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The effects of biotic and abiotic factors on the spatial heterogeneity of alpine grassland vegetation at a small scale on the Qinghai–Tibet Plateau (QTP), China

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Abstract Understanding the complex effects of biotic and abiotic factors on the composition of vegetation is very important for developing and implementing strategies for promoting sustainable grassland development. The vegetation–disturbance–environment relationship was examined in degraded alpine grasslands in the headwater areas of three rivers on the Qinghai–Tibet Plateau in this study. The investigated hypotheses were that (1) the heterogeneity of the vegetation of the alpine grassland is due to a combination of biotic and abiotic factors and that (2) at a small scale, biotic factors are more important for the distribution of alpine vegetation. On this basis, four transects were set along altitudinal gradients from 3,770 to 3,890 m on a sunny slope, and four parallel transects were set along altitudinal gradients on a shady slope in alpine grasslands in Guoluo Prefecture of Qinghai Province, China. It was found that biological disturbances were the major forces driving the spatial heterogeneity of the alpine grassland vegetation and abiotic factors were of secondary importance. Heavy grazing and intensive rat activity resulted in increases in unpalatable and poisonous weeds and decreased fine forages in the form of sedges, forbs, and grasses in the vegetation composition. Habitat degradation associated with biological disturbances significantly affected the spatial variation of the alpine grassland vegetation, i.e., more pioneer plants of poisonous or unpalatable weed species, such as *Ligularia virgaurea* and *Euphorbia fischeriana*, were found in bare patches. Environmental/abiotic factors were less important than biological disturbances in affecting the spatial distribution of the alpine grassland vegetation at a small scale. It was concluded that rat control and light grazing should be applied first in implementing restoration strategies. The primary vegetation in lightly grazed and less rat-damaged sites should be regarded as a reference for devising vegetation restoration measures in alpine pastoral regions.

Keywords Species composition · Grassland degradation · Biotic factors · Abiotic factors · Canonical

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Introduction

Degradation of grasslands is an extremely serious environmental problem around the world (Day and Buckley 2013; Harris 2010; Zhang et al. 2011; Wiesmeier et al. 2009), especially on the Qinghai–Tibet Plateau (QTP), affecting not only the survival of local pastoralists but also the well-being of people who live downstream. To devise ecological restoration strategies and actions, it is first necessary to reveal the processes and causes associated with grassland degradation, which are not yet fully understood. Previous researchers have attributed grassland degradation to different causes, such as overgrazing, the collection of herbs for medicine, resource allocation, and destruction by rodents, global climate change, and local government policing (Brandta et al. 2013; Gao et al. 2009, 2013; Harris 2010; Luo et al. 2009; Shang and Long 2007; Wen et al. 2012). However, which factors are the major driving forces for the degradation of vegetation is still uncertain. Therefore, in the present study, we conducted a field survey of an alpine grassland on the QTP to examine the relationship between the environment, disturbance, and vegetation.

The headwater area of three major rivers in Asia, the Yangtze River, Yellow River, and Lancang–Mekong River, which is located in the center of the QTP, is one of the most important eco-regions in China. Over 85 % of the 18.9 million km^2 of QTP is covered by alpine grasslands (including alpine meadow, alpine shrub–meadow, and alpine steppe), which are grazed by indigenous herbivores such as yak and Tibetan sheep (Wang and Chen 2001). The grasslands in this area have served as the dominant pastures for Tibetan communities over a long history and are regarded as one of the major pastoral production bases in China (Ma and Li 1999). They also provided ecosystem functions and services, such as carbon sequestration, biodiversity conservation, soil and water protection, and playing a role in Tibetan culture and tradition. Alpine grasslands represent good genetic pools for alpine vegetation and coupled human–natural systems for maintaining Tibetan culture (Dong et al. 2010). However, degradation of alpine grasslands limits the sustainable development of ecological, social, and economic systems at local and regional scales (Ma and Li 1999; Shang and Long 2007; Wang and Chen 2001). Nearly half of the alpine grasslands in this area have been degraded over the past 40 years, with an increasing rate of degradation observed, from 3.9 % in the early 1970s to 7.6 % in the late 1990s (Wang and Chen 2001). Currently, approximately 26 % of the alpine grasslands are severely degraded to what is referred to as “black beaches” or “black soil land,” characterized by bare “black” land in winter and “green” land sparsely covered by annual weeds or poisonous plants in summer (Li and Huang 1995; Ma et al. 2002; Ma and Li 1999; Shang and Long 2007).

A total of 15–23 % of the indigenous plant species have been described as endangered due to the degradation of the alpine grasslands, especially meadows, which are key habitats for many alpine organisms in these headwater areas (Dong et al. 2002). The amount of water transported from the upper watershed in Qinghai Province to the Yellow River has decreased by 23 % since the 1970s due to the shrinkage and loss of lakes and the drying up of some river branches in the headwater areas, while the sediment loads have increased to 4,600× 10^{4}t annually due to increased soil erosion from these alpine grasslands (Lan 2004). This critical situation has challenged both professionals and practitioners to develop technical and managerial strategies to restore the degraded grasslands in the headwater areas of the QTP and maintain upstream–downstream relationships along the Yangtze, Yellow, and Lancang–Mekong Rivers.

The plant communities of the alpine grasslands on the QTP have changed from primary vegetation dominated by sedges or sedge–grasses to secondary vegetation dominated by poisonous weeds due to the process of grassland degradation (Li and Huang 1995; Ma and Li 1999). The succession of vegetation in the alpine grassland during degradation has varied greatly at a large spatial scale (Ma et al. 2006; Wang et al. 2006), although few publications have documented the causes and effects of the spatial heterogeneity of the vegetation of the degraded alpine grassland. For alpine vegetation, some researchers have concluded that both recent ecological and historical factors determine the floristic richness of a plant community (Onipchenko and Semenova 1995; Onipchenko et al.

1998). Additionally, some authors have stressed that the variations in grassland vegetation can be attributed to abiotic processes, such as frost and snowmelt, as well as biotic processes, such as trampling, digging, and grazing by herbivores (Brown et al. 1980; Evju et al. 2009; Forbes and Jefferies 1999; Olofsson et al. 2002, 2005; Walker and Walker 1991). For the alpine grassland on the QTP, the causes of degradation remain uncertain (Harris 2010). Most scholars have linked the alpine rangeland degradation to overgrazing or inappropriate livestock management and land-use (Cao et al. 2004; Chen et al. 2010, 2008; Zhou et al. 2006). However, Klein et al. (2007) investigated the effects of experimental warming and simulated grazing on rangeland quality at a plot scale and concluded that warming was the main reason for the decrease in grassland quality. Thus, we hypothesized that (1) the vegetation composition and distribution of the degraded alpine grassland vary at a spatial scale with both environmental factors, such as geographic location, land coverage, and soil fertility, and biological disturbances, such as livestock grazing and rat damage, and (2) biological disturbances are the dominant driving forces leading to the spatial heterogeneity of the vegetation in the alpine grassland at a small scale.

On this basis, this study was conducted to examine vegetation–disturbance–environment relationships to clarify the vegetation patterns in the degraded alpine grassland and the associated driving forces and to test our hypothesis about the coupled effects of environmental factors and biological disturbances in altering the vegetation composition and distribution. The conclusion reached in this study can provide a theoretical basis for restoration management of degraded grasslands in alpine regions worldwide.

Materials and methods

Site description

The study site is located at Dawu village in Maqin County of Guoluo Tibetan Autonomous Prefecture, Qinghai Province. The average altitude of this area is 4,200 m, and it presents a typical continental climate. The annual average temperature is −0.6 °C; the lowest temperature is −34.9 °C, and the annual cumulative temperatures above 0 and 5 °C are 1,202.6 and 865.0 °C, respectively. The annual precipitation is 513 mm, which occurs mainly from May to September. The annual evaporation is 1,459 mm. The annual sunshine duration is 2,571 h. There is no absolutely frost-free period in the study area. The soil is silt-clay, or alpine meadow soil, according to the Chinese Soil Classification System. The alpine grasslands extending from low to high altitude on the sunny slope were degraded to different extents, while those on the shady slope were not degraded according to the criteria of alpine grassland degradation forwarded by Ma et al. (2002). The grasslands on sunny slopes are normally grazed by Tibetan sheep in the cold season from October to the next May, lasting for almost 200 days. Degraded grasslands on the sunny slope suffered damage from overgrazing and zokor (*Myospalax baileyi*) activities. The vegetation composition is different between the sunny and shady slopes due to the water, heat, and melting snow in the area.

Field survey and sampling

A vegetation survey and sampling were conducted from July to August of 2008. Four 250-m transects were set on the sunny slope (south facing) along an altitudinal gradient. Four 250-m transects were set on the shady slope (north facing), on the same mountain, to compare the differences in terms of both the vegetation composition and the effects of environmental factors on the vegetation composition. The forb-dominated vegetation on the sunny slope was sampled within 30 100 cm×100-cm quadrats at fixed altitudinal intervals (50 m) within each transect. The vegetation on the shady slope was dominated by shrubs with a forb/herbaceous under canopy. The vegetation on the shady slope was sampled in four 500 cm×500-cm quadrats for shrubs and 12 50 cm×50-cm quadrats for underneath forb at 50 m altitudinal intervals between the neighboring transects. In each quadrat, on both slopes, the plant numbers, density, coverage, height, and biomass were measured. The coverage of plants was estimated visually (Floyd and Anderson 1987). The density/abundance of individual plants was estimated by recording the numbers of each species per unit area. The frequency of the plants was measured by recording the number of individuals of each species occurring in all quadrats. According to the criteria for grading alpine grassland degradation (Ma et al. 2002), each quadrat was divided into five levels of degradation: severe degradation (SD), heavy degradation (HD), moderate degradation (MD), light degradation (LD), or non-degraded grassland (ND).

In each quadrat, the geographic location, including the altitude and slope, and soil conditions, including the bare patch size, soil pH, soil total carbon (SC), total nitrogen (SN), and total dissolved salt (TDS), were analyzed, and biological disturbance parameters, including the grazing intensity and density of rats, were all recorded. Together with vegetation sampling, five soil samples (0–10 cm) were collected from each quadrat with a soil auger (D=3.5 cm). The soil samples from each plot were pooled, air-dried, and passed through 0.85 and 0.15 mm sieves to determine the pH, SC, SN, and TDS (Gerlacha et al. 2006). SC and SN were assayed using a Vario El automatic elemental analyzer (Elementar Company, Germany). pH and TDS were determined by performing electrical conductivity analysis with a glass electrode (HI255, Italy) in a suspension of 10 g of soil material and 25 ml of distilled water (Sobek et al. 1978). Along the examined altitudes, the water and heat conditions changed on both the shady and sunny sides, so we investigated the effects of moisture and heat accordingly. The grazing intensity was defined as light grazing (2 sheep units/ha), moderate grazing (4 sheep units/ha), heavy grazing (8 sheep units/ha), or severe grazing (12 sheep units/ha) based on the number of grazing animals in winter, according to a survey of herdsman. The grasslands on the shady slope were dominated by shrubs, which were inedible for livestock. The rat density was estimated by recording the effective number of zokor holes in the grasslands. The relationships between environmental factors, biological disturbance, and the vegetation composition and distribution in the degraded alpine grassland were clarified.

The importance values (IV) for herbage on the sunny slope ($\mathrm{IV_h}$), shrubs on the shady slope ($\mathrm{IV_s}$), and herbage on the shady slope ($\mathrm{IV_h}'$) were calculated using the following formulae recommended by Ren (1998):

$$\mathrm{IV_h} = (\mathrm{C}' + \mathrm{H}' + \mathrm{F}' + \mathrm{B}' + \mathrm{D}')/5;$$
$$\mathrm{IV_s} = (\mathrm{C}' + \mathrm{B}')/2;$$
$$\mathrm{IV_{h'}} = (\mathrm{C}' + \mathrm{F}' + \mathrm{D}')/3.$$

where C' is the relative coverage, H' is the relative height, F' is the relative frequency, B' is the relative aboveground biomass, and D' is the relative density.

The similarity of vegetation from different sampling plots was estimated using the Jaccard Classic Similarity Index (JC) based on the following formula recommended by Jaccard (1912):

$$\mathrm{JC} = \mathrm{c}/(\mathrm{a} + \mathrm{b}),$$

where a represents the number of species in quadrat A, b the number of species in quadrat B, and c the number of species in both quadrats A and B.

Statistical analysis

Canonical correspondence analysis (CCA) using Canoco 4.5 and Canodraw for Windows was applied to analyze the vegetation–environment relationship. CCA associations provide a multivariate ordination of the species occurrence data, with a constrained regression maximizing the correlation between the species ordination axes and selected environmental variables (Austin 2002). It was assumed that distributions of species along the environmental gradients are unimodal. The species matrix was composed of the species' abundance data, and the environmental matrix consisted of the means of each environmental variable. Logarithmic transformation [$y'=\log(y+1)$] was performed to reduce the weight attributed to a single and dominant species. The significance of the most influential environmental factors was tested using automatic forward selection (Monte Carlo test, 499 permutations). In the ordination graph, the variables are represented by arrows pointing in the direction of maximum variation, with their length proportional to the rate of change (ter Braak 1986). Each arrow determines an axis on which the species points can be projected. Generally, these projected points estimate the optima of the species distribution for each environmental variable (Petillon et al. 2008). According to the results of detrended correspondence analysis (DCA) for species on the sunny slope, the length of the gradient represented by axis 1 was 3.173, indicating that both unimodal and linear methods work well (ter Braak and Smilauer 2002). Therefore, CCA was carried out to examine the site–species relationship on the sunny slope. In terms of the results of DCA for species on the shady slope, the length of the gradient represented by axis 1 was less than 2, indicating that the linear method works better than the unimodal method (ter Braak and Smilauer 2002). Thus, for the shady slope, RDA was carried out for the site–species–environment relationship.

Results

Vegetation composition

From a total of 184 quadrats surveyed on the two slopes, 132 vascular plants belonging to 88 genera and 31 families were collected and identified. The most popular families of plants recorded were Asteraceae, Cyperaceae, Ranunculaceae, Poaceae, Rosaceae, Gentianaceae, Fabaceae, Polygonaceae, and Scrophulariaceae (Table 1). The most common genera were Kobresia, Potentilla, and Saussurea. Among all of the plants sampled, none occurred in all of the 184 quadrats. Some species exhibited a wide distribution range, e.g., for *Kobresia humilis*, *Thalictrum alpinum*, *Kobresia pygmaea*, and *Swertia bifalia*, 174, 159, 152, and 151 records were observed, respectively. The most frequent occurrence of a species (*K. humilis*) approached 94.3 %. The distribution of the vegetation on the sunny slope was different from that on the shady slope. More families were observed on the sunny slope than on the shady slope, e.g., Plantaginaceae, Elaeagnaceae, Chenopodiaceae, Geraniaceae, Rubiaceae, Solanaceae, Caprifoliaceae, and Dipsacaceae only occurred on the sunny slope.

Each quadrat on the sunny slope was divided into four levels of degradation (Table 2), whereas all quadrats on the shady slope were all categorized as ND. On the sunny slope, 96 plants representing 88 genera and 28 families were collected and identified. Two primary plants, *K. humilis* and *K. pygmaea*, occurred as accidental species in all of the quadrats on the sunny slope. The dominant species varied greatly with grassland degradation along altitudinal gradients (Table 3). Pioneer forbs, such as *Ligularia virgaurea* and *Leontopodium nanum*, co-dominated the severely degraded grasslands at low altitudes, whereas primary forbs, such as *Polygonum viviparum* or *Polygonum macrophyllum* and pioneer forbs consisting of individuals of *Ligularia virgaurea* co-dominated the heavily, moderately, and lightly degraded grasslands at medium to high altitudes. On the shady slope, 93 plant species including five shrub species and 88 herbage species from 66 genera and 24 families were recorded in a total of 48 quadrats. Three shrub species, *Salix cupularis*, *Potentilla fruticosa*, and *Spiraea salicifolia*, occurred in all quadrats, while none of the forb species were present in all of the quadrats. Eight herbage species, *K. humilis*, *Carex sabulosa*, *Fcstuca ovina*, *Kobresia capillifolia*, *Astragalus weigoldianus*, *Saussurea supcrba*, *Swertia bifalia*, and *T. alpinum*, were identified in the majority of the plots, representing 97.92–91.67 % of the total flora on the shady slope. There was no great variation observed in the dominant species along altitudinal gradients (Table 3). *Salix cupularis*, *Potentilla fruticosa*, and *Spiraea salicifolia* co-dominated the shrub communities. *Leontopodium nanum*, *T. alpinum*, and *Carex tristachya* co-dominated the herbage community.

Site–environment relationship

The eigenvalues of the CCA indicated that the importance of the first CCA axis was 0.297 (F ratio=12.6, $p<0.01$), the second 0.109, the third 0.030, and the fourth 0.025. The sum of the eigenvalues of all of the canonical axes was 0.461 (F ratio=6.4, $p<0.01$). The four CCA axes explained 9.4, 3.4, 1.0, and 0.7 % of the total variation in the species data, respectively. The first two axes explained 68.6 and 25 % of the variation in the relationship between the species and environment, respectively. The results showed that on the sunny slope, heavy grazing was positively correlated with the rat intensity, while light grazing was negatively related to the rat intensity. There was a significant relationship between the soil pH and soil TDS. These two factors were negatively correlated with total

Table 1 The most popular families and genera on both sunny and shady slopes

	Family/genera name	*n*	Frequency (%)	Family/genera name	*n*	Frequency (%)	Family/genera name	*n*	Frequency (%)
Family	Asteraceae	20	100	Poaceae	11	96.60	Fabaceae	10	92.00
	Cyperaceae	9	98.30	Rosaceae	8	96.60	Polygonaceae	6	89.70
	Ranunculaceae	11	97.10	Gentianaceae	6	93.70	Scrophulariaceae	8	87.90
Genera	Kobresia	3	97.70	Potentilla	4	95.40	Saussurea	7	92.50

n represents how many species appearing at the study sites belonged to this family

Table 2 Characteristics of the sampling plots

Degradation grade	Altitude (m), mean±SE	Rat burrows (ha^{-1})	Bare patch (%)	Slope degree	Grazing intensity	SC (%)	SN (%)	pH	TDS (mg/L)	Slope
ND	3,839.3±6.6	0	0	23.6	LG	12.841	0.880	5.82	198.5	Shady
LD	3,909.3±2.2	0.2	1	18.4	LG	10.757	0.831	6.1	220	Sunny
MD	3,873.9±2.3	3.9	1	16.7	MG	9.448	0.811	6.34	278	Sunny
HD	3,830.6±1.8	13.9	2	21.3	OG	7.861	0.591	6.66	319	Sunny
SD	3,790.3±2.2	23.4	5	15.1	HG	8.253	0.673	6.43	297	Sunny

ND not degraded, *LD* light degradation, *MD* moderate degradation, *HD* heavy degradation, *SD* severe degradation, *LG* light grazing, *MG* moderate grazing, *OG* over grazing, *HG* heavy grazing. *SC* soil total carbon, *SN* soil total nitrogen, *TDS* total dissolved salt

soil carbon and nitrogen. Soil carbon and nitrogen were significantly correlated. These two factors were positively related to light grazing. For the sunny slope, the results of the CCA imply that the grazing intensity decreased along the altitudinal gradient; heavy grazing was negatively correlated with the altitude, while light grazing was positively correlated with the altitude. There was a positive relationship between the area of bare patches and the rat destruction intensity. The area of bare patches was significantly correlated with both heavy grazing and the rat intensity, which was negatively associated with the altitude.

For the sunny slope, the CCA results indicate that SD due to overgrazing was positively correlated with the size of bare patches and the number of rat holes, but negatively correlated with altitude. LD associated with light grazing was positively correlated with high altitudes, rich soil with high soil total carbon and nitrogen contents, whereas LD was negatively correlated with the soil pH and soil TDS. HD associated with heavy grazing and MD associated with moderate

Table 3 The important values (IV) for dominant shrubs and forbs in the plots on the sunny and shady slopes

Slopes	Degradation grade	Shrubs		Forb	
		Species	IV	Species	IV
Sunny	SD	–	–	*Ligularia virgaurea*	13.4
		–	–	*Leontopodium nanum*	11.8
		–	–	*Kobresia pygmaea*	8.3
	HD	–	–	*Polygonum viviparum*	16.2
		–	–	*Ligularia virgaurea*	9.5
		–	–	*Leontopodium nanum*	4.8
	MD	–	–	*Polygonum macrophyllum*	35.0
		–	–	*Ligularia virgaurea*	22.2
		–	–	*Kobresia capillifolia*	14.7
	LD	–	–	*Polygonum macrophyllum*	11.1
		–	–	*Ligularia virgaurea*	9.2
		–	–	*Anaphalis lactea*	6.0
Shady	ND	*Salix cupularis*	40.8	*Leontopodium nanum*	4.9
		Potentilla fruticosa	26.6	*Dracocephalum heterophyllum*	4.8
		Spiraea alpina	24.0	*Ranunculus japonicus*	4.7

Abbreviations as in Table 2

grazing were not evidently correlated with any of these environmental factors.

For the shady slope, the eigenvalues of the RDA showed that the importance of the each axes fell in the following order: The first was 0.234, the second 0.061, the third 0.032, and the fourth 0.159, implying that these four axes can explain 23.4, 5.1, 3.2, and 15.9 %, respectively, of the variation in the herbage abundance. The results of the RDA show that axis 1 and axis 2 can explain 71.6 and 18.6 % of the variation in the relationship between the species and environment. Furthermore, the first three axes can explain all of the variation in the species–environment correlation. There were almost no biological disturbances recorded on the shady slope. Altitude was positively correlated with soil total carbon, total nitrogen, and pH. Soil TDS showed no correlation with other abiotic factors.

Plant–site relationship

Pioneer plants (aggressive weeds), including *Ajuga lupulima*, *Artemisia frigida*, and *Aconitum pendulum*, were distributed intensively around SD sites (Fig. 1), i.e., those consisting of bare soil patches/severely degraded habitat. Secondary plants, such as *Colaria longifolia*, *Saussurea stella*, *Plantago depressa*, *Sibiraea angustata*, *Stipa krylovii*, and *Potentilla anserina*, were aggregated around MD and HD sites. Primary plants, including *Allium chrysanthum*, *Viola philippica*, *Astragalus speciel*, *Saxifraga atrata*, *Parnassia palustris*, *Gentiana*

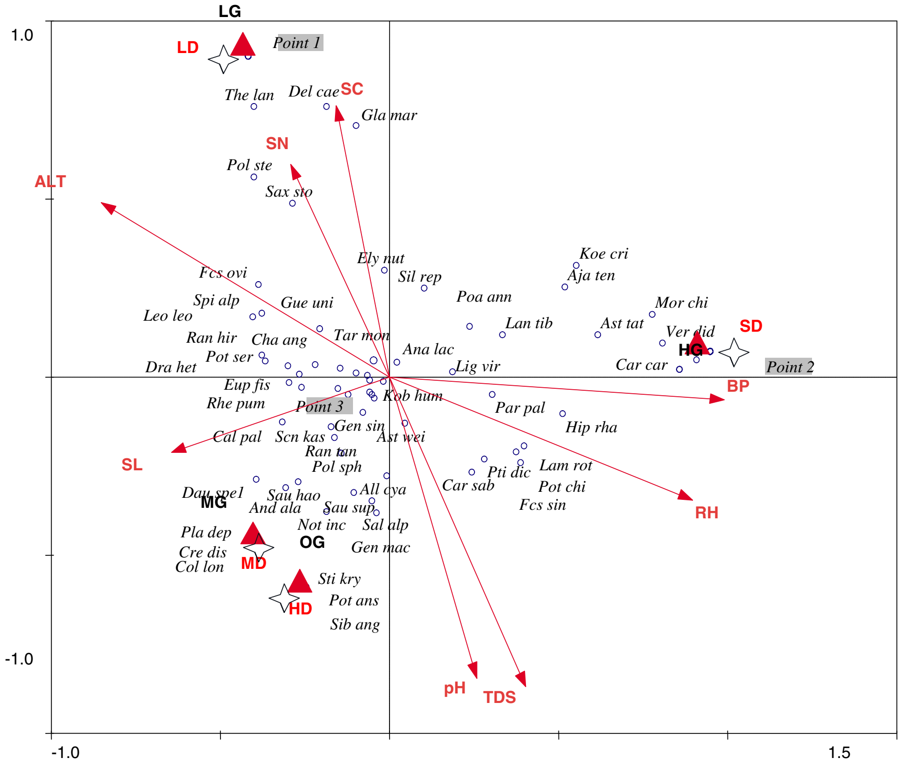

Fig. 1 CCA ordination diagram for herbage species, sites, and environmental variables on the basis of the species abundance on the sunny slope. *ALT* altitude, *SL* slope, *BP* bare patch, *SC* soil total carbon, *SN* soil total nitrogen, *TDS* total dissolved salt, *RH* number of zokor holes, *ND* not degraded, *LD* light degradation, *MD* moderate degradation, *HD* heavy degradation, *SD* severe degradation, *LG* light grazing, *MG* moderate grazing, *OG* over grazing, *HG* heavy grazing. Point 1 included the following species: All chr, Vio phi, Ast spe1, Sax atr, Par tri, Sor hoo, Gen aqu, Ger pyl. Point 2 included the following species: Ste med, Art san, Prz tan, Ste cha, Aco gym, Dra nem, Rub cor, Ped ala, Els den, Koe isl, Aco tan, Sil ten, Sti cap, Lag bre, Gal ver, Ped lon1, Lon min, Aco pen, Aju lup, Che ilj, Art fri. Point 3 included the following species: Kob cap, Pot fru, Oxy och, Swe bif, Pol viv, Leo nan, Iri gin, Tha alp, Kob pyg. Species abbreviations are given in the "Appendix"

spathulifolia, *Soroseris hookeriana*, and *Geranium pylzowianum*, were aggregated near LD sites. A few primary plants, such as *K. capillifolia*, *Polygonum viviparum*, and *K. humilis*, were not confined any of these habitats (LD, MD, HD, and SD). The Jaccard similarity values of 37.4 % found between SD and HD, 40.1 % between HD and MD, and 33.1 % between MD and LD indicate that there were significant variations in species composition between the four sampled habitats (Table 3). However, the similarity index values among the non-degraded grassland quadrats on the shady slope were all greater than 50 %.

Plant–environment relationship

The species–environment relationship shown in the biplot indicates that the species data were strongly correlated with the environmental variables (Fig. 1). Figure 1 displays the ordination of species constrained by nine variables. Interpretation of the ordination axes using the canonical coefficients and intersect correlations shows that only three out of nine variables were significant. These variables were the bare soil area (F=12.6, p<0.01), the altitude (F=4.7, p<0.01), and the number of zokor hole (F=1.5, p<0.05), which together explained 43 % of the total variance.

The high absolute correlation coefficient means that these variables exerted a great influence over the species distribution. The slope and total soil nitrogen were less important in explaining the variations in species abundance than the other variables. The triplot diagram of the CCA ordination (Fig. 1) indicates that the bare soil patch size was strongly associated with the distribution of most species. The bare patch size was positively correlated with the distribution of pioneer plants, i.e., poisonous or unpalatable forbs. The primary plants, i.e., the sedges and grasses, such as *K. humilis* and *K. capillifolia*, were negatively correlated with the bare patch size. It is also shown in Fig. 1 that heavy grazing was positively correlated with bare soil patches.

The results of the CCA show that the number of zokor holes, bare patch size, and TDS were negatively (p<0.05) correlated with the altitude. Rat holes were negatively (p<0.05) correlated with the bare patch area. Positive correlations (p<0.05) were found between total soil carbon and soil nitrogen. Both of these factors were significantly (p<0.05) related to the altitude and the number of zokor holes. Soil TDS was negatively correlated (p<0.05) with the altitude, soil total carbon, and nitrogen, but positively correlated (p<0.05) with the pH and grazing intensity. There were no significant correlations (p>0.05) found between the slope and other factors.

On the shady slope, only three environmental variables, the pH (F ratio=11.1, p<0.01), slope (F ratio=5.1, p<0.01), and altitude (F ratio=3.3, p<0.01), can be applied to the RDA model for forbs (Fig. 2). The first axis can be defined by the altitude and pH and the second by the SC, slope, and SN. The distributions of most forbs were associated with the altitude, soil pH, SC, and SN (Fig. 2), e.g., *K. humilis*, *Polygonum sibiricum*, and *Senecio kaschkarowii* occurred at sites with a high soil TDS, and *Poa annua*, *Delphinium caeruleum*, and *F. ovina* were found at sites with a high altitude, soil pH, SN, and SC.

Discussion

The results indicated that the observed vegetation heterogeneity could be attributed to both environmental factors such as the geographic location, land coverage, and soil fertility and biological disturbances such as livestock grazing and rat damage. Unpalatable weeds/forbs appeared while palatable grasses disappeared associated with heavy disturbance on the sunny slope. This conclusion is consistent with the finding of Xu et al. (2008) that edible grasses were replaced by poisonous weeds as degradation was aggravated. However, on the shady slope, *Salix cupularis*, *Potentilla fruticosa*, and *Spiraea alpine* were the dominant species, with no change along the altitudinal gradients. This result indicates that there were no significant variations in the species composition along the altitudinal gradient on the shady slope. Heavy grazing might be one of the causes of large areas of bare soil patches and alteration of the vegetation composition in the alpine region. In contrast, light grazing may maintain the vegetation composition, e.g., *Allium chrysanthum*, *Viola philippica*, *Astragalus* spp., *Saxifraga atrata*, *Parnassia palustris*, *Gentiana spathulifolia*, *Soroseris hookeriana*, and *Geranium pylzowianum* were observed in the habitats disturbed by light grazing. The variation in the vegetation composition

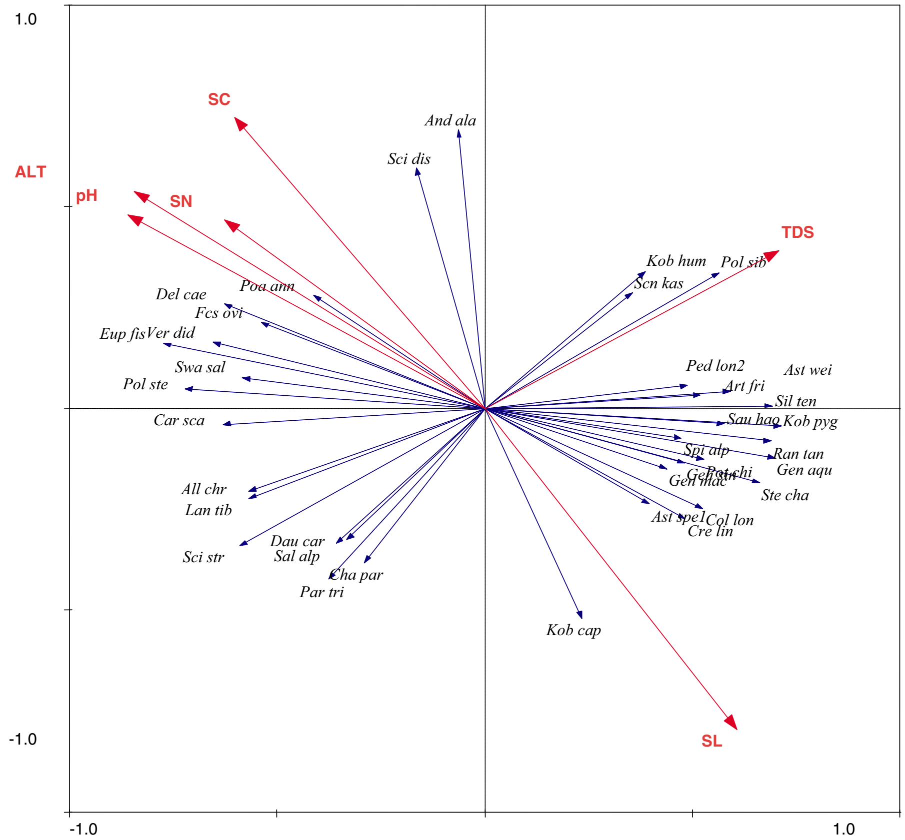

Fig. 2 RDA ordination diagram for herbage species and environmental variables on the basis of the species abundance on the shady slope. Abbreviations as in Fig. 1

associated with different slope may be attributed to the differences in the distribution sunlight and evaporation.

The vegetation in the shady plots was dominated by shrubs, which are plants that are inedible for indigenous grazing ruminants, and thus, the biological disturbance associated with grazing animals can be overlooked. Moreover, the absence of rat burrows indicates that there was no *M. baileyi* activity on the shady slope.

On the sunny slope, the grazing intensity was negatively correlated with the altitude, which supports the hypothesis that grazing intensity decreases as the distance from settlements increases (Fu et al. 2002; Tong 2000). The present study shows that light disturbance caused by herbivores can favor the persistence of primary vegetation and promote the coexistence of different palatable forbs belonging to different functional groups (forbs, sedges, and grasses) in alpine grasslands, whereas severe disturbance by herbivores altered the compositions of functional groups and reduces the weights of palatable forbs in alpine grasslands. This is consistent with other researchers' findings that herbivores may influence plant community structure directly by reducing the abundance of preferred forage species (Brathen et al. 2007; Huffman et al. 2009; Kohyani et al. 2008; Wang et al. 2008) and depleting nitrogen-fixing plants within the vegetation composition (Wang et al. 2008), or indirectly via modifying competitive interactions between plants (Evju et al. 2009; Mulder and Ruess 1998) and altering nutrient availability (Olofsson 2009; Olofsson and Okasnen 2002). Some researchers have found that overgrazing can not only change the floristic composition and soil nutrients but also disrupts the soil structure of alpine grasslands on the QTP (Li et al. 2007; Li 2002; Li and Huang 1995; Zhou et al. 2003). However, other investigators have stressed that rat activity damages the vegetation and soil structures, resulting in the promotion of grassland degradation in the alpine region of the QTP (Li 2002; Shang and Long 2007; Zhou et al. 2005). In this study, we found that the degradation of alpine grassland vegetation was highly correlated with both the grazing intensity and the number of zokor burrows, implying that the coupled effects of overgrazing and rat damage may lead to the formation of bare patches and, ultimately, severely degraded grassland. This conclusion is supported by the findings of other researchers that the coupled disturbances from grazing animals and rats significantly decreased vascular plant heights and abundances (Austrheim et al. 2007; Olofsson et al. 2004) and long-term impacts of severe rat disturbance were detected on a grazing resistant plant (Austrheim et al. 2007; Moen and Oksanen 1998; Olofsson et al. 2004). Fan et al. (2010) found that the climate change was also a factor associated with reductions in grassland yields. But, in this small scale study, the effect of global climate change on vegetation heterogeneity was not discussed.

It can be concluded that biotic drivers are more important than abiotic drivers with respect to the vegetation heterogeneity on the investigated sunny slope of the degraded alpine grassland at a small scale. The heterogeneity of the vegetation on the sunny slope was higher than on the shady slope according to CCA and similarity analysis (Fig. 1; Table 4). The high similarity of the vegetation sampled in different altitudinal gradients on the shady slope showed that there were no remarkable variations in the vegetation composition along environmental and geographical gradients at small scales. On this basis, the great difference of the vegetation composition on sunny slope can be attributed to the biological disturbances of livestock grazing and rat activity. This is consistent with the findings of previous researchers showing that the interactions between herbivores and disturbance may significantly, but slowly, shape the dynamics and structure of arctic plant communities (Mulder and Ruess 1998; Olofsson et al. 2002, 2005).

Table 4 Similarity of the species composition between different degradation levels

	HD (%)	MD (%)	LD (%)
SD	37.4	33.6	33.5
HD		40.1	34.8
MD			33.1

Abbreviations as in Table 2

Furthermore, it can be concluded from the present study that biotic factors, rather than abiotic factors, caused the heterogeneity of the vegetation of the investigated degraded alpine grassland at a small scale in the headwater areas of the QTP. Thus, to prevent the degradation of grassland, the primary task should be to carry out rational grazing management on non-degraded grassland. For lightly degraded grassland, we recommended that zokor controls be implemented and grazing be limited to low stock levels (2 sheep units/ha), and the primary vegetation in lightly grazed and less patchy sites should be referenced in devising a restoration planning. Other research also demonstrated that the exclusion of grazing using fencing was an effective way to restore degraded grassland (Aronson et al. 1993; Fan et al. 2010). Given the serious consequence of grassland degradation on the QTP, the Chinese government launched an ecological restoration program involving the retirement of livestock and the restoration of pastures in 2003. It was reported by the Ministry of Agriculture of the People's Republic of China that this program promoted an increase in productivity by 43.9 %, while edible forage productivity was increased by 49.1 %. However, considering there were many bare patches observed in the investigated severely degraded grassland, grazing exclusion and rat control alone cannot restore the SD grasslands. Previous studies have shown that the development of artificial grasslands was effective method for the restoration of severely degraded grassland (Feng et al. 2009; Gao et al. 2009). Therefore, we conclude that the diagnosis of the state of a grassland is an important first step in grassland ecosystem management. According to the level of degradation, different measurements should be taken. For healthy and lightly degraded grasslands, scientific grazing management and rat control appears to be an effective strategy. These conclusions can be viewed as a theoretical basis for restoring degraded grassland and promoting the sustainable management of alpine grassland ecosystem in similar regions worldwide\.

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Appendix

Abbreviation	Full name of species
Aco gym	*Aconitum gymnandrum*
Aco pen	*Aconitum pendulum*
Aco tan	*Aconitum tangutcum*
Aja ten	*Ajania tenuifolia*
Aju lup	*Ajuga lupulina*
All chr	*Allium chrysanthum*
All cya	*Allium cyaneum*
Ana lac	*Anaphalis lactea*
And ala	*Androsace pomatosace*
And inc	*Androsace integra*
Ane kan	*Anemone kansuensis*
Art fri	*Artemisia frigida*
Art san	*Artemisia santolinaefolia*
Ast spe1	*Astragalus* spp.
Ast tat	*Aster tataricus*
Ast wei	*Astragalus weigoldianus*
Bra jun	*Brassica juncea*
Cal pal	*Caltha palustris*
Car alr	*Carex atrofusca*
Car bre	*Caragana brevifolia*
Car car	*Chamaesium carvi*
Car moo	*Carex moorcroftii*
Car sab	*Carex sabulosa*
Car sca	*Carex scabrirostris*
Cha ang	*Chamaenerion angustifolium*
Cha par	*Chamaesium paradoxum*
Che ilj	*Chenopodium iljinii*
Cle chi	*Cleistogenes chinensis*
Col lon	*Coluria longifolia*
Cor cri	*Corydalis cristata*
Cot rou	*Cotoneaster rotundifolius*
Cre dis	*Cremanthodium discoideum*
Cre lin	*Cremanthodium lineare*
Dau car	*Daucus carota*
Dau spe1	*Daucus* spp.
Del cae	*Delphinium caeruleum*
Des sop	*Descurainia sophia*

(continued)

Abbreviation	Full name of species
Dra het	*Dracocephalum heterophyllum*
Dra nem	*Draba nemorosa*
Els den	*Elsholtzia densa*
Ely nut	*Elymus nutans*
Eup fis	*Euphorbia fischeriana*
Fcs ovi	*Festuca ovina*
Fcs sin	*Festuca sinensis*
Gal ver	*Galium verum*
Gen aqu	*Gentiana aquatica*
Gen mac	*Gentiana macrophylla*
Gen pal	*Gentianopsis paludosa*
Gen sin	*Gentiana sino*
Gen spa	*Gentiana spathulifolia*
Ger pyl	*Geranium pylzowianum*
Gla mar	*Glaux maritima*
Gue uni	*Gueldenstaedtia multiflora*
Hel tib	*Helictotrichon tibeticum*
Hip rha	*Hippophae rhamnoides*
Iri gin	*Iris ginghainica*
Kob cap	*Kobresia capillifolia*
Kob hum	*Kobresia humilis*
Kob pyg	*Kobresia pygmaea*
Koe cri	*Koeleria cristata*
Koe isl	*Koenigia islandica*
Lag bre	*Lagotis brevituba*
Lam rot	*Lamiophlomis rotata*
Lan tib	*Lancea tibetica*
Leo leo	*Leontopodium leontopodi*
Leo nan	*Leontopodium nanum*
Lig vir	*Ligularia virgaurea*
Lon min	*Lonicera minuta*
Mec sep1	*Meconopsis* spp.
Med lup	*Medicago lupulina*
Mor chi	*Morina chinensis*
Not inc	*Notopterygium incisum*
Oxy kan	*Oxytropis kansuensis*
Oxy och	*Oxytropis ochrocephala*
Par pal	*Parnassia palustris*
Par tri	*Parnassia trinervis*
Ped ala	*Pedicularis alaschanica*
Ped kan	*Pedicularis kansuensis*
Ped lon1	*Pedicularis longiflora* var.
Ped lon2	*Pedicularis longiflora*
Ped pil	*Pedicularis pilostachya*

(continued)

Abbreviation	Full name of species
Pla dep	*Plantago depressa*
Poa ann	*Poa annua*
Pol sib	*Polygonum sibiricum*
Pol sph	*Polygonum sphaerostachyum*
Pol ste	*Polygonum stenophyllum*
Pol viv	*Polygonum viviparum*
Pot ans	*Potentilla anserina*
Pot chi	*Potentilla chinensis*
Pot fru	*Potentilla fruticosa*
Pot ser	*Potentilla sericea*
Prz tan	*Przewalskia tangutica*
Pti dic	*Ptilagrostis dichotoma*
Ran hir	*Ranunculus hirtellus*
Ran lin	*Ranunculus lingua*
Ran tan	*Ranunculus tanguticus*
Rhe pum	*Rheum pumilum*
Rho sim	*Rhododendron simsii*
Rub cor	*Rubia cordifolia*
Sal alp	*Salix cupularis*
Sau gra	*Saussurea graminea*
Sau hao	*Saussurea haon*
Sau hao	*Saussurea haoi*
Sau jap	*Saussurea japonica*
Sau ste	*Saussurea stella*
Sau sup	*Saussurea superba*
Sax atr	*Saxifraga atrata*
Sax sto	*Saxifraga stolonifera*
Sci dis	*Scirpus distigmaticus*
Sci str	*Scirpus strobilinus*
Scn kas	*Senecio kaschkarowii*
Sib ang	*Sibiraea angustata*
Sil rep	*Silene repens*
Sil ten	*Silene tenuis*
Sor hoo	*Soroseris hookeriana*
Spi alp	*Spiraea alpina*
Ste cha	*Stellera chamaejasme*
Ste med	*Stellaria media*
Sti cap	*Stipa capillata*
Sti kry	*Stipa krylovii*
Sti pur	*Stipa purpurea*
Swa sal	*Swainsona salsula*
Swe bif	*Swertia bifalia*
Tar mon	*Taraxacum monogolicum*
Tar spe1	*Taraxacum* spp.
Tha alp	*Thalictrum alpinum*
The lan	*Thermopsis lanceolata*
Tro pum	*Trollius pumilus*
Ver did	*Veronica didyma*
Vio phi	*Viola philippica*

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