1	Predicting parameters of degradation succession processes					
2	of Tibetan Kobresia grasslands					
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4	$L Lin^1$ , Y. K. $Li^{1*}$ , X. L. $Xu^{2*}$ , F. W. Zhang $^1$ , Y. G. $Du^1$ , S. L. $Liu^1$ , X. W. $Guo^1$ , G. M. $Cao^1$					
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6	<sup>1</sup> Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, China					
7	<sup>2</sup> Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences					
8	and Natural Resources, Chinese Academy of Sciences, Beijing 100101, China					
9						
10	*Correspondence to: Y.K. Li, E-mail: liyikang501@163.com, and X.L. Xu, E-mail:					
11	xuxingl@hotmail.com					
12						

**Abstract** In the past two decades, increasing human activity (i.e., overgrazing) in the Tibetan Plateau has strongly influenced plant succession processes, resulting in the degradation of alpine grasslands. Therefore, it is necessary to diagnose the degree of degradation to enable implementation of appropriate management for sustainable exploitation and protection of alpine grasslands. Here, we investigated environmental factors and plant functional groups quantity factors (PFGs) during the alpine grassland succession processes. Principal component analysis (PCA) was used to identify the parameters indicative of degradation. We divided the entire degradation process into six stages. PFG types shifted from rhizome bunch grasses to rhizome plexus and dense plexus grasses during the degradation process. Leguminosae and Gramineae plants were replaced by Sedges during the advanced stages of degradation. The PFGs were classified into two reaction groups: the grazing-sensitive group, containing Kobresia humilis Mey, and Gramineae and Leguminosae plants, and the grazing-insensitive group, containing Kobresia pygmaea Clarke. The first group was correlated with live root biomass in the surface soil (0-10 cm), whereas the second group was strongly correlated with mattic epipedon thickness and K. pygmaea characteristics. The degree of degradation of alpine meadows may be delineated by development of mattic epipedon and PFG composition. Thus, meadows could be easily graded and their use adjusted based on our scaling system, which would help prevent irreversible degradation of important grasslands. Because relatively few environmental factors are investigated, this approach can save time and labor to formulate a conservation management plan for degraded alpine meadows.

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**Key words:** Degradation grassland, grazing, alpine meadow, grassland health estimate

# 1 Introduction

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Alpine grasslands are one of the most important grassland types on earth, and they are distributed across the tundra zone of North Eurasia and North America. More than 48% of alpine grasslands are distributed on the Tibetan Plateau of China (Sun and Zheng, 1998; Wang et al., 1998; Harmsen and Grogan, 2008). Alpine grasslands represent one of the major natural types of pastures for pastoralists living in alpine regions, especially for those living on the Tibetan Plateau where livestock grazing is the most important human activity (Zhang et al., 2003a). Livestock mainly affects alpine grasslands through two ways. First, their grazing can affect the structure and composition of plant community, and the constitution of plant life forms and ecotypes in alpine grasslands (de la Paix et al., 2013; Zhao et al., 2013; Mekuria and Aynekulu, 2013). Second, their trampling can reduce infiltration rates, surface sealing, and physical crust formation (Cerda and Lavee, 1999; Angassa, 2014). With increased grazing, a part of alpine grasslands gradually degrade and become bare soil due to decreased vegetation protection (Zhang et al., 2003b; Zhang et al., 2003c; Wang et al., 2007a, b; Foggin, 2008). Consequently, this reduces the role of alpine grasslands in soil and water protection (Wen et al., 2010; Brandt et al., 2013; You et al., 2014). Such grazing-induced degradation of alpine grasslands has been observed in the early 2000s (Wang et al., 1997; Liu et al., 2008; Wang et al., 2009; Harris, 2010; Lin et al., 2013a, b), mainly because livestock number increased from approximately  $0.8 \times 10^8$  in 1997 to  $1.08 \times 10^8$  sheep unit in 2011 on the Tibetan Plateau (Yang, 2002; He et al., 2008; Sun, 2012). In the past decade, degradation in alpine grasslands has been getting more and more serious due to increasing grazing density. This has started to affect the living of pastoralists and the development of local economy. How to restore those degraded grasslands and maintain sustainable development

of alpine grasslands is a big challenge. An important prerequisite for this is how to diagnose the degree to which alpine grasslands have degraded (Li et al., 2014). So far, numerous studies separately used plant community (Han et al., 2008; Lin et al., 2013a,b; Angassa, 2014; Giangiacomo, 2014) or environmental indexes (Lin et al., 2010, 2013a, b) as indicators to diagnose grassland degradation (Li et al., 2014; Wang et al., 2015). However, grassland degradation caused by grazing is a very complicated ecological process, including changes in both vegetation and soil. This emphasizes the importance of the plant-soil system for improving degradation of alpine grasslands.

Among the plant-soil system, plants are the link of the atmosphere, biosphere, hydrosphere, and lithosphere (Brevik et al., 2015). The existence of plants can protect the soil surface against kinetic energy of drops, reduces runoff and increases infiltration (Groen and Wood, 2008). Therefore, the vegetation cover play a fundamental role in the soil development and soil erosion (Cerdà 2002; Keesstra et al., 2014), and soil degradation (Ziadat and Taimeh, 2013), and also in the geomorphological (Nanko et al., 2015) and hydrological (Keesstra, 2007; Gabarrón-Galeote et al., 2013) behaviour of the Earth System and their interactions with the biota (Ara Go et al., 2014; Bochet et al., 2015). At the same time, plants can shape soil microenvironments through living roots (Bardgett, 2002; Puente et al., 2004; Cerdà 2002; Dai et al., 2013; Keesstra et al., 2014; Shang et al., 2014; Keesstra, 2014; Gabarrón-Galeote et al., 2013) and affects microbial function (Wang et al., 2015; Pereg and McMillan, 2015). In contrast to the vegetation, the soil system provides an important carrier for growth of plants and microorganisms. Almost all nutrient transformation processes operate by microorganisms in the soil. Therefore, the analysis on the soil-plant system must be approached from a multidisciplinary strategy (Brevik et al., 2015).

To identify the degradation stages of the Tibetan Kobresia grasslands, we conducted a large

field investigation in alpine grasslands across the Qinghai province. We collected a large number of indicators, including visible (e.g., species diversity, plant height, vegetation coverage, and plant biomass, plant functional groups) and invisible (e.g., root biomass, organic matter content, total nitrogen, and available nutrients in the soil). To reduce the parameters dimensionality (Lin et al., 2012), ordination and classification approaches were used for the multivariate analysis because it has been used to explore which factors contribute most to plant community change (Ali et al., 2014; Christopher, 2014). Therefore, our objectives of this study are to: (1) analyze the degree of degradation in grasslands through reducing the parameter dimensionality from a large number of visible and invisible parameters, and (2) develop a useful approach to diagnose and predict the extent of degradation of alpine grasslands for the sustainable development of alpine grasslands.

## 2 Materials and methods

## 2.1 Study area

- The experimental sites were located in the flat ground which slopes are less than 5°. And the experimental sites were distributed in districts of Haibei, Guoluo, and Yushu in Qinghai Province, China. These sites are characterized by a typical alpine climate and are dominated by typical alpine grasslands. Detailed information on these sites is presented in Fig 1.
  - In this study, we investigated 96 plots (100 m  $\times$  100 m) from 32 counties in three districts. These plots were selected according to the following criteria: similar annual average precipitation (509.2  $\pm$ 23.7 mm) and temperature (-1.04  $\pm$ 0.4 °C), along with the same grassland type (alpine *Kobresia* meadow) over the past two decades, according to the grassland resource map of China at the 1:1000000 scale (1992), at that time the grasslands were the same class in grassland resource

map of China in 1992, but two decades past those grasslands were degraded into different degrees. On the basis of the change in plant communities, we divided the 96 plots into 6 vegetation types, and choose 2-3 plots in every type to study the plant community and soil properties (Fig. 1, Table 1, Lin et al., 2012): (1) Gramineae grass-*Kobresia humilis* Mey community (stage I), (2) *K. humilis* community (stage II), (3) thickening-in-mattic-epipedon of the *Kobresia pygmaea* Clarke community (stage III), (4) cracks-in-mattic-epipedon of the *K. pygmaea* community (stage IV), (5) collapse-in-mattic-epipedon of the *K. pygmaea* community (stage V), and (6) forbs-"black-soil beach" (stage VI). Detailed information about the vegetation types of typical experimental sites is presented in Table 1.

# 2.2 Field investigations and laboratory analyses

Total vegetation coverage, the percentage coverage of each functional plant group, and the aboveground/belowground biomass proportion in all plots were investigated in August 2009. Aboveground biomass was estimated by harvesting plants from five  $0.25 \text{ m}^2$  quadrats selected randomly within each plot.

Gramineae and sedge are divided into three major plant life forms (PLFs) in Tibetan *Kobresia* meadows. All the three PLFs are edible, but have different traits. One is a rhizome bunch type. This type propagates by rhizomes and seeds. In general, this type germinates in early spring, and the seeds mature in early autumn. This PLF is highly sensitive to grazing because the period of grazing by animals and high growth sensitivity of the plants coincide. The second PLF is the rhizome plexus-type. This type propagates mainly through its rhizomes. They often dominate the lower layer (3-5 cm) of the plant community. The third PLF is the rhizome dense plexus type. Due to the dense

plexus, this type is able to accelerate the development of the mattic epipedon. The soil surface of alpine meadows contains a mixture of live and dead roots of different ages. It is an active layer where nutrients and energy exchange occur very quickly. As a result, excess root growth causes an imbalance between soil nutrients and soil moisture, which accelerates the degradation of alpine grasslands. *K. pygmaea* is a typical species that contributes to this process.

On the basis of the stated traits, plants were divided into six PFGs: Gramineae, other sedges, *K. humilis*, *K. pygmaea*, Leguminosae, and forbs (Table 2). Roots were collected from two soil depths (0–10 cm and 10–20 cm) with an earth-auger (6 cm diameter). In each plot, 25 cores were randomly collected, with every 5 cores being pooled together as a combined sample. In each plot, there were 5 combined samples. The cutting ring method was used to estimate bulk density in the top 10 cm of soil. Large root fragments were washed after the associated soil was passed through a 0.25-mm sieve. The proportion method was used to distinguish live from dead roots (Lu et al., 2007). All plant materials were dried in an oven at 80 °C for 48 h and weighed for biomass determination (Chinese Ecosystem Research Network Scientific Committee, 2007). Plant community importance values included estimates of the average of relative coverage and relative aboveground biomass of PFGs.

# 2.3 Statistical analysis

All statistical analyses and construction of graphs were performed by the Canoco 4.5 software package for Windows. Euclidean Cluster Analysis (ECA) was used to divide the 96 plots into 6 stages. Live root biomass, dead root biomass, soil bulk density, and the thickness of mattic epipedon were used as the environmental factors in the principal component analysis (PCA). Pearson's correlation coefficient was calculated to identify any correlations between variables. Arithmetic

means with standard errors were calculated for all of the data. Plant community importance values were based on the equation:  $IV = \frac{C+B}{2}$ , in the equation "IV" represented "important value", "C" represented "average of the relative coverage" and "B" represented "relative aboveground biomass". Values were considered significant at the P < 0.05 level.

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#### 3 Results

## 3.1 PFG characteristics

The succession process of the alpine Kobresia grassland involved the replacement of functional plant groups (Fig. 2). Gramineae was the dominant edible forage type, and had the highest husbandry value of all forage matter during community succession. The highest importance value was 40.7±1.8% presented in Stage I, it was significant higher than any Stage IV, V and VI, and had no difference between Stage II and III. The lowest one was 9.5 ±2.3% presented in Stage IV, and it was significant lower than Stage I, II,III and V, but had no significant difference to Stage VI (Fig. 3A). The important values of Gramineae ranged from 28.6%  $\pm 2.1\%$  to 40.8%  $\pm 1.8\%$ . The highest values were recorded in stage III, and there was no significant difference between the first three stages. K. humilis belongs to the Cyperaceae family, and was widely distributed among the dwarf plants during the entire growing season. By comparison, K. humilis disappeared from stage V onwards (Fig. 3B). During the succession process, K. pygmaea gradually replaced Gramineae. The contribution of K. pygmaea was minimal during the first three stages of succession, but increased from stage IV onwards. The highest importance value (48.7±3.9%) of K. pygmaea appeared in the stage V (Fig. 3C).

As the grassland became increasingly degraded, the importance values of Leguminosae initially

increased and then decreased (Fig. 3E). The importance values of Forbs were low during stages I and VI, but were similarly high during all other stages (Fig. 3 A-F).

## 3.2 Root biomass and distribution

The quantity of both live and dead roots increased during early succession, and then decreased with increasing grassland degradation. The highest live-root biomass in the top 10 cm of soil occurred at stage IV (19.4  $\pm$  1.8 kg m<sup>-2</sup>), while the highest dead-root biomass occurred at stage V (29.3  $\pm$  2.31 kg m<sup>-2</sup>). Dead-root biomass was consistently higher than live-root biomass in the top 10 cm soil (Fig. 4A).

Live- and dead-root biomass in the 10–20 cm soil layer increased during the early stages of succession, with a steep decrease in the final stage (Fig. 4). Similar live-root biomass was recorded between stages II and III, but was significantly higher at stage IV compared to stages I and VI. The highest dead-root biomass was recorded at stage V (Fig. 4B).

# 3.3 Thickness of the mattic epipedon and soil bulk density

The thickness of the mattic epipedon increased over the first 5 stages of succession; however, the mattic epipedon disappeared at the final stage, because it was destroyed. The greatest thickness of the mattic epipedon occurred at stage V (18.4  $\pm 0.8$  cm). In comparison, stage IV represented a transition stage, before which the thickness was approximately 5cm (Fig. 5).

Soil bulk density in the top 10 cm decreased with the succession process, due to increased root biomass, with the lowest value being recorded at stage IV, and then increased in the final stage, with

the highest value of  $1.1 \pm 0.1$ g cm<sup>-3</sup> (Fig. 6).

## 3.4 Bare ground coverage in the plant community

Bare ground coverage in the plant community increased during community succession, showing three states. The first state was in stage I, in which almost all soil was covered (93% coverage). The second state included stages II and III, with approximately 20% bare ground coverage. The third state encompassed stages IV to VI, with approximately 50% space coverage (Fig. 7).

# 3.5 Relationship between PFGs and the environment

The principal component analysis of the PFG and environmental factors matrices showed that two important principal components explained 82.9% of the total variance (Fig. 8). The first axis explained 49.1% of the total variance, showing a strong positive correlation with *K. pygmaea* and a negative correlation with Leguminosae and Gramineae. The first principle axis also showed a positive correlation with the thickness and area of the mattic epipedon and a negative correlation with live-root biomass. The second principle axis explained 33.8% of total variance, showing a positive correlation with forbs and a negative correlation with Leguminosae, Gramineae, and *K. pygmaea*. The second axis was positively correlated with soil bulk weight and negatively correlated with live- and dead-root biomass (Fig. 8).

The environmental factors were divided into two new types: (1) the first environmental axis was related to mattic epipedon characteristics, whereas (2) the second environmental axis was related to soil bulk weight. The first PFG group was strongly related with the plexus-type plant group. The

second functional plant group was strongly related with the forage-type plant group (Fig. 8). The thickness of mattic epipedon had a strong positive correlation with *K. pygmaea*. Soil bulk density was strong positive correlation with herbs, but negatively correlation with Gramineae and Leguminosae.

## 4 Discussion

As *Kobresia* grasslands became degraded, there was a clear shift in dominant PFGs. This shift has been previously linked to trampling and selective grazing by livestock (Cao et al., 2007; Du et al., 2007; Lin et al., 2012; Lin et al., 2013a,b), and the shift was Leguminosae and Gramineae plants were replaced by Sedges when the livestock grazing intensity increased. In alpine grasslands, *Stipa* spp. and *Festuca* spp. are highly edible Gramineae forage (Wang et al., 2008). These plants turn green in early spring and continue to have high aboveground biomass in autumn when the plant community withers. Overgrazing at the turning-green period (i.e., early spring) and the fructicative period in autumn interrupts the normal growing cycle of these plants and reduces their dominance in the plant community. Consequently, the dominance of low feeding-value plants (e.g. non-leguminous broad-leaved herbs) or low-growing plants (e.g., *K. pygmaea* and *K. humilis*) increases (Lin et al., 2012). Therefore, PFGs are expected to reflect the effects of grazing on alpine grasslands and the degradation process.

A clear changing pattern in PFG characteristics and environmental factors during the degradation process (Fig. 8) is mainly caused by a shift from sensitive to endurable plants in response to grazing pressure. As livestock number increases in alpine grasslands, dense-plexus plants

(K. pygmaea) replace rhizome plexus-type plants (e.g. Scirpus spp. and K. humilis) as the dominant vegetation type in the community. K. pygmaea differing from other sedges, such as Scirpus spp. and K. humilis, may help to maintain the community structure despite substantial livestock grazing (Lin et al., 2008; Wang et al. 2008), because it increases root biomass, which safeguards plants against livestock pressure and increases the activity of the plant community. This response causes the thickness of the mattic epipedon to increase and form a developed cushion to alleviate livestock trampling (Lin et al., 2008), with K. pygmaea being a major contributor. Therefore, the thickness of the mattic epipedon represents a critical environmental index for describing the extent of grassland degradation. The increasing dominance of K. pygmaea in the plant community serves as an early alert for degradation in alpine grasslands.

The thickening of the mattic epipedon represents a reciprocal response between the plant community and associated environmental factors during the succession process. As the mattic epipedon thickens, many environmental factors such as the thickness of mattic epipedon, and soil bulk as soil moisture and temperature have been changed, generating positive feedback to overgrazing that has dual effects on alpine grasslands. Initially, increased root biomass enhances water retention and nutrient uptake in the soil (Li et al., 2012). To a certain extent, this action improves the quality of alpine grassland soils. However, increased biomass leads to higher ratios of roots to soil due to high root volume (Wang et al., 2007a; Wang et al., 2008). Subsequently, the number of dead roots increased due to altered environmental factors. The decomposition of these dead roots was not enhanced because there are two reasons. First, thick mattic epipedon obstructs the air diffusion and water infiltration, decreasing microbial activity and decomposition. Second, low temperature also leads to slow decomposition of dead roots. Consequently, root activity decreases

and causes an imbalance among soil nutrients. At this point, the degradation of alpine meadows is inevitable (Cao et al., 2007).

Therefore, alpine meadow degradation involves two processes. The first process is passive, and is driven by overgrazing (Lin et al., 2008; Wang et al., 2008). The second process is active, and initiated when the mattic epipedon thickens due to the increasing dominance of *K. pygmaea* in the plant community and ends as forbs-"black soil beach." In the first stage of succession, alpine grasslands may be rapidly recovered by excluding livestock. However, it is difficult to recover alpine grasslands by excluding livestock once the second stage of the succession process has been reached. At this point, it would be necessary to use artificial approaches to restore the degradation grasslands. However, the mechanisms causing grassland degradation need to be elucidated to fully understand the factors that contribute to this process. Future studies should integrate new tools, such

## **5 Conclusions**

(1) PFGs numerical features and root activity, together with certain physical properties of soil, could be used as indicators of the degree of degradation in alpine grasslands. The visible properties such as PFGs and the thickness of mattic epipedon were correlated with invisible properties such as root activities. Therefore, the degree of degradation of alpine grasslands can be predicted by development of mattic epipedon and changes in PFGs.

as molecular and isotope approaches, to clarify these mechanisms.

(2) Alpine grasslands are very fragile to grazing and are easily degraded. Based on our study above, the degree of degradation in alpine grasslands can be well predicted using relatively few environmental factors. This approach can save time and easily help pastoralists to efficiently manage their grasslands.

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Table 1. Detailed information about the six degradation successional stages of alpine *Kobresia* grasslands.

Succession stage	Abbrevi ation	Study area	Geographical position	Plot general situation
Gramineae grass-K. humilis community	Stage I	Maqin County of Guoluo	34 '28'N, 100 '12'E 3751 m asl	Dominant plants are <i>Elymus nutans</i> , <i>Poa</i> sp., <i>Festuca rubra</i> , coverage 93%, the thickness of the mattic epipedon is 1.66 cm, the average livestock number is 4 sheep units per ha
		Huangcheng County of Haibei	37 40' N, 101 11' E 3232 m asl	
		Ebo County of Haibei	37 56 N, 100 58 E, 3419 m asl	
K. humilis community	Stage II	Huangcheng County of Haibei	37 40'N, 101 11'E 3232 m asl	Dominant plants are <i>K. humilis</i> , subdominant species are <i>E. nutans</i> , <i>Poa</i> sp. and <i>F. rubra</i> , coverage 96.7%, the average thickness of the mattic epipedon is more than 2 cm but less than 3, the average livestock number is 8 sheep units per ha.
		Batang County of Yushu	35 °51'N, 96 °60'E 3907 m asl	
Thickening-in-mattic-epipedon <i>K. pygmaea</i> community	Stage III	Maqin County of Guoluo	34 °28'N, 100 °12'E, 3751 m asl	Dominant plants are <i>K. pygmaea</i> , coverage 81%, the meadow has a rugged surface, the average thickness of the mattic epipedon is more than 3 cm but less than 5 cm, the average livestock number is 11 sheep units per ha
		Huangcheng County of Haibei	37 40'N, 101 11' E 3232 m asl	
Cracks-in-mattic-epipedon <i>K. pygmaea</i> community	Stage IV	Maqin County of Guoluo	37 40'N, 101 11' E, 3232 m asl	Dominant plant is <i>K. pygmaea</i> , the alpine <i>K. pygmaea</i> species mottling are not less than 85%; there are many crannies dividing the meadow into big alpine <i>K. pygmaea</i> mottling, there is hypogenesis of <i>K. pygmaea</i> within the mottling, the average thickness of the mattic epipedon is more than 5 cm but less than 7 cm, the average livestock number is 13 sheep units per ha
		Batang River beaches of Yushu	35 %1'N, 97 00 'E 3907 m asl	
Collapse-in-mattic-epipedon <i>K</i> . <i>pygmaea</i> community	Stage V	Maqin County of Guoluo	34 <sup>2</sup> 8'N, 100 <sup>9</sup> 2'E 3751 m asl	Dominant plant is <i>K. pygmaea</i> , the meadow surface are intensity collapsed into a lot of insulation mattic epipedon islands, the collapse ground are parent material, the average thickness of the mattic epipedon is more than 7 cm, the average livestock number is 14 sheep units per ha
		Huangcheng County of Haibei	37 40' N, 101 91' E, 3232 m asl	
		Ebo County of Haibei	37 56 N, 100 58 E, 3429m asl	
Forbs-"Black-soil beach"	Stage VI	Maqin County of Guoluo	34 °28'N, 100 °12'E, 3751 m asl	The dominant plants are forbs, with <i>K. pygmaea</i> , coverage is 46%, there is no mattic epipedon, the surface is loose, in winters there are no plants covering the ground, there is no edible plant for grazing.
		Menyuan County of Haibei	37 37 N, 101 19 E 3196 m asl	

Table 2. Plant functional groups and their composition or traits

Plant functional group	Main composition or traits			
Gramineae	Composition: Festuca spp., Stipa spp., Poa spp., etc.			
	Trait: rhizome bunch type, rhizome plexus-type, and rhizome dense-plexus type.			
K. humilis	Trait: rhizome plexus-type.			
K. pygmaea	Trait: rhizome dense-plexus type.			
Other sedges	Composition: Carex spp., Cyperus spp., Kobresia spp. (exclusively K. humilis and K.			
	pygmaea), etc.			
	Trait: rhizome bunch type, rhizome plexus-type and rhizome dense-plexus type.			
Leguminosae	Composition: Gueldenstaedtia verna, Melissilus ruthenicus, Oxytropis spp., Astragalus			
	spp., etc.			
	Trait: Axis root plants.			
Forbs	Composition: Asteraceae, Gentianaceae, etc.			
	Trait: Non-leguminous broad-leaved herbs.			

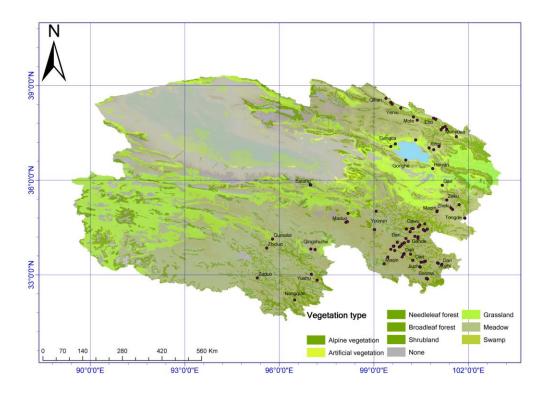


Fig 1 The location of experimental sites.



Fig. 2 The degradation-succession of Tibetan alpine *Kobresia* grasslands was divided into six stages: (A) The *Gramineae* grass-*K. humilis* community (stage I), (B) The *K. humilis* community (stage II), (C) The thickening-in-mattic-epipedon of the *K. pygmaea* community (stage III), (D) The cracks-in-mattic-epipedon of the *K. pygmaea* community (stage IV), (E) The collapse-in-mattic-epipedon of the *K. pygmaea* community (stage V), and (F) The forbs-"black-soil beach" (stage VI).

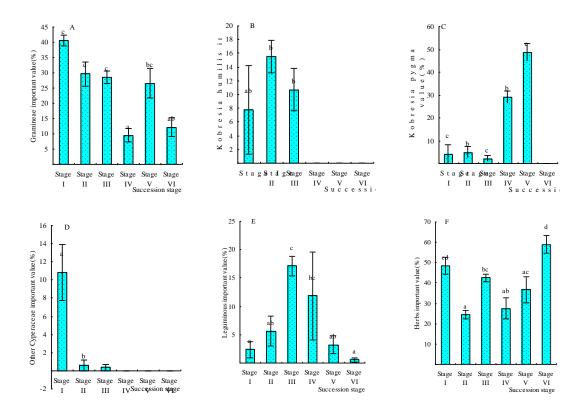


Fig. 3. The characteristics of the four plant functional groups in a degradation successional series of Tibetan alpine grasslands: (A) *Gramineae*, (B) *Kobresia humilis*, (C) *Kobresia pygmaea*, (D) other sedges, (E) *Leguminosae*, and (F) Forbs. Different letters in the figures indicate significant differences between the stages at P < 0.05.

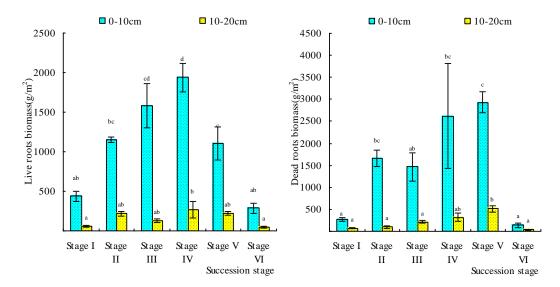


Fig. 4. Living-root biomass (a) and dead-root biomass (b) at 0–10 cm and 10–20 cm depths. The values represent the means  $\pm$  1SD of four replicates. Different letters in the figures indicate significant differences between the stages at P < 0.05. The stage details refer to Fig. 2.

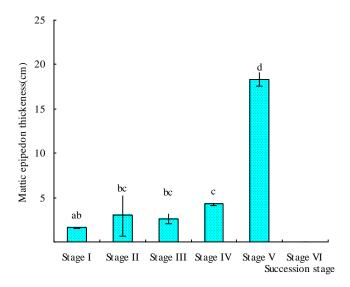


Fig. 5. The thickness of mattic epipedon over the course of succession. The values represent the means  $\pm$  1SD of four replicates. Different letters in the figures indicate significant differences between stages at P < 0.05. The stage details refer to Fig. 2.

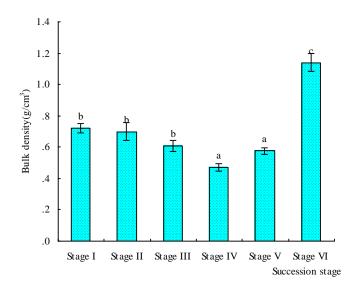


Fig. 6. Surface soil-bulk density over the course of succession. The values represent the means  $\pm 1SD$  of four replicates. Different letters in the figures indicate significant differences between stages at P < 0.05. The stage details refer to Fig. 2.

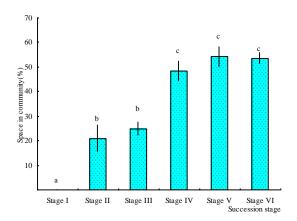


Fig. 7. The space coverage over the course of succession. The values represent the means  $\pm$  1SD of four replicates. Different letters in the figures indicate significant differences between stages at P < 0.05. The stage details refer to Fig. 2.

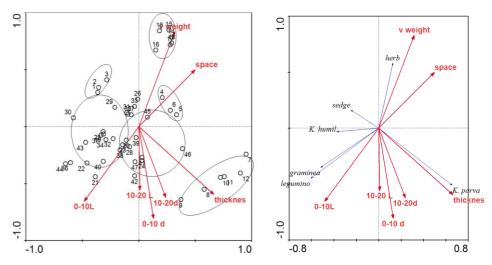


Fig. 8. The plant functional groups and environment PCA ordination bioplot. Black items denote plant functional groups, red items denote environmental factors. "V weight" denotes the soil bulk density, "space" denotes the space in community (bared place), "thickness" denotes the thickness of mattic epipedon, 0–10L denotes the live roots in the 0–10 cm soil layer, 10–20L denotes the live roots in the 10–20 cm soil layer, 0–10 d denotes the dead roots in the 0–10 cm soil layer, 10–20 d denotes the dead roots the10–20 cm soil layer, herb denotes the non-leguminous broad-leaved herb plant functional group, sedge denotes the sedge plant functional group (excluding *K. humilis* and *K. pygmaea*), Gramineae denotes the Gramineae plant functional group, *legumino* denotes the Leguminosae plant functional group, *K. humili* denotes the *K. humilis*, and *K. parva* denotes the *K. pygmaea*.