but for many species, even common and dominant ones, ploidy status is unknown.

**Study species**

*Kobresia* Willdenow is a genus of Cyperaceae that comprises some 54 species with a mainly temperate distribution. In China 44 species occur, 16 of which are endemic (Zhang & Noltie 2010). *Kobresia* species are perennial herbs that spread by short rhizomes. The inflorescences are terminal and flowers are unisexual (Zhang & Noltie 2010). Sedges of the genus are wind-pollinated and seeds are enclosed by an open perigynium, which separates them from the closely related genus *Carex* with a closed perigynium (Yen & Olmstead 2000). Although interspecific hybridization is generally assumed to be low in Cyperaceae, and especially in the closely related genus *Carex* (Heilborn 1939), recent hints towards hybridization within *Kobresia* have been revealed by morphological studies (S. Miehe, pers. communication). Populations of *Kobresia* species have high levels of within-population diversity (Zhao *et al.* 2006).

The genus *Kobresia* is of ecological relevance as species such as *K. pygmaea*, *K. myosuroides* (Vill.) Fiori and *K. humilis* dominate plant communities of cold environments in China and worldwide (Bowman *et al.* 1993; Miehe *et al.* 2008b; Mühlmann & Peintner 2008; Wang *et al.* 2010). Some members of the genus are mycorrhizal (Gai *et al.* 2006; Mühlmann & Peintner 2008).

Of particular importance is the species *Kobresia pygmaea*, endemic to the Tibetan Plateau and adjacent mountain ranges of Bhutan, India, Myanmar, Nepal and Pakistan (Zhang & Noltie 2010). This species is the main constituent of the *Kobresia* pastures. Although this dwarf sedge is of only 2 to 3 cm in height, it colonizes all exposures (Miehe *et al.* 2008b) and habitats ranging from dry, open grasslands and rocky slopes to wet habitats beside rivers (Zhang & Noltie 2010). The species covers an extraordinary wide altitudinal range of nearly 3000 m between the highest outposts on the northern slope of Mt. Everest at 5960 m a.s.l. down to the sunny slopes at 3000 m a.s.l. in the north-eastern declivity on the plateau (Miehe *et al.* 2008b; Zhang & Noltie 2010). As such, *K. pygmaea* covers a hygric range of between

200 mm per year on the western reach to more than 1000 mm per year on the eastern parts of the Tibetan highlands (Miehe *et al.* 2008b).

The growing period ranges from May until dormancy commences in October (Miao *et al.* 2008), while flowering and fruiting takes place in the rainy season between May and September (Zhang & Noltie 2010). Experimental warming led to a phenological delay and reduced inflorescence production (Dorji *et al.* 2013). Inflorescences are dense, ovoid spikes with (mostly) two terminal male, and two to four female, spikelets (Fig. 1). The fruits are one-seeded nutlets of 1.5-2 × 1 mm in size (Zhang & Noltie 2010). About 24% of the diaspore yield is integrated into the soil seed bank (Deng *et al.* 2002). Germination rates are low, ranging from 0 to 13% (Miao *et al.* 2008; Huang *et al.* 2009), while vegetative reproduction by short rhizomes being described as the main reproductive strategy (Deng *et al.* 2002).

*Kobresia pygmaea* is assumed to be highly grazing-tolerant, as below-ground biomass substantially exceeds above-ground biomass, thereby acting as storage for resources and facilitating resprouting (Li *et al.* 1996). Still, the economical importance of this sedge comprises from its value as high nutrient forage, mainly during spring and summer (Long *et al.* 1999; Miao *et al.* 2008).

With respect to the extraordinary economical and ecological importance of *K. pygmaea*, data on its biology are relatively limited. Additionally, data have often been derived from populations below the natural range (e.g. Li *et al.* 1996; Deng *et al.* 2002; Li *et al.* 2003), while there is a general lack of information from altitudes well above 4000 m a.s.l.


**Figure 1:** (a) Fruiting ramets of *Kobresia pygmaea* and (b) yaks grazing on a *Kobresia* pasture (Chapter 3, Supplementary Material).

**Study sites**

Studies were mainly conducted at two key sites: Kema (Tibetan Autonomous Region, China), which represents the core area of *K. pygmaea* distribution at alpine altitudes (Miehe *et al.* 2008b); and near Xinghai (Qinghai, China) situated in the montane belt on the north-eastern plateau.

The study site in Kema lies approximately 20 km south of Nagqu (31.27418°N, 92.11037°E, Fig. 2) at 4450 m a.s.l. in the upper reaches of the Salween River. Here, the use of *Kobresia* pastures ranges from seasonal summer or winter pastures to year-round grazing grounds for yak, sheep and goat. On these pastures, average cover of *Kobresia pygmaea* was about 61%, indicating light to medium degradation. The vegetation community consists of around 45 species, of which monocotyledons such as *Kobresia pusilla* N.A. Ivanova and *Stipa purpurea* Griseb., and herbs such as *Lagotis brachystachya* Maxim., *Lamiophlomis rotata* Kudô, *Lancea tibetica* Hook.f. & Thomson and *Potentilla* species are most frequent. However, only 70% of the landscape is covered by *Kobresia* pastures, while the remainder is dominated by degraded sites without turf cover (22%) and *Kobresia schoenoides* (C.A. Mey.) Steud. swamps (7%; Chapter 3).

The soil is characterized as stagnic (mollic) Cambisol comprising of thin layers of silty loess that overlay metamorphous rocks with occasional morainic and fluvial-lacustrine sediments (Babel *et al.* 2014). The root turf attains a thickness of about 14 cm. The rhizomull acts as an isolation layer, and temperatures below the *Kobresia* mats do not fall much below 0°C, providing favourable conditions for soil-dwelling mammals (Miehe *et al.* 2008b).

The study site at Kema has an alpine semi-humid monsoon climate with a long-term average precipitation of 447 mm (nearest climate station Nagqu; 1971-2005), which mainly falls between June and September (Miehe *et al.* 2014). Heavy snowfall occurs irregularly between December and March and leads to livestock losses (Miehe *et al.* 2008b). The mean annual temperature is -0.5°C (1971-2005, mean July temperature 9.0°C), while frost between September and May restricts the growing season to approximately 150 days (Wei *et al.* 2007).

The study site in Xinghai is located on a loess-covered gravel terrace of the Huang He/ Yellow River (Chapter 6) and has an average altitude of 3440 m a.s.l. (35.53882°N, 99.84920°E; Fig. 2). Here, *Kobresia* pastures are assumed to be replacement communities of taller grasslands, scrublands and probably forests (Miehe *et al.* 2008b). The cover of *K. pygmaea* rarely exceeds 10%, while dicotyledons are the overwhelmingly dominant plant group comprising mainly grazing weeds such as *Stellera chamaejasme* L. or *Gentiana straminea* Maxim. Typical alpine companion species are also frequent, such as *Lagotis* *brachystachya*, *Lamiophlomis rotata*, *Lancea tibetica* and *Potentilla* species. About 20% of the turf is covered with Cyanophyceae and crustose lichens. The *Kobresia* pastures serve mainly as winter pastures for yak and sheep, or as year-round grazing ground for weak livestock, while summer pastures are located at higher altitudes.

The prevailing soils have developed from unconsolidated Aeolian silts and have characteristics of Haplic Kastanozem, with an Ah mollic horizon. The root turf has a thickness of about 5 cm (Chapter 6).

The nearest climate station is in Xinghai, where the recorded long-term (1971-2001) mean annual temperature is 1.4°C, with mean July temperatures of 12.3°C. Precipitation is concentrated in the thermal growing season between May and September, and the mean annual total is 353 mm (Babel *et al.* 2014). Project gauges on the study site obtained a higher mean of 582 mm for the period 2002 to 2010 (Miehe *et al.* 2008a).

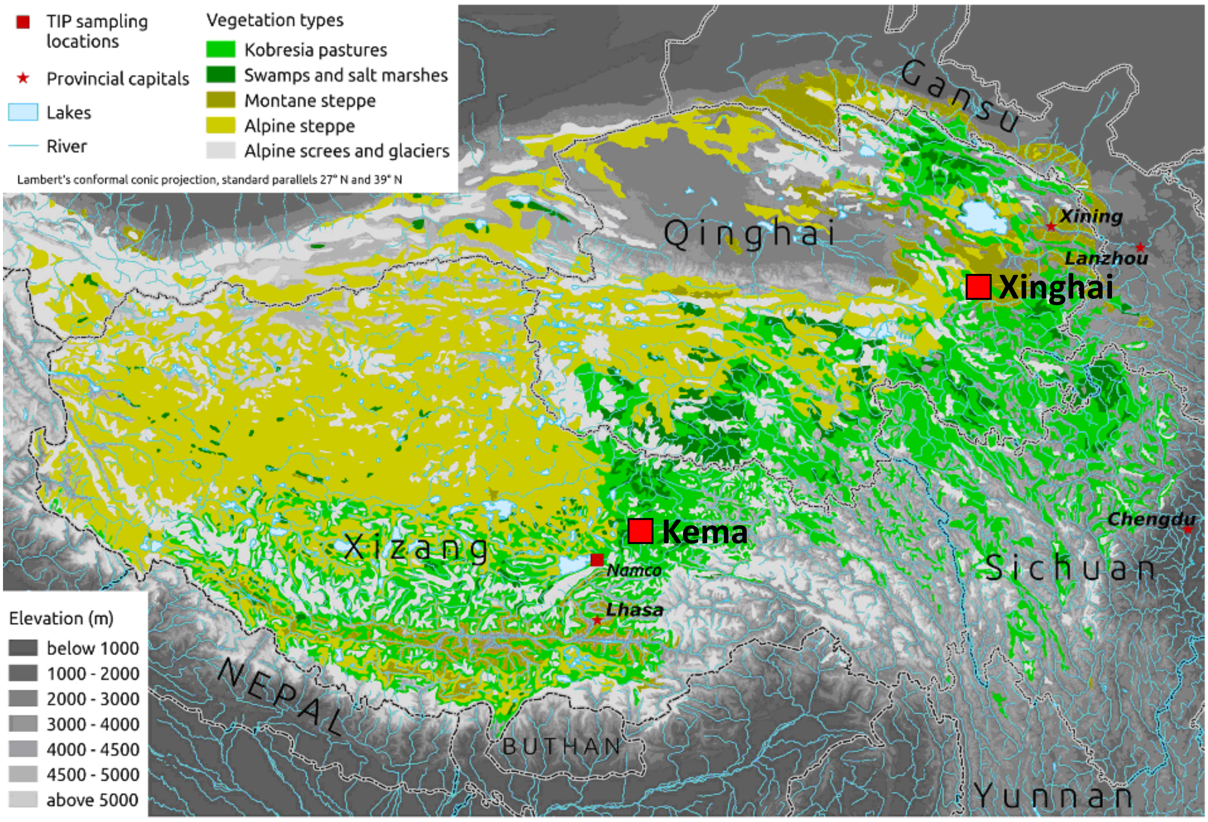


**Figure 2:** Distribution of *Kobresia* pastures (light green) on the Tibetan Plateau and localities of study sites within Xinghai in the montane belt and Kema in the alpine belt (after **Babel *et al.* 2014**).

## The framework of TiP

The work of this thesis was embedded in the project called "The making of a Tibetan landscape: Identification of parameters, actors and dynamics of the *Kobresia pygmaea* pastoral ecosystem” and part of the subproject “Monitoring of vegetation dynamics in the *Kobresia* ecosystem in relation to grazing intensity”. Alpine ecosystems are complex, and integrative studies should consider edaphic properties, hydrological budgets and climatic conditions, all of which were ensured by the integration of the project with a multi-institutional collaboration within the "Atmosphere-Ecology-Glaciology Cluster" (TiP-AEG) funded by the DFG (German Research Foundation) Priority Programme 1372 "Tibetan Plateau; Formation, Climate, Ecosystems" (TiP), which included soil scientists (University Hannover, Göttingen, Koblenz), ecosystem hydrologists (University Göttingen), micrometeorologists (University Bayreuth) and ecologists (University of Marburg, Göttingen, Senckenberg Natural History Museum Görlitz).

From 2011 to 2013, joint field campaigns were conducted with scientists of the BMBF (German Federal Ministry of Education and Research) programme “Central Asia – Monsoon dynamics and geo-ecosystems”.

## Objectives of the thesis

This thesis investigates the biology and ecology of alpine *Kobresia pygmaea*, centering around the questions how the species attains and maintains dominance across the Tibetan Plateau (Fig. 3). The studies that support the thesis were presented in the various chapters and focused on the sexual and clonal reproduction of *K. pygmaea* as well as polyploidy and associated genetic structure. The effects of abiotic and biotic factors on the ecology and ecosystem services of these economically and ecologically important alpine *Kobresia* pastures were also tested.

The first study (Chapter 2) assessed the ploidy status of *K. pygmaea* and determined whether polyploidy is a general characteristic of the genus. It was based on a combined application of chromosome counts, newly established microsatellite markers from high-throughput sequencing and flow cytometry. The study sets the basics for further research on *K. pygmaea,* as it reports on newly established microsatellite markers and protocols which were adapted to species’ dwarf size and the consequently limited amount of available tissue for sampling.

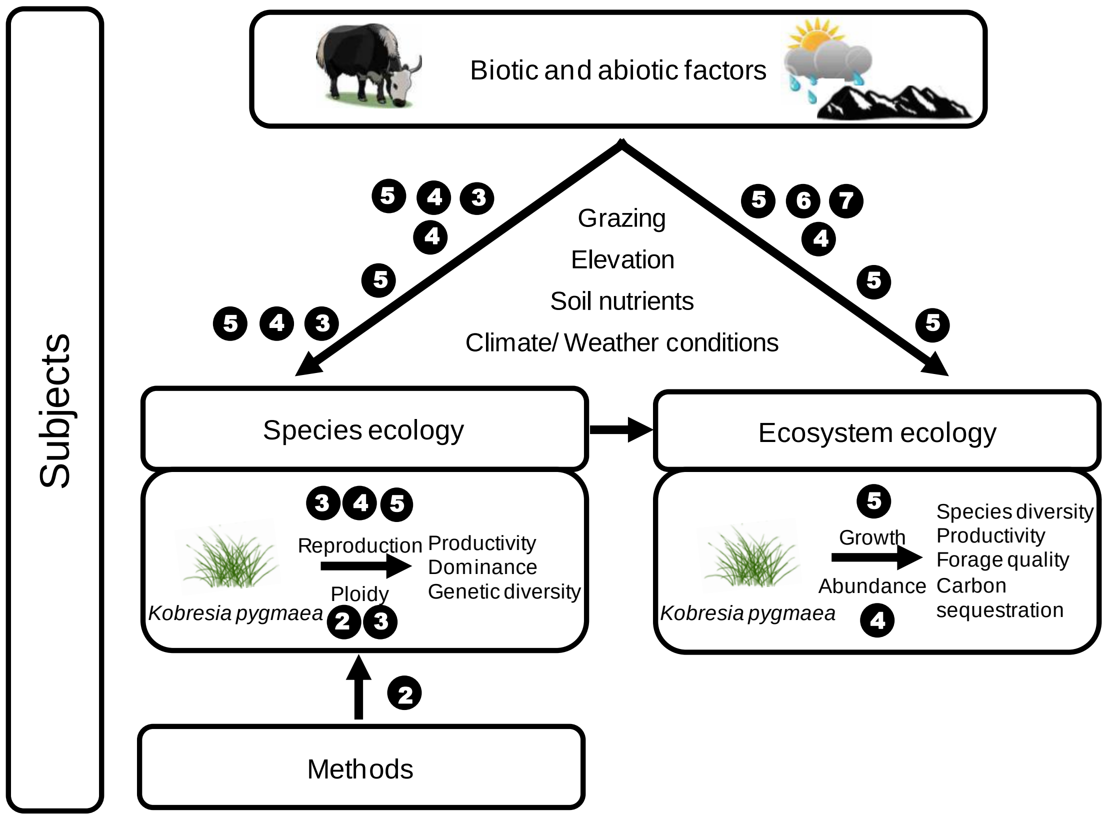


**Figure 2:** Summary of the subjects in this thesis. The numbers refer to the chapters with the corresponding investigations.

The next two chapters present studies on the reproductive strategy of *K. pygmaea* at the key alpine site in Kema (Chapter 3) and along an altitudinal transect in Qinghai ranging from 3440 to 4800 m a.s.l. (Chapter 4). It was tested whether populations persist by sexual or clonal reproduction and how pasture management, weather and climatic conditions as well as altitude influence the trade-off between reproductive strategies. In addition, genetic diversity within and among populations was tested and whether such diversity was influenced by polyploidy.

The following three chapters investigate biotic and abiotic factors at the ecosystem level, placing particular emphasis on *K. pygmaea* as the key species. The fourth study (Chapter 5) determined the effects of grazing, nutrient availability and of highly variable weather conditions on above- and below-ground productivity as well as on forage value of plant functional groups such as sedges, grasses, annuals and perennial herbs of alpine *Kobresia* pastures. The study also tested whether such factors alter the level of allocation to reproduction in the dominant sedge *K. pygmaea*.

The next two chapters focus on carbon pools and fluxes in *Kobresia* pastures. Chapter 6 investigated whether long-term grazing cessation of montane sites in Xinghai altered carbon partitioning patterns between above- and below-ground pools; the approach was based on $^{13}CO_2$ pulse labeling. The sixth study (Chapter 7) tested for short-term effects of grazing at the key alpine site in Kema, with a special emphasis on the role of the turf layer for carbon storage and cycling by coupling $^{13}CO_2$ pulse labeling with continuous eddy covariance measurements.

The overall aim of this thesis was to improve knowledge on the alpine biology of *K. pygmaea*, the relevance of the root turf and factors influencing species abundance at the ecosystem level. The findings support both an ecosystem services approach to sustainability appraisal for the region and locally adopted conservation measures aimed at reducing pasture degradation.

Most of the chapters represent published articles or submitted manuscripts, and this is reflected in the formatting, which follows individual journal guidelines and may differ between chapters.

# CHAPTER 2

Ploidy in the alpine sedge *Kobresia pygmaea* (Cyperaceae) and related species: combined application of chromosome counts, new microsatellite markers and flow cytometry

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## ABSTRACT

Polyploidy is a fundamental mechanism in evolution, but is hard to detect in taxa with agmatoploidy or aneuploidy. We tested whether a combination of chromosome counting, microsatellite analyses and flow cytometric measurements represents a suitable approach for the detection of basic chromosome numbers and ploidy in *Kobresia* (Cyperaceae). Chromosome counting resulted in $2n = 64$ for *Kobresia pygmaea* and *K. cercostachys*, $2n = 58$ and 64 for *K. myosuroides*, and $2n = 72$ for *K. simpliciuscula*. We characterized eight microsatellite loci for *K. pygmaea*, which gave a maximum of four alleles per individual. Cross-species amplification was tested in 26 congeneric species and, on average, six of eight loci amplified successfully. Using flow cytometry, we confirmed tetraploidy in *K. pygmaea*. Basic chromosome numbers and ploidy were inferred from chromosome counts and the maximum number of alleles per locus. We consider the basic numbers as $x = 16$ and 18, with irregularities derived from agmatoploidy and aneuploidy. Across all *Kobresia* taxa, ploidy ranged from diploid up to heptaploid. The combination of chromosome counts and microsatellite analyses is an ideal method for the determination of basic chromosome numbers and for inferring ploidy, and flow cytometry is a suitable tool for the identification of deviating cytotypes.

ADDITIONAL KEYWORDS: 454 sequencing – basic chromosome number – cross-amplification – *Kobresia pygmaea* ecosystem – next-generation sequencing – palaeopolyploidy – Tibetan Plateau.

# CHAPTER 3

Mixed reproduction strategy and polyploidy facilitate dominance of *Kobresia pygmaea* on the Tibetan Plateau

Elke Seeber, Georg Miehe, Isabell Hensen, Yongping Yang, Karsten Wesche

*Journal of Plant Ecology* (2015). doi: 10.1093/jpe/rtv035.

## ABSTRACT

*Aims:* The sedge *Kobresia pygmaea* is the dominant species of high-altitude pastures in Tibet, and it is the most important source of forage in animal husbandry. We present the first comprehensive reproduction study for this perennial key species that adopts a molecular approach and tests how sexual and vegetative reproduction, as well as ploidy, relate to survival and dominance under harsh conditions.

*Methods:* We assessed inflorescence numbers of *K. pygmaea* across two Tibetan alpine pastures with differing grazing regimes. Germination was tested in untreated diaspores and then following mechanical and chemical scarification. In a 4-year experiment, we assessed diaspore viability and seed bank formation. Using eight microsatellite markers, we recorded multilocus genotypes in hierarchical grids and measured their ploidy using flow cytometry. Adjusted ANOVA models were used to analyse data on sexual reproduction, while the complement of the Simpson index and the Shannon diversity index were used to characterise the spatial distribution of multilocus genotypes and clonal richness.

*Important Findings:* Inflorescence production was high and differed significantly between years (2010: 617 ± 460 s.d.; 2012: 2,015 ± 1,213 s.d.) but not between grazing regimes. Diaspore viability was high (94%) and gradually decreased after three and four years of storage in the soil. Diaspores not exposed to further scarification failed to germinate, while mechanical and chemical ($H_2SO_4$) scarification increased germination to 9% and 44%, respectively. Clonal diversity was high, although *in situ* germination was rarely observed. Multilocus genotypes intersected and covered a mean area of 0.74 $m^2$. Most individuals were found to be tetraploid, with only 0.8% of all ramets being triploid. We conclude that *Kobresia pygmaea* survives on the Tibetan Plateau by employing a mixed reproduction strategy involving both sexual and clonal propagation. The species' adaptability and dominance is further facilitated by its polyploidy. As pasture restoration using diaspores would be difficult, existing *Kobresia* pasture should be managed more sustainably.


*Keywords*: alpine rangelands, clonal diversity, flow cytometry, grazing, microsatellite analyses

# CHAPTER 4

## From allele to species level: Genetic diversity and mode of reproduction of the dominant species shape plant community composition along an elevational transect on the Tibetan plateau

Elke Seeber, Georg Miehe, Isabell Hensen, Jianquan Liu, Xinmin Tian, Pauline M. Nowak, Karsten Wesche

*Global Ecology and Biogeography* (submitted).

**ABSTRACT**

**Aim** Ecological research along elevational gradients provides valuable knowledge about future trends in the course of climatic changes. Biodiversity variables are assumed to show unimodal responses along elevational gradients or approximately linear responses at upper elevations.

We studied elevation–diversity patterns in an ecosystem with a well-defined dominant and a set of subordinate species and tested how the existence of the dominant *Kobresia pygmaea* C.B.Clarke ex Hook.f. and its reproductive and gentic characteristics affect diversity and elevational dynamics in this ecosystem.

**Location** Qinghai, China

**Methods** We compared community-level species richness, Shannon species diversity and evenness, as well as within-species genetic and clonal diversity along an elevational transect of *Kobresia* pastures spanning over ~1500 m. Within-species diversity of the overwhelmingly dominant species, *K. pygmaea*, was assessed in altitudinal steps of ~200 m using eight microsatellite markers. We mapped the extent of clones, and counted inflorescences as an indicator for sexual reproduction

**Results** Estimates of richness and diversity at species-, clone- and allele levels followed the same inverse hump-shaped pattern with increasing elevation. The genetic diversity of *K. pygmaea* was high and influenced by the trade-off between sexual and clonal reproduction. Maxima of clonal growth and minima of sexual reproduction occurred at intermediate elevations, where species' abundance reached its maximum, while community diversity was low. Populations of *K. pygmaea* were hardly differentiated.

**Main conclusions** The unusual inverse hump-shaped elevational pattern of genetic and clonal diversity of a single dominant species can shape species' abundance and thereby the elevation–diversity relationship on community level. Other factors, apart from elevation and linearly correlated climatic variables, are important for growth of *K. pygmaea*, such as grazing, soil conditions and the availability of open substrate, indicating resilience to climate changes. Phenotypic plasticity rather than genetic differentiation facilitates adaption of the dominant sedge across its elevational range.

**KEYWORDS**

Clonal mapping, diversity–elevation pattern, *Kobresia* pastures, *Kobresia pygmaea*, microsatellite analyses, species diversity.

# CHAPTER 5

## Co-limitation by nitrogen and phosphorus rather than climate shapes plant performance in alpine Tibetan pastures

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*Oecologia* (submitted).

## Abstract

Grasslands worldwide have been exposed to grazing and nutrient removal for several centuries, suggesting that they are nutrient-limited and sensitive to nutrient input from aerial sources. Fertilization experiments in various Chinese grasslands yield contrasting results, and no data are available on alpine *Kobresia pygmaea* pastures of the Tibetan highlands well above 4000 m a.s.l., despite their immense distribution range and importance for animal husbandry. We investigated responses of soil parameters, above- and below-ground biomass, tissue nutrient contents and sexual reproduction to 3-years single and combined application of potassium (K), nitrogen (N) and phosphorus (P) in artificially grazed and ungrazed plots. Fertilization enhanced nutrient availability in the soil but did not change below-ground biomass. Total above-ground biomass of water controls after 3-year grazing exclusion was 153 g $m^{-2}$. Artificial grazing resulted in ~50% reduction of the standing crop and complete disappearance of litter. In spite of the harsh alpine climate, productivity of the dominant *K. pygmaea* and herbs was limited by nitrogen and co-limited by phosphorous for both grazing treatments. Annual variability of climatic conditions affected productivity only after N and NP addition. Fertilization increased tissue nutrient contents of *K. pygmaea* and herbs but not of other Cyperaceae and Poaceae. Resource allocation to inflorescences and seed yield of *K. pygmaea* was not improved by nutrient addition but significantly decreased after 3-year grazing exclusion. We conclude that N deposition will have limited effects on forage yield due to a strong co-limitation by P, while tissue N contents may increase.

**Keywords:** grazing, *Kobresia pygmaea*, *Kobresia* turf, nutrient limitation, Tibetan Plateau

# CHAPTER 6

Effect of grazing on carbon stocks and assimilate partitioning in a Tibetan montane pasture revealed by $^{13}CO_2$ pulse labeling

Silke Hafner, Sebastian Unteregelsbacher, Elke Seeber, Lena Becker, Xingliang Xu, Xiaogang Li, Georg Guggenberger, Georg Miehe, Yakov Kuzyakov

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**Abstract**

Since the late 1950s, governmental rangeland policies have changed the grazing management on the Tibetan Plateau (TP). Increasing grazing pressure and, since the 1980s, the privatization and fencing of pastures near villages has led to land degradation, whereas remote pastures have recovered from stronger overgrazing. To clarify the effect of moderate grazing on the carbon (C) cycle of the TP, we investigated differences in below-ground C stocks and C allocation using *in situ* $^{13}CO_2$ pulse labeling of (i) a montane *Kobresia* winter pasture of yaks, with moderate grazing regime and (ii) a 7-year-old grazing exclosure plot, both in 3440 m asl. Twenty-seven days after the labeling, $^{13}C$ incorporated into shoots did not differ between the grazed (43% of recovered $^{13}C$) and ungrazed (38%) plots. In the grazed plots, however, less C was lost by shoot respiration (17% vs. 42%), and more was translocated below-ground (40% vs. 20%). Within the below-ground pools, <2% of $^{13}C$ was incorporated into living root tissue of both land use types. In the grazed plots about twice the amount of $^{13}C$ remained in soil (18%) and was mineralized to $CO_2$ (20%) as compared to the ungrazed plots (soil 10%; $CO_2$ 9%). Despite the higher contribution of root-derived C to $CO_2$ efflux, total $CO_2$ efflux did not differ between the two land use types. C stocks in the soil layers 0–5 and 5–15 cm under grazed grassland were significantly larger than in the ungrazed grassland. However, C stocks below 15 cm were not affected after 7 years without grazing. We conclude that the larger below-ground C allocation of plants, the larger amount of recently assimilated C remaining in the soil, and less soil organic matter-derived $CO_2$ efflux create a positive effect of moderate grazing on soil C input and C sequestration.

*Keywords*: $^{13}C$ pulse labeling, C allocation, grazing exclosure experiment, grazing intensity, montane *Kobresia* pasture, Qinghai-Tibetan Plateau, soil organic carbon

# CHAPTER 7

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

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ABSTRACT

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

HIGHLIGHTS

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

*Keywords*: Alpine grassland, Carbon cycle, Land use changes, Grazing, Tibetan-Plateau

# CHAPTER 8

General discussion and conclusions

## CHARACTERISTICS OF *KOBRESIA PYGMAEA* – SPECIES ECOLOGY

### Reproductive biology of *Kobresia pygmaea* and genetic consequences

Resource allocation to sexual reproduction is high in *K. pygmaea*, and consequently clonal diversity, which give rise to a high overall genetic diversity, although germination was limited to years with favourable conditions (Chapter 2, 3, 4; Fig. 4). The results support the recent shift in ecology from assuming that alpine plants generally employ low levels of sexual reproduction, leading to low genetic diversity (Billings & Mooney 1968; Bauert *et al.* 1998), towards an assumption that even infrequent, low levels of sexual recruitment are sufficient to maintain high levels of genetic diversity in long-living, clonal species (Watkinson & Powell 1993). However, reproductive and genetic characteristics are subject to high spatial and inter-annual variability due to differences in soil conditions, elevational gradients, grazing patterns and changing weather/ climatic conditions (Chapter 3, 4, 5). Thereby, populations of *K. pygmaea* show a high phenotypic variability rather than genetic differentiation. This fact, together with the overall high genetic diversity, suggests that *K. pygmaea* can cope with future changes in environmental conditions such as aerial nutrient deposition and climate change.

Although high genetic diversity is apparently a common feature of the genus *Kobresia*, values obtained for *K. pygmaea* were outstanding compared to other clonal species and species within the genus (Chapter 3; e.g. Ellstrand & Roose 1987; Zhao *et al.* 2006; Zheng *et al.* 2009). This raises the question of a self-incompatibility system promoting outcrossing, such as in the alpine *Campanula thyrsoides* L. (Ægisdóttir *et al.* 2007). For the genus *Kobresia*, no information is available from pollination experiments, while self-compatible and incompatible species are reported for other Cyperaceae (e.g. Whitkus 1988; Charpentier *et al.* 2000; Snyder & Richards 2005). Further studies on pollination are necessary to analyze self-compatibility in the genus *Kobresia*.

### Polyploidy and genetic consequences

This thesis proved that the genus *Kobresia* exhibits various levels of ploidy ranging from di- to heptaploids, with about half of the tested species being polyploid (Chapter 2). Considering that polyploids are generally assumed to better tolerate harsh alpine conditions than diploids and that the genus is mainly distributed across cold habitats, i.e. at high latitudes or altitudes (Zhang *et al.* 1995), the high proportion of polyploids is not surprising (Hagerup 1932;

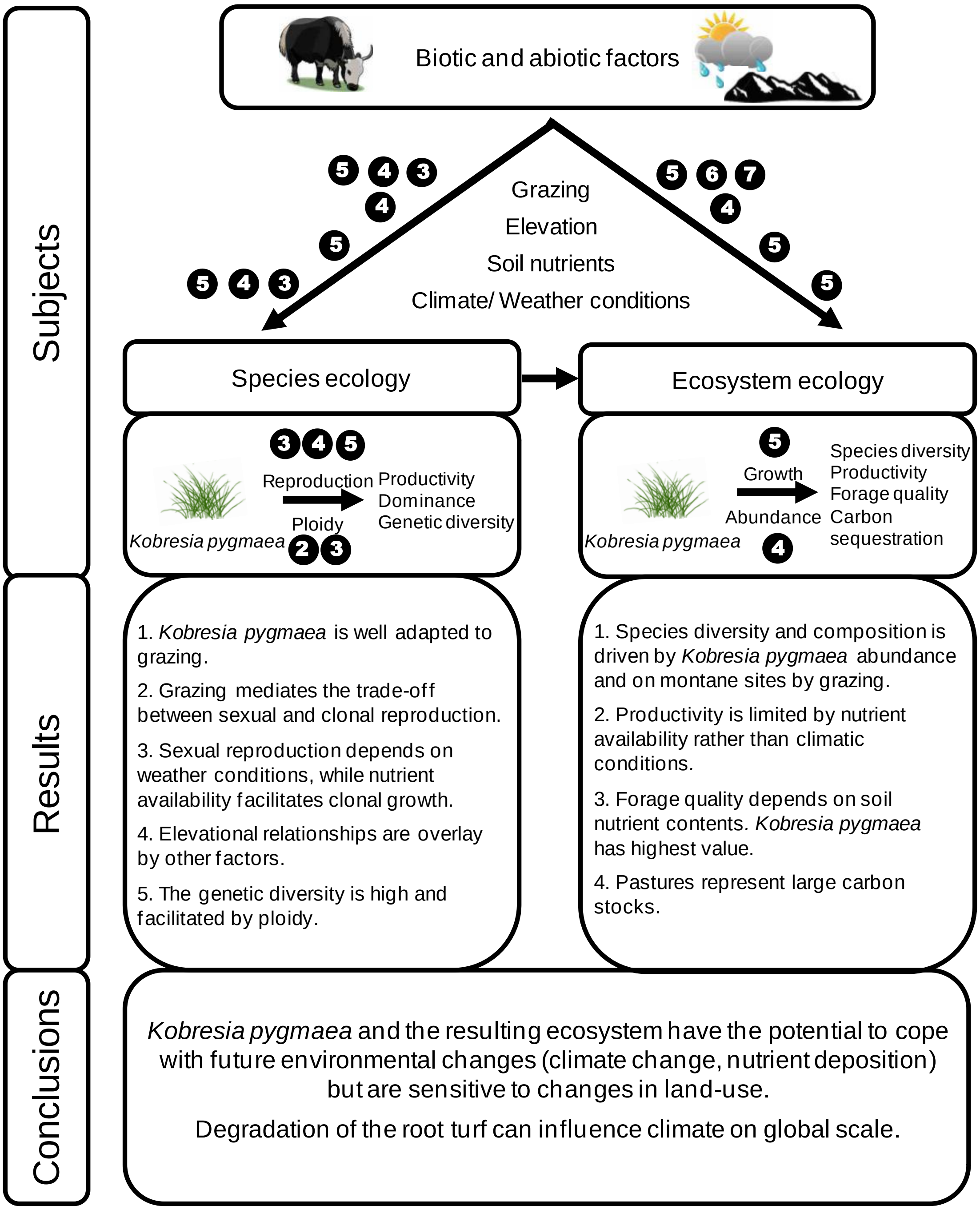


**Figure 4:** Summary of the subjects, results and conclusions of this thesis. The numbers refer to the chapters with the corresponding investigations.

Stebbins 1950; Hijmans *et al.* 2007). However, in contrast with other alpine floras, ploidy is the exception rather than the rule on the Tibetan Plateau, and it is only limited to a few genera (Liu *et al.* 2001; Liu 2004; Nie *et al.* 2005 and references therein). Ploidy thus may account for the high number of common and dominant species in this genus.

*Kobresia pygmaea* is mainly tetraploid (Chapter 2; 3), a configuration which enhances the competitive advantage of the dominant sedge by means of increasing the genetic diversity on individual level, compared to most other accompanying species of alpine *Kobresia* pastures that are diploids (e.g. Liu *et al.* 2011b; Fang *et al.* 2007). However, there are a few exceptions. Surprisingly, an octaploid cytotype was found in Qinghai, which was highly overrepresented in patches of bare soil (E. Seeber unpublished data). Whether this reflects a high proportion of octaploid diaspores, higher germination capacity and/or increased survival by adaptation to the dry conditions remains to be tested. In any case, this octaploid cytotype potentially represents a natural resource for pasture restoration programs and it is therefore of particular relevance both ecologically and economically.

The mode of cytotype formation is one of the most discussed issues in studies on speciation (Soltis *et al.* 2004). For tetraploid *K. pygmaea,* we initially assumed autopolyploidization, as this is the prevailing mode in the closely related genus *Carex* and is assumed to apply for Cyperaceae in general (Heilborn 1939). Still, a few specimens showed genotypic and/ or phenotypic variation, which would be expected for hybrids (Ford *et al.* 1993). This supports recent morphological studies by S. Miehe indicating hybridization as well (pers. communication). However, none of the deviating cytotypes of potential hybridogenic origin, produced fertile inflorescences, which otherwise would have allowed for further morphological analyses.

Microsatellite markers have previously been proved valuable to identify hybrids (e.g. Lalit *et al.* 2014). The newly established markers in the genus *Kobresia* have a high potential for cross-amplification, but large ranges of overlapping allele sizes prevent species and hybrid identification by this approach (Chapter 2). We therefore cannot draw any final conclusion on the origin of these presumably hybridogenic specimens. However, if cytotypes resulted from allopolyploid formation, further insights into hybridization patterns might be obtained from investigations of plastid DNA. Suitable sequences from *K. pygmaea* are available from high-throughput sequencing performed during the study, which can be used again to facilitate the initial establishment of selective primers. In the case of autopolyploidization, investigation of the frequency of unreduced pollen formation might be crucial. In any case, special emphasis should be laid on the octaploid cytotype.

# BIOTIC AND ABIOTIC ACTORS ON *KOBRESIA* PASTURES – ECOSYSTEM ECOLOGY

## Effects of grazing

Species of alpine *Kobresia* pastures, and in particular *K. pygmaea,* are well adapted to moderate grazing pressure. This not only refers to a mixed strategy with persistence through vegetative growth and at least occasional sexual reproduction, it is also applicable to fast and high allocation of assimilated carbon to below-ground pools (Chapter 7). This indicates that *K. pygmaea* invests strongly in below-ground plant tissue (i.e. for growth and maintenance of root biomass; Chapter 7), which most likely ensures efficient nutrient uptake (i.e. nitrogen; Schleuss *et al.* 2015) in the nitrogen- and phosphorus-limited ecosystems (Chapter 5) and it enables fast regrowth after grazing (Spielvogel *et al.* in preparation).

Grazing exclosure experiments revealed that montane and alpine *Kobresia* pastures develop increasing standing crop and accumulate litter within a few growing seasons compared to moderately grazed sites (Chapter 5, 6, 7; Miehe *et al.* 2008a). While in montane pastures grazing cessation goes along with changes in species composition (Chapter 6; Miehe *et al.* 2008a), the results do not support such changes at the alpine key site in Kema within three growing seasons (Chapter 7; E. Seeber, unpublished data). Thus, the study supports suggestions of a grazing-driven ecosystem (Miehe *et al.* 2008a) only for montane elevations, while first results on short-term exclosures suggest alpine *Kobresia* pastures to be the natural vegetation, in accordance with assumptions of Kaiser (2007). Alpine species of the Tibetan Plateau are generally small (at the study site <5 cm; exceptions include inflorescences of *Stipa* spec. and *Elymus* spec. at ~10 cm) as they are most likely adapted to the harsh climate, nutrient limitation (Chapter 5) and water limitation caused by high evapotranspiration rates (Babel *et al*. 2014; Coners *et al.*, submitted). The size of such species only marginally increases after grazing exclusion and thus effects of competition are generally low; however, litter accumulation can affect species composition by decreasing or fostering the availability of safe sites for germination, altering the microclimate or directly suppressing small species (Jensen & Meyer 2001; Quested & Eriksson 2006). The long-term effects of litter accumulation at alpine sites require further investigation, as accumulation is slow due to overall low productivity, removal by strong winds or surface run-off after heavy precipitation events.

Grazing regimes also influenced rangeland carbon cycles and again, montane and alpine pastures had different characteristics. On a montane pasture, grazing exclusion led to higher carbon losses by shoot respiration and increased total above-ground carbon stocks, while below-ground carbon stocks declined (Chapter 6), indicating a weakening of the root turf, thereby making it vulnerable to the trampling and digging activities of small mammals (Chapter 6; Miehe *et al.* 2008b). In contrast, in the alpine pasture, neither shoot respiration and total above-ground carbon stocks, nor below-ground biomass, as an indicator of turf density, differed after grazing cessation for one and three growing seasons (Chapter 5, 7). This accounts for the overall large below-ground pools and cold temperatures decelerating microbial activity and decomposition in alpine habitats (Chapter 7) and demonstrates that long-term studies, probably for decades, are necessary to identify effects of grazing cessation in alpine environments. Independent of elevation, the root turf (below-ground biomass, necromass and soil) stores huge amounts of carbon (Chapter 6, 7) and due to this fact and the immense spatial extension of the ecosystem, *Kobresia* pastures are of relevance for global carbon cycles. A comparison of grazing intensities proved that moderate to high stocking rates (~2-3 yaks $ha^{-1}$) are optimal in terms of ecosystem carbon storage (Gao *et al.* 2007). In contrast, overgrazing and anthropogenic factors such as construction, can lead to decreasing carbon stocks through weakening and removal of the turf layer, which can result in so called “black soil beaches”, or open patches with bare soil. The loss of the turf layer followed by erosion of the whole soil profile can cause $CO_2$ emissions to the atmosphere, which is of global relevance with regard to climate change (Wang *et al.* 2010; Babel *et al.* 2014). Counteractive measures against degradation include long-term exclosures. This thesis proved that this is not a suitable tool, especially not for montane pastures, as the species composition changes comparably fast and the root turf degrades. Pastures could be mowed or grazed at intervals of a few years, which would also provide winter forage and decrease grazing pressure on free ranges. Further, grazing from the end of the growing season to spring should be preferred as this allows for diaspore maturity and enhances seed bank formation.

This thesis represents the first attempt to compare grazing effects on montane an alpine sites. The results suggest that alpine ecosystems are more stable in species composition and carbon cycling, due to short growing periods, low microbial activity and cold climatic conditions. However, long-term exclosure experiments in alpine sites are still pending, which are essential for drawing final conclusions.

### Effects of nutrient and moisture availability

Above-ground productivity of *K. pygmaea* and herbs is limited by nitrogen and co-limited by phosphorus (Chapter 5). A comparative study between montane and alpine pastures on total above-ground biomass confirmed the same mode of nutrient limitation over a larger elevational range (Träger *et al.* in preparation). The results contradict the general assumption of prevailing nitrogen limitation in mountain ecosystems (Körner 2003). Annual variability of productivity in response to precipitation was only detectable in fertilized plots (Chapter 5). This indicates that the net primary productivity of the ecosystem is mainly restricted by nutrients, rather than water availability and it may accounts for the long history of nutrient removal by animal husbandry. This is in contrast to Babel *et al.* (2014), who assumed a generally strong hydrological limitation of *Kobresia* pastures as evapotranspiration rates almost exceed precipitation. Results are also of economical importance, as they prove that pastures of different nutritional status, or those subject to fertilization, do not produce uniform forage yields in different years.

Nutrient addition, in contrast, increased tissue nutrient contents and decreased C:N ratios as a proxy for forage quality (Chapter 5). Thereby, tissue contents seem to be more sensitive than overall productivity and might even be positively affected by low quantities of aerial nutrient deposition.

The common pattern of changes in species composition by nutrient addition (e.g. Bowman *et al.* 1993; Bowman 1994; Clark & Tilman 2008) could not be confirmed in this thesis. Three years of experimental nutrient addition may not represent a sufficiently appropriate period to produce detectable changes of species diversity and composition for such low productivity alpine ecosystems with high community stability, which is caused by clonal growth and long cycles of sexual reproduction. Further long-term studies on effects of nutrient and water availability at the ecosystem level are thus needed.

The results of this thesis expand the available knowledge on *Kobresia pygmaea*, the dominant sedge of *Kobresia* pastures, and they have implications for both the applied management and general understanding of plant population ecology in harsh environments. The results do, however, emphasize the need for further research. In particular, species diversity and composition responses are revealed to be slow in this habitat as a result of the short growing seasons, the high persistence of individuals associated with longevity and clonal reproduction in *K. pygmaea*, and its ability to recover from vegetative organs. Further, the high inter-annual variability of ecosystem responses to environmental factors, such as grazing or fertilization, calls for long-term, *in situ* studies.

## CONCLUSION

The results suggest that abiotic and biotic factors influence sexual and clonal recruitment of *K. pygmaea* and thus determine the genetic diversity of populations. The high allelic diversity at the individual level is fostered by tetraploidy. Further, *K. pygmaea* has exceptional high root:shoot ratios, highlighting the species' tolerance to grazing. The abundance of *K. pygmaea* resulting from these characteristics controls the characteristics of the whole ecosystem, such as species diversity and composition or potential for carbon sequestration. Still, species characteristics and practices of pastoral communities varied widely between altitudes, proving that further studies must compare differences between montane and alpine habitats. The species' large elevational distribution range, as well as its high genetic diversity and the recent formation of an octaploid cytotype that is probably adapted to drier conditions, suggests a high potential of *K. pygmaea* to cope with global climate change in most of its distribution range. However, anthropogenic factors, such as inappropriate grazing regimes or removal for construction purposes, can lead to considerable changes of vegetation and soil properties of these pastures, which may affect carbon cycles and precipitation regimes at local as well as global scales.

Counteractive measures should be initiated at an early stage of degradation along with sustainable land-use - incorporating flexible grazing management relative to weather conditions and nutritional status, combined with moderate stocking densities - should be favoured in order to maintain ecological and economically sustainable ecosystem functioning. Long-term grazing exclosures are not suitable to restore pastures, as the root turf becomes progressively decomposed and species diversity decreases. For the restoration of heavily degraded pastures with a complete loss of the root turf, usage of the octaploid cytotype of *K. pygmaea* found on open sites may be a future prospect.

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# APPENDICES

# APPENDICES

## Publications of the dissertation

Hafner S, Unteregelsbacher S, **Seeber E**, Becker L, Xu X, Li X, Guggenberger G, Miehe G, Kuzyakov Y (2011). Effect of grazing on carbon stocks and assimilate partitioning in Tibetan montane pasture revealed by $^{13}CO_2$ pulse labeling. *Global Change Biology* **18**: 528–538.

Ingrisch J, Biermann T, **Seeber E**, Leipold T, Li M, Ma Y, Xu X, Miehe G, Guggenberger G, Foken T, Kuzyakov Y (2015). Carbon pools and fluxes in a Tibetan alpine *Kobresia pygmaea* pasture partitioned by coupled eddy-covariance measurements and $^{13}CO_2$ labeling. *Science of the Total Environment* **505**: 1213–1224.

**Seeber E**, Miehe G, Hensen I, Yang Y, Wesche K (2015). Mixed reproduction strategy and polyploidy facilitates dominance of *Kobresia pygmaea* on the Tibetan Plateau. *Journal of Plant Ecology*. doi:10.1093/jpe/rtv035.

**Seeber E**, Miehe G, Nowak P, Hensen I, Liu J, Wesche K (submitted). From allele to species level: Genetic diversity and mode of reproduction of the dominant species shape plant community composition along an elevational transect on the Tibetan Plateau. *Global Ecology and Biogeography*.

**Seeber E**, Träger S, Hensen I, Guggenberger G, Miehe G, Yang Y, Wesche K (submitted). Climate, soil nutrients and land-use determine productivity and reproduction in alpine pastures of the Tibetan Plateau. *Oecologia*.

**Seeber E**, Winterfeld G, Hensen I, Sharbel TF, Durka W, Liu J, Yang Y, Wesche K (2014). Ploidy in the alpine sedge *Kobresia pygmaea* (Cyperaceae) and related species: combined application of chromosome counts, new microsatellite markers and flow cytometry. *Botanical Journal of the Linnean Society* **176**: 22–35.

## Other publications of the author within the framework of TiP

### Peer-reviewed publications

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

Miehe G, Miehe S, Bach K, Wesche K, **Seeber E**, Behrendes L, Kaiser K, Reudenbach C, Nölling J, Hanspach J, Herrmann M, Ma Y, Mosbrugger V (2013). Resilience or Vulnerability? Vegetation

Patterns of a Central Tibetan Pastoral Ecotone. In: Prieto MBM, Diaz JT [eds]: *Steppe Ecosytems – Biological Diversity, Management and Restoration*, *Environmental Research Advances*, New York: Nova publishers.

### Non peer-reviewed publications

Biermann T, Leipold T with contributions from Babel W, Becker L, Coners H, Foken T, Guggenberger G, He S, Ingrisch J, Kuzyakov Y, Leuschner C, Miehe G, Richards K, **Seeber E**, Wesche K (2011). *Joint Kobresia Ecosystem Experiment: Documentation of the first intensive observation period summer 2010 in Kema Tibet*. Arbeitsergebnisse Nr 44. Bayreuth: Eigenverlag der Universität Bayreuth Abt. Mikrometeorologie.

Biermann T, **Seeber E**, Schleuß P, 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 Atmosphere-Ecology-Glaciology Cluster Joint Kobresia Ecosystem Experiment: Documentation of the second intensive observation period summer 2012 in KEMA Tibet*. Arbeitsergebnisse Nr 54. Bayreuth: Eigenverlag der Universität Bayreuth Abt. Mikrometeorologie.

### Publications in preparation

Coners H, **Seeber E**, Willinghöfer S, Becker L, Biermann T, Yang Y, Guggenberger G, Foken T, Wesche K, Leuschner C (in preparation). Water requirement of *Kobresia pygmaea* mats – an *in situ* irrigation experiment on the Tibetan Plateau

Coners H, Babel W, Willinghöfer S, Biermann T, Köhler L, **Seeber E**, Foken T, Ma Y, Yang Y, Leuschner C (submitted). Evapotranspiration and water balance of high-elevation grasslands on the Tibetan Plateau. *Journal of Hydrology.*

Schleuss P-M, Heitkamp F, **Seeber E**, Spielvogel S, Miehe G, Guggenberger G, Kuzyakov Y (in preparation). Intensive soil organic carbon losses followed by soil degradation on alpine grassland of the Tibetan Plateau

Spielvogel S, Weiss J, Schleuss P, Hüllen J, Deggelmann A, Sauheitl L, Bange U, **Seeber E**, Kuzyakov Y, Guggenberger G (in preparation). Effects of grazing on the physical and chemical protection of grassland soil carbon: A multifactorial meta-analysis

Träger S, **Seeber E**, Hensen I, Glaser B, Guggenberger G, Wesche K (in preparation). Analysis of the productivity of *Kobresia pygmaea* pastures on the Tibetan Plateau

Wang Y, Lehnert LW, Holzapfel M, Schultz R, Heberling G, Görzen E, Meyer H, **Seeber E**, Pinkert S, Ritz M, Ansorge H, Bendix J, Seifert B, Miehe G, Long R, Yang Y, Wesche K (major revision). Testing congruence among multiple grazing indicators: a multi-site study across the Tibetan Plateau. *Journal of Applied Ecology.*

# Conference contributions

## Talks

Schleuss P-M, Heitkamp F, **Seeber E**, Spielvogel S, Miehe G, Guggenberger G, Kuzyakov Y **(**2015). Intensive soil organic carbon losses by degradation of alpine *Kobresia* pastures on the Tibetan Plateau. Talk at the EGU General Assembly, 12.-17.04.2015, Vienna

**Seeber E**, Hensen I, Wesche K (2012). A microsatellite study on the importance of clonal growth in the high alpine sedge *Kobresia pygmaea*. Talk at the 45th Population Genetics Group Meeting, 04.-07.01.2012, Nottingham, Abstract p 45

**Seeber E**, Maussion F, Dietze E (2011). Pictures tell more than words: impressions from TiP Young Scientist courses. Talk at the 7th Sino-German Workshop on Tibetan Plateau Research, 03.-06.03.2011, Hamburg

**Seeber E**, Wesche K, Miehe G, Miehe S **(**2014). The ecology of the *Kobresia pygmaea* pastures. Talk at the 10th Sino-German Workshop on Tibetan Plateau Research, 09.-12.12.2014, Berlin

Wesche K, **Seeber E**, Miehe G, Miehe S, Leuschner C, Coners H (2009). The Making of a Tibetan Landscape – Identification of Parameters Actors and Dynamics of the *Kobresia pygmaea* Pastoral Ecosystem. Talk at the 6th Sino-German Workshop on Tibetan Plateau Research, 10.-13.10.2009, Qingdao

Wesche K, **Seeber E**, Miehe G, Miehe S, Leuschner C, Coners H, Yang YP, Ma Y (2011). The Making of a Tibetan Landscape – Identification of Parameters Actors and Dynamics of the *Kobresia pygmaea* Pastoral Ecosystem. Talk at the 7th Sino-German Workshop on Tibetan Plateau Research, 03.-06.03.2011, Hamburg

Wesche K, Wang Y, **Seeber E**, Holzapfel M, Schultz R, Ansorge H, Miehe G, Seifert B, Görzen E, Heberling G, Träger S, Yang Y, Long RJ (2013). Grazing degradation in Central Asia: a view from Tibet. Invited plenary talk at 4th International Conference on Sustainable Animal Agriculture for Developing Countries, 28.-31.7.2013, Lanzhou

## Poster (Selection)

Becker L, Miehe G, Miehe S, **Seeber E**, Li X, Kuzyakov Y, Guggenberger G (2011). Suberin and Cutin as biomarkers for shifts in plant community composition following land use changes on the Tibetan Plateau. Poster at the 7th Sino-German Workshop on Tibetan Plateau Research, 03.-06.03.2011, Hamburg

Becker L, **Seeber E**, Wesche K, Shibistova O, Hafner S, Unteregelsbacher S, Kuzyakov Y, Miehe G, Li X, Guggenberger G (2009). Grazing effects on soil carbon and nitrogen of the northern Qinghai-

Tibetan Plateau. Poster at the 6th Sino-German Workshop on Tibetan Plateau Research, 10.-13.10.2009, Qingdao

Becker L, **Seeber E**, Wesche K, Shibistova O, Haffner S, Unteregelsbacker S, Kuzyakov Y, Miehe G, Li X, Guggenberger G (2011). Does grazing exclusion improve montane grasslands on the Tibetan Plateau? The joint Xinghai-experiment 2009. Poster at the 7th Sino-German Workshop on Tibetan Plateau Research, 03.-06.03.2011, Hamburg

Biermann T, Babel W, Becker L, Coners H, Foken T, Guggenberger G, He S, Ingrisch J, Kuzyakov Y, Leuschner C, Leipold T, Li M, Li X, Miehe G, Ma Y, Richards K, Rose L, **Seeber E**, Shibostova O, Shi P, Unger M, Wesche K, Xu X, Yang Y (2011). TiP-AEG Joint *Kobresia* Ecosystem Experiment 2010, Poster at the 7th Sino-German Workshop on Tibetan Plateau Research, 03.-06.03.2011, Hamburg

Biermann T, Babel W, Becker L, Coners H, Hafner S, He S, Ingrisch J, Leipold T, **Seeber E**, Shibostova O, Unteregelsbacher S, Shi P, Ma Y, Yang Y, Richards K, Wesche K, Miehe G, Leuschner C, Kuzyakov Y, Guggenberger G, Foken T (2011). Effects of land use change and monsoon variability on atmosphere-ecosystem exchange in high alpine grasslands on the Tibetan Plateau. 3rd iLEAPS Science Conference, 18.-23.09.2011, Garmisch-Partenkirchen

Hafner S, Unteregelsbacher S, **Seeber E**, Xu X, Li X, Guggenberger G, Miehe G, Kuzyakov Y (2011). Effect of grazing on C stocks and assimilate partitioning in Tibetan montane pasture revealed by $^{13}CO_2$ pulse labeling. Poster at the 7th Sino-German Workshop on Tibetan Plateau Research, 03.-06.03.2011, Hamburg

Miehe G, Miehe S, Wesche K, **Seeber E**, Zhao X, Liu J (2009). “Alpine Meadows” of the Tibetan Plateau are a synanthropic pseudoclimax, Poster at the 6th Sino-German Workshop on Tibetan Plateau Research, 10.-13.10.2009, Qingdao

**Seeber E**, Winterfeld G, Sharbel T, Durka W, Hensen I, Liu Jianquan, Miehe G, Wesche K (2011). How *Kobresia pygmaea* maintains dominance – A study on generative reproduction, clonal growth and polyploidy. Poster at the 7th Sino-German Workshop on Tibetan Plateau Research, 03.-06.03.2011, Hamburg

Wang Y, Lehnert L, Holzapfel M, Schulz R, Heberling G, Görzen E, Meyer H, **Seeber E**, Pinkert S, Ritz M, Ansorge H, Bendix J, Seifert B, Miehe G, Long RJ, Yang YP, Wesche K (2015). Testing congruence among multiple grazing indicators: a multi-site study across the Tibetan plateau. Poster at the EGU General Assembly, 12.-17.04.2015, Vienna

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|---|---|
| 2009-2011 | Wissenschaftliche Mitarbeiterin (Priority Programme 1372, „Tibetan Plateau: Formation, Climate, Ecosystems“), Georg-August-Universität Göttingen<br>Thema: “Monitoring of vegetation dynamics in the *Kobresia* ecosystem in relation to grazing intensity” |
| 2011-2014 | Wissenschaftliche Mitarbeiterin (Priority Programme 1372, „Tibetan Plateau: Formation, Climate, Ecosystems“), Senckenberg Museum für Naturkunde, Görlitz<br>Thema: “Monitoring of vegetation dynamics in the *Kobresia* ecosystem in relation to grazing intensity” |
| Seit Nov 2014 | Wissenschaftliche Mitarbeiterin, Philipps Universität Marburg<br>Herbarmanagement Myanmar |

**Praktische Erfahrungen**

| | |
|---|---|
| 2006 | •Vegetationskartierung im Naturschutzgebiet Federsee, Deutschland |
| 2007 | •Phytopathologisches Forschungsgruppenpraktikum (Leibniz-Institut für Pflanzenbiochemie, Halle)<br>•Praktikum zu molekularen Methoden in der Medizin (Institut für Medizin, MLU) |

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| | •Praktikum zur Bestäubungsökologie und Vegetationskunde, Hustai-Nationalpark, Mongolei<br>•Studentische Hilfskraft: DNA-Extraktion (Institut für Geobotanik, MLU) |
| 2008 | •Vetationskundliches Praktikum, Erzgebirge, Deutschland<br>•Studentische Hilfskraft: Molekulare Systematik afrikanischer *Erica*-Arten (DNA-Extraktion, RAPD, Auswertung) (Institut für Geobotanik, MLU)<br>•Vetationskundliche Exkursion, Schweiz<br>•Studentische Hilfskraft: FUPERS-Deutsche Biodiversitäts-exploratorien (Helmholtz-Zentrum für Umweltforschung) |
| 2009 | •Studentische Hilfskraft: DNA-Extraktion und Bodenanalysen (Institut für Geobotanik, MLU) |
| 2010 | •Lehrauftrag für Ökologisches Grundpraktikum (Institut für Geobotanik, MLU) |
| 2012 | •Durchführung des internationalen Symposiums „Biodiversity Research in Mongolia“ in Halle/Saale |
| 2014 | •Durchführung des „Biodiversity and Ecosystems Retreat“ in Görlitz, Germany<br>•Organisation und Durchführung des „Young Scientist Retreats 2014“ in Görlitz, Germany |

**Forschungsaufenthalte im Ausland**

Feldarbeiten in China und Tibet im Rahmen des Priority Programme 1372, „Tibetan Plateau: Formation, Climate, Ecosystems“ (DFG) und seit 2011 des BMBF Projektes PaDeMoS (Pasture Developing Monitoring System)

2009: 4 Monate; 2010: 3 Monate; 2011: 3 Monate; 2012: 2 Monate; 2013: 3 Monate

**Betreuung von Abschlussarbeiten**

| | |
|---|---|
| 2011-2012 | •Catherina Wypior: „Genetic diversity of *Salvia pratensis* in connection with population size“ (Masterarbeit)<br>•Sabrina Träger: „Analysis of the productivity of *Kobresia pygmaea* pastures on the Tibetan Plateau“(Masterarbeit) |

**Fremdsprachen**

Deutsch (Muttersprache)
Englisch (fließend in Wort und Schrift)
Französisch (Grundkenntnisse)
Latein (Grundkenntnisse)
Chinesisch (Grundkenntnisse)

## Erklärung über den persönlichen Anteil an den Publikationen

**CHAPTER 2:** Seeber E, Winterfeld G, Hensen I, Sharbel TF, Durka W, Liu J, Yang YP, Wesche K (2014). Ploidy in the alpine sedge *Kobresia pygmaea* (Cyperaceae) and related species: combined application of chromosome counts, new microsatellite markers and flow cytometry. *Botanical Journal of the Linnean Society* **176**: 22–35.

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|---|---|
| Field work: | **Elke Seeber** (100 %) |
| Laboratory work: | **Elke Seeber** (75%); G Winterfeld (20%); TF Sharbel and W Durka (advisory 5%) |
| Data analysis: | **Elke Seeber** (90%); G Winterfeld (5%); K Wesche (advisory 5%) |
| Writing: | **Elke Seeber** (80%); corrections by all co-authors (together 20%) |

**CHAPTER 3:** Seeber E, Miehe G, Hensen I, Yang YP, Wesche K (2015) Mixed reproduction strategy and polyploidy facilitate dominance of *Kobresia pygmaea* on the Tibetan Plateau (2015). *Journal of Plant Ecology* doi:10.1093/jpe/rtv035.

| | |
|---|---|
| Field work: | **Elke Seeber** (100 %) |
| Laboratory work: | **Elke Seeber** (100%) |
| Data analysis: | **Elke Seeber** (90%); K Wesche (advisory 10%) |
| Writing: | **Elke Seeber** (80%); corrections by all co-authors (together 20%) |

**CHAPTER 4:** Seeber E, Miehe G, Hensen I, Liu J, Tian X, Nowak PM, Wesche K (submitted). From allele to species level: Genetic diversity and mode of reproduction of the dominant species shape plant community composition along an elevational transect on the Tibetan Plateau. *Global Ecology and Biogeography*.

| | |
|---|---|
| Field work: | **Elke Seeber** (50 %); G Miehe, J Liu, X Tian and PM Nowak (Vegetation records 50%) |
| Laboratory work: | **Elke Seeber** (100%) |
| Data analysis: | **Elke Seeber** (90%); K Wesche (advisory 10%) |
| Writing: | **Elke Seeber** (80%); corrections by all co-authors (together 20%) |

**CHAPTER 5:** Seeber E, Träger S, Hensen I, Guggenberger G, Miehe M, Wesche K (submitted). Co-limitation by nitrogen and phosphorus rather than climate shapes plant performance in alpine Tibetan pastures. *Oecologia.*

Field work: **Elke Seeber** (95 %); S Träger (5%)
Laboratory work: **Elke Seeber** (100%)
Data analysis: **Elke Seeber** (90%); K Wesche (advisory 10%)
Writing: **Elke Seeber** (80%); corrections by all co-authors (together 20%)

**CHAPTER 6:** Hafner S, Unteregelsbacher S, Seeber E, Becker L, Xu X, Li X, Guggenberger G, Miehe G, Kuzyakov Y (2012). Effect of grazing on carbon stocks and assimilate partitioning in a Tibetan montane pasture revealed by $^{13}CO_2$ pulse labeling. *Global Change Biology* **18**: 528–538.

Field work: **Elke Seeber** (10 %); S Hafner, S Unteregelsbacher (90%)
Data analysis: **Elke Seeber** (5%); other authors (together 95%)
Writing: **Elke Seeber** (5%); other authors (together 95%)

**CHAPTER 7:** Ingrisch J, Biermann T, Seeber E, Leipold T, Li M, Ma Y, Xu X, Miehe G, Guggenberger G, Foken T, Kuzyakov Y (2015). Carbon pools and fluxes in a Tibetan alpine *Kobresia pygmaea* pasture partitioned by coupled eddy-covariance measurements and $^{13}CO_2$ pulse labeling. *Science of the Total Environment* **505**:1213–1224.

Field work: **Elke Seeber** (20 %); J Ingrisch and T Biermann (80%)
Laboratory work: **Elke Seeber** (10%); J Ingrisch (90%)
Writing: **Elke Seeber** (5%); other authors (together 95%)

## Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig und ohne fremde Hilfe verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Wörtliche oder inhaltliche Zitate wurden von mir als solche kenntlich gemacht.
Darüber hinaus erkläre ich, dass diese Dissertationsschrift erstmalig der Naturwissenschaftlichen Fakultät I (Biowissenschaften) der Martin-Luther-Universität Halle-Wittenberg zur Promotion vorgelegt wird und auch bei keiner anderen Universität eingereicht ist oder war.

Marburg, den 06. Juli 2015

Elke Seeber