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Predicting parameters of degradation succession processes of Tibetan *Kobresia* grasslands

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], and G. M. Cao[1]

[1]Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, China
[2]Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources, Chinese Academy of Sciences, Beijing 100101, China

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Correspondence to: Y. K. Li (liyikang501@163.com) and X. L. Xu (xuxingl@hotmail.com)

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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 group 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.

1 Introduction

The soil system is a key component of the Earth system and must be approached from a multidisciplinary strategy (Brevik et al., 2015). 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; Serrano Muela et al., 2015) and hydrological (Keesstra, 2007; Gabarrón-Galeote et al., 2015) behaviour of the Earth System and their interactions with the biota (Araujo et al., 2014; Bochet et al., 2015).

Plants are the link of the atmosphere, biosphere, hydrosphere, and lithosphere (Brevik et al., 2015). Plant cover protects soil against erosion, assembles organic matter, shapes soil, contributes to biofertilization by plant-growth-promoting rhizospheric (PGPR) microbes, and so on (Pereg and McMillan, 2015). Organisms especially in soil including plant root and rhizospheric microbes perform vital roles in shaping the soil environment through formation and modification of the soil architecture with pores and tunnels, the transportation of soil particles, and the creation of new soil habitats through the weathering of rocks (Puente et al., 2004). While the diversity and abundance of soil organisms influence soil functioning, the diversity and activity of soil organisms also depend on soil properties (Bardgett, 2002). The health of plant-soil system is the focus issue in natural eco-system, and plant and soil properties can reflect the health of the ecosystem.

Alpine grasslands are one of the most important types of grassland on earth. Alpine grasslands are distributed across the tundra zone of North Eurasia and North America, but mainly occur on the Tibetan Plateau (Harmsen and Grogan, 2008). A large area of alpine grasslands has been subject to different extents of degradation due to increased grazing of livestock. Alpine grasslands are important for pastoralists who rely on livestock for survival. Additionally, these grasslands play an important role in protecting soils and water (Wen et al., 2010; Brandt et al., 2013; You et al., 2014). Their degradation often causes hydrological disturbances and dust storms, in addition to leading to a scarcity of livestock products and uprooting people (Van et al., 1989; Zhang et al., 2003, Zhang et al., 2003a, b; Q. L. Wang, et al., 2007; Foggin, 2008). Thus, it is important to develop useful approaches to diagnose and predict the extent of degradation of alpine grasslands and to elucidate the mechanisms responsible for their degradation, which could provide a model for the sustainable development of alpine grasslands worldwide.

The Tibetan Plateau is termed the "roof" of the world, because it is a vast elevated plain (exceeding 4500 m) covering over 2.5 million km^2 (Dong et al., 2010). Alpine grasslands cover more than 48 % of the total area of the plateau (Sun and Zheng, 1998), and are regarded as one of the major natural types of pastures in China (Wang et al., 1998). Grasslands provide important ecosystem functions and services, including water conservation, livestock products and so on. Vegetation in the ecosystem plays a key role in soil development due to its influence on nutrient cycling, hydrological processes and soil erosion (de la Paix et al., 2013; Zhao et al., 2013). It protects the soil surface against kinetic energy of drops, reduces the amount of runoff generated, decreases runoff velocity and increases infiltration (Groen and Wood, 2008; Yasmina et al., 2014). It also produces a suitable environment by the roots and plant aboveground to raise more soil microorganisms to join in the material and energy cycling (Wang et al., 2015), to provide nutrients for plant growth, to adjust soil pH, or to induce positive effects on soil properties such as cation exchange capacity, bulk density and water-holding capacity (Dai et al., 2013; Shang et al., 2014). For example, pH value, live root, dead root, bulk density in the soil can reflect the plant aboveground healthy condition whether in grassland or forest ecosystems. Alpine meadows dominated by *Kobresia* spp. are inherently fragile and instable, with both human activity and climate change causing detrimental changes. Livestock grazing is the most important human activity on the Tibetan Plateau (Zhang et al., 2003b). Grazing can affect seed propagation and litter production, and alter the floristic composition of herbaceous species and thus decrease the grazing capacity of grasslands (Mekuria and Aynekulu, 2014). Over grazing can lead to an increase of bare soil due to increased erosion, e.g., trampling by livestock reduces infiltration rates, surface sealing, and physical crust formation (Cerda and Lavee, 1999; Angassa, 2014). Since the 1980s, the intensity of grazing has increased, causing varying degrees of degradation to alpine grasslands. The grazing-related degradation of most alpine grasslands on the Tibet Plateau started during the 2000s (Wang et al., 1997, 2009; Liu et al., 2008; Harris, 2010). Such grazing has substantially altered the plant species composition, and thus plant functional groups, in these alpine grasslands, as well as influencing abiotic factors (Lin et al., 2013a, b).

Diagnosing the degree to which these grasslands have become degraded is a prerequisite for their ecological restoration and sustainable management (Li et al., 2014). Consequently, numerous plant community and environmental indexes have been used as indicators for the mechanisms responsible for grassland degradation (Li et al., 2014; Wang et al., 2015). However, grassland degradation cannot be ascribed to a single factor. Therefore, elucidating ecological processes alone are not sufficient to improve our understanding about alpine grassland degradation (Harris, 2010; Han et al., 2014). It seems that more ecological factors you use, more appropriate it is to describe the ecological system. Thus, the challenge of identifying and predicting the degree of grassland degradation using easily obtainable indices remains.

In this regard, selecting the tools required to extract such indices form a large number of numerical indices is considered to be very important. If we can predict the degradation stages of Tibetan *Kobresia* grasslands by using visible indicators such as plant functional groups compositions as well as invisible indicators of plant root biomass, instead of so large number of parameters to elucidate the process of the degradation process of *Kobresia* grasslands, it will save so much time to relevant researches. Ordination and classification represent potential tools for developing specific quantitative approaches to capture the characteristics of grassland degradation (Lin et al., 2012). These tools have been often used for multivariate analyses of community structure, to explore which factors contribute most to plant community change (Ali et al., 2014; Christopher, 2014) and how we can use the multivariate analyzing to reduce the parameters dimensionality, in order to use less parameters to describe the more information hiding in the research subjects. So finding out the relationships between different factors in ecological system is the base to reduce the parameter dimensionality. Plant functional types (PFTs) is a group of combinations of plant species which have the common features to specific environmental factors and mechanisms of ecosystem processes to the similar reactions and impacts coming from environment. Many studies have investigated the relationship between environmental factors and plant community characteristics both basing on individual plant species and plant functional groups during the process of degradation succession using visible indicators, such as species diversity, plant height, vegetation coverage, and plant biomass (Han et al., 2008; Lin et al., 2013a, b; Angassa, 2014; Giangiacomo, 2014). There are so many technologies to divide grassland plant species into different plant functional groups, which is convenient than using species in field sampling. However, few studies have been considered in invisible indexes than visible indexes, such as organic matter content, total nitrogen, and available nutrients in the soil (Lin et al., 2010, 2013a, b).

In this study, we used the ordination and classification approaches to investigate the relationships between visible indexes (e.g., the growth of mattic epipedon characteristics) and invisible indexes (e.g., root activity, root biomass, and soil bulk density) in the degradation succession process of alpine grasslands. We aimed to reduce the parameter dimensionality and indentify the indices that could be used in visible parameter in the ecological system instead of invisible parameter to predict the degree of degradation in grasslands, and to improve the management of degraded alpine meadows.

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 Table 1.

In this study, we investigated 96 plots (100 m × 100 m) from 32 counties in three districts. These plots were selected according to the following criteria: similar annual average precipitation (509.2 ± 23.7 mm) and temperature (−1.04 ± 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 : 1 000 000 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 (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 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 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 periods 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 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. 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 average of the relative coverage and relative aboveground biomass. Values were considered significant at the $P < 0.05$ level.

3 Results

3.1 PFG characteristics

The succession process of the alpine *Kobresia* grassland involved the replacement of functional plant groups (Fig. 1). Gramineae was the dominant edible forage type, and had the highest husbandry value of all forage matter during community succession. The importance values of Gramineae decreased over the first four stages, increased at stage V, and again decreased during the final stage (Fig. 2a). The important values of Gramineae ranged from 28.6 ± 2.1 to 40.8 ± 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. 2b). 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. 2c).

As the grassland became increasingly degraded, the importance values of Leguminosae initially increased and then decreased (Fig. 2e). The importance values of Forbs were low during stages I and VI, but were similarly high during all other stages (Fig. 2a–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 degree. The highest live-root biomass in the top 10 cm of soil occurred at stage IV (19.4 ± 1.8 kg m^{-2}), while the highest dead-root biomass occurred at stage V (29.3 ± 2.31 kg m^{-2}). Dead-root biomass was consistently higher than live-root biomass in the top 10 cm soil (Fig. 3a).

SED
7, 2185–2211, 2015

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. 3). 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. 3b).

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 ± 0.8 cm). In comparison, stage IV represented a transition stage, before which the thickness was approximately 5 cm (Fig. 4).

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 ± 0.1 g cm^{-3} (Fig. 5).

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. 5).

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. 7). 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. 7).

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. 7). The thickness of mattic epipedon had a strong positive correlation with *K. pygmaea*. Soil bulk density was strong positive correlation with forbs, 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, 2013a, b). 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.

SED
7, 2185–2211, 2015

A clear changing pattern in PFG characteristics and environmental factors during the degradation process (Fig. 7) 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 have been changed, generating positive feedback to overgrazing that has dual effects on alpine grasslands. Initially, increasing 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, increasing biomass requires soil volume to hold roots (G. X. Wang, et al., 2007, Wang et al., 2008). Because the number of dead roots increases, 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

SED
7, 2185–2211, 2015

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.

In summary, 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 most important index is the thickness of the mattic epipedon. 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 as molecular and isotope approaches, to clarify these mechanisms.

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

Succession stage	Abbreviation		Study area	Geographical position	Plot general situation
Gramineae grass-*K. humilis* community	HC	Stage I	Maqin County of Guoluo Huangcheng County of Haibei Ebo County of Haibei	34°28′ N, 100°12′ E 3751 m a.s.l. 37°40′ N, 101°11′ E 3232 m a.s.l. 37°56′ N, 100°58′ E, 3419 m a.s.l.	Dominant plants are *Elymus nutans, Poa* sp., *Festuca rubra*, coverage 93 %, the thickness of the mattic epipedon is 1.66 cm, the average livestock number is 4 sheep units per ha
K. humilis community	AS	Stage II	Huangcheng County of Haibei Batang County of Yushu	37°40′ N, 101°11′ E 3232 m a.s.l. 35°51′ N, 96°60′ E 3907 m a.s.l.	Dominant plants are *K. humilis*, subdominant species are *E. nutans*, *Poa* sp. and *F. rubra*, 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.
Thickening-in-mattic-epipedon *K. pygmaea* community	XS1	Stage III	Maqin County of Guoluo Huangcheng County of Haibei	34°28′ N, 100°12′ E 3751 m a.s.l. 37°40′ N, 101°11′ E 3232 m a.s.l.	Dominant plants are *K. pygmaea*, 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
Cracks-in-mattic-epipedon *K. pygmaea* community	XS2	Stage IV	Maqin County of Guoluo Batang River beaches of Yushu	37°40′ N, 101°11′ E, 3232 m a.s.l. 35°51′ N, 96°60′ E 3907 m a.s.l.	Dominant plant is *K. pygmaea*, the alpine *K. pygmaea* species mottling are not less than 85 %; there are many crannies dividing the meadow into big alpine *K. pygmaea* mottling, there is hypogenesis of *K. pygmaea* 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
Collapse-in-mattic-epipedon *K. pygmaea* community	XS3	Stage V	Maqin County of Guoluo Huangcheng County of Haibei Ebo County of Haibei	34°28′ N, 100°12′ E 3751 m a.s.l. 37°40′ N, 101°11′ E, 3232 m a.s.l. 37°56′ N, 100°58′ E,	Dominant plant is *K. pygmaea*, 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
Forbs-“Black-soil beach”	HZ	Stage VI	Maqin County of Guoluo Menyuan County of Haibei	34°28′ N, 100°12′ E 3751 m a.s.l. 37°37′ N, 101°19′ E 3196 m a.s.l.	The dominant plants are forbs, with *K. pygmaea*, 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

SED
7, 2185–2211, 2015

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.

SED
7, 2185–2211, 2015

Figure 1. 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).

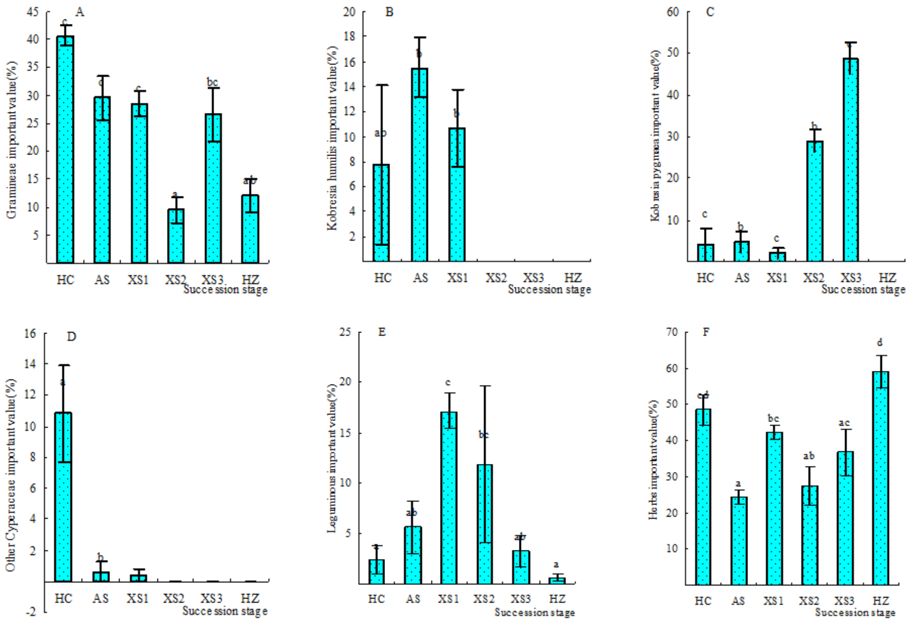

Figure 2. The characteristics of the four plant functional groups in a degradation successional series of Tibetan alpine grasslands: **(a)** *Gramineae*, **(b)** *Kobresia humilis*, **(c)** *Kobresia pygmaea*, **(d)** other sedges, **(e)** *Leguminosae*, and **(f)** forbs. Different letters in the figures indicate significant differences between the stages at $P < 0.05$.

SED
7, 2185–2211, 2015

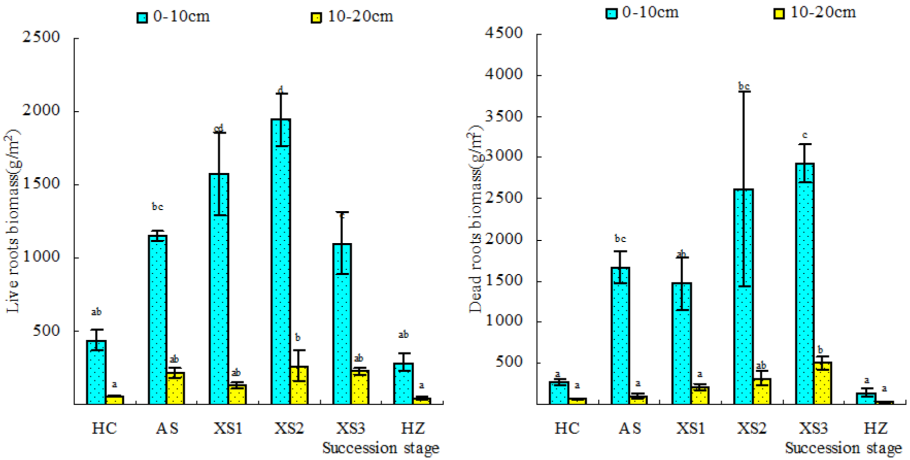

Figure 3. Living-root biomass **(a)** and dead-root biomass **(b)** at 0–10 and 10–20 cm depths. The values represent the means ±1 SD of four replicates. Different letters in the figures indicate significant differences between the stages at $P < 0.05$. The stage details refer to Fig. 1.

SED
7, 2185–2211, 2015

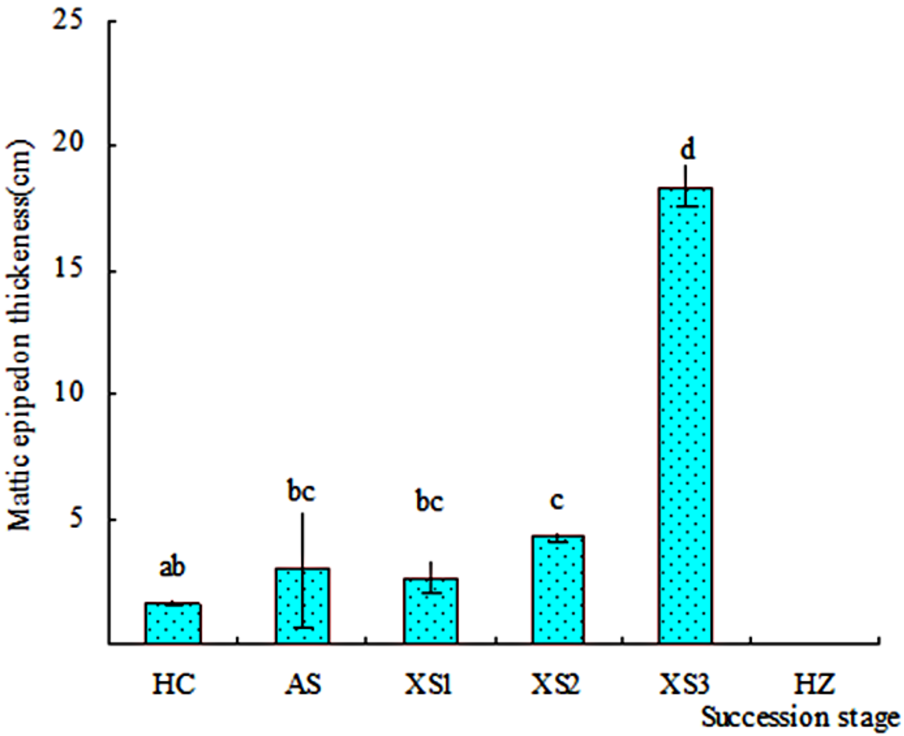

Figure 4. The thickness of mattic epipedon over the course of succession. The values represent the means ±1 SD of four replicates. Different letters in the figures indicate significant differences between stages at $P < 0.05$. The stage details refer to Fig. 1.

SED
7, 2185–2211, 2015

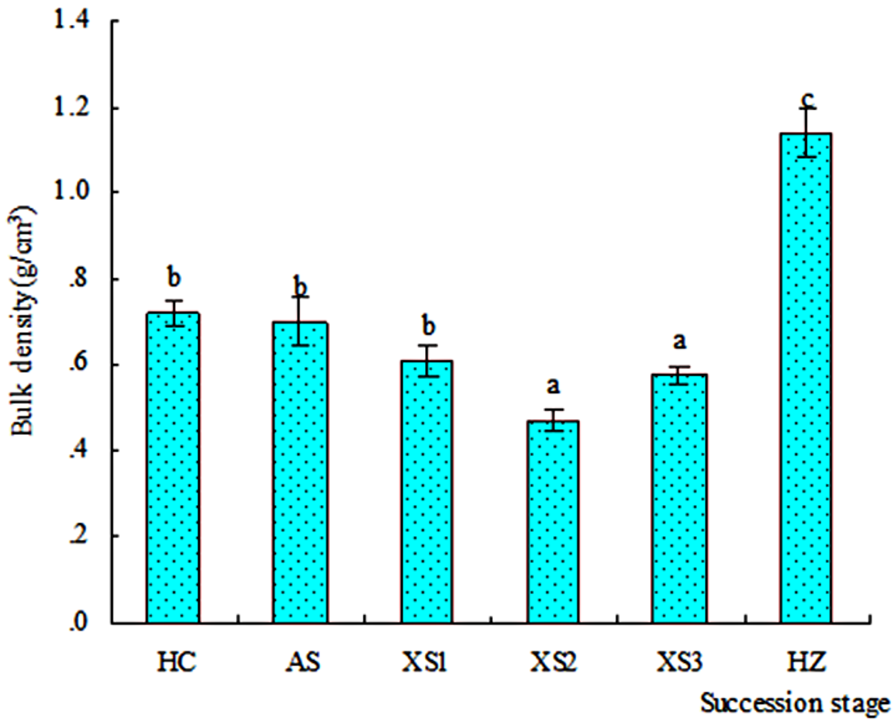

Figure 5. Surface soil-bulk density over the course of succession. The values represent the means ±1 SD of four replicates. Different letters in the figures indicate significant differences between stages at $P < 0.05$. The stage details refer to Fig. 1.

SED
7, 2185–2211, 2015

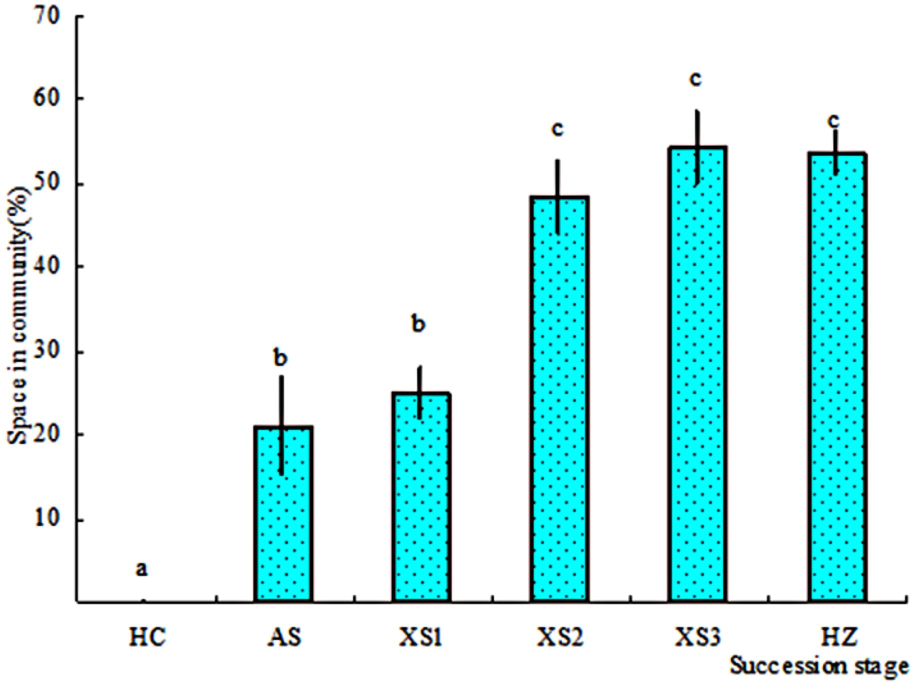

Figure 6. The space coverage over the course of succession. The values represent the means ±1 SD of four replicates. Different letters in the figures indicate significant differences between stages at $P < 0.05$. The stage details refer to Fig. 1.

SED
7, 2185–2211, 2015

Predicting parameters of degradation succession processes

L. Li et al.

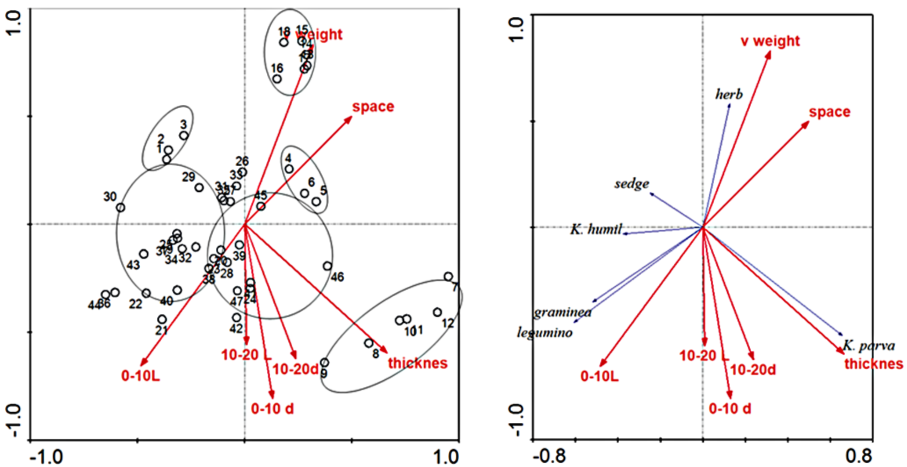

Figure 7. The plant functional groups and environment RDA ordination bioplot. Black items denote plant functional groups, red items denote environmental factors. "V weight" denotes the soil bulk density, "space" denotes the space in community (bared place), "thickness" denotes the thickness of mattic 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, 0–10d denotes the dead roots in the 0–10 cm soil layer, 10–20d 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. humil* denotes the *K. humilis*, and *K. parva* denotes the *K. pygmaea*.

SED
7, 2185–2211, 2015

Predicting parameters of degradation succession processes

L. Li et al.

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◂◂ | ▸▸
◂ | ▸
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion