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Response of the plant community and soil water status to alpine *Kobresia* meadow degradation gradients on the Qinghai–Tibetan Plateau, China

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Abstract Degradation of alpine *Kobresia* meadow in the Qinghai–Tibetan Plateau is a serious problem, but its effect on the plant community and soil water status is not fully understood. We chose four homogeneous sites with <20, 20–70, 70–90, and >90 % absolute abundance of palatable grasses, and classified them as degradation gradient categories of poor, fair, good, and excellent, respectively. The lowest aboveground biomass and infiltration rate, and the highest root biomass, thickness of mattic epipedon, topsoil (<10 cm) organic matter content and volumetric ratio of root/soil all occurred in fair plots. There was little fluctuation in plant community diversity and topsoil bulk density among the degradation gradients. Results of non-metric multidimensional scaling suggested that vegetation dynamics along degradation processes were non-equilibrium in the alpine *Kobresia* meadow. The effects of degradation on soil water content and retention were the highest in the top layer (>10 cm). The minimum topsoil water content and maximum topsoil water retention both occurred in fair plots, indicating asynchrony between soil water content and holding capacity along degradation gradients, which likely resulted in a non-equilibrium plant community pattern through physiological desiccation and nutrient deficits. Our findings should be highly informative for threshold-based management of the degraded alpine *Kobresia* meadow in the future.

Keywords Soil water retention · Plant community · Non-equilibrium · Mattic epipedon · Non-metric multidimensional scaling

Introduction

Grazing is considered one of the most important factors influencing plant diversity, vegetation productivity, and soil properties within grassland ecosystems (van de Koppel et al. 1997; Perevolotsky and Seligman 1998). Rangeland degradation induced by overgrazing is a serious environmental issue worldwide (Milton et al. 1994; Asner et al. 2004). Rangeland degradation has impacted not only biotic productivity (O'Connor et al. 2001; Swemmer et al. 2007) and landscape heterogeneity (Whitford et al. 1998), but also the abiotic environment and related hydrological processes such as rainfall infiltration, soil erosion (Mwendera et al. 1997; Mills and Fey 2003), local water resources (Feddesma 1998), and spatiotemporal water balance (Wilcox et al. 2006). Conservation of biodiversity, soil, and water is critical for maintaining healthy grassland ecosystems (Whitford et al. 1998). This process varies depending on vegetation type and grazing management, and is poorly understood in alpine regions, where the headwaters of major rivers are located (Snyman 2000; Wang et al. 2008). It is important to quantify how the plant community transitions and how the soil water status changes with degradation in order to devise restoration strategies and ensure sustainable utilization of alpine grasslands (Cheng et al. 2008).

The alpine *Kobresia* meadow occupies one-third of the Qinghai–Tibetan Plateau (QTP) area and plays a critical role in regional sustainable development and water resource conservation in Asia (Wang and Fu 2004; Kang et al. 2007). Degradation of alpine *Kobresia* meadow is widespread and has recently been increasing over the QTP because of overgrazing and climate change (Wang et al. 2012). Severely degraded meadow (“black soil beach”) is estimated to account

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for approximately 15 % of degraded grassland (Wang et al. 2006). With the decrease in vegetation coverage, the abundance and biomass of sedge and grass species has decreased (Wang et al. 2012), soil water content and quality has declined (Wang et al. 2007; Cheng et al. 2008), and soil water content and thermal conditions in the active layer have worsened. These changes have resulted in deterioration of plant growth and further degradation of alpine *Kobresia* meadow (Wang et al. 2008).

Mattic epipedon (ME) is an extremely resilient dense turf peculiar to alpine *Kobresia* meadow, and consists of felty fine dead and living roots, amorphous humus, and minerogenic matter. ME plays an important role in nutrient supply and ecosystem health. The thickness of ME greatly increased and topsoil organic matter content was mostly sequestered because of firm Cyperaceae turf, as well as slow decomposition activity under alpine climate conditions (Miehe et al. 2008; Li et al. 2012). Consequently, circulation of nutrient elements has gradually become intermittent (Wang and Fu 2004). Over-growth of ME has facilitated rodent infestations by providing them with suitable habitats and food, which has subsequently led to destruction of ME, revealing bare mineral soil (Kang et al. 2007). Furthermore, weedy species and black soil beach have become widespread (Wang et al. 2006). Alpine meadow degradation has long-lasting effects on soil properties (Wang et al. 2008) and how soil water status and vegetation transition are affected by such changes is not fully understood.

The objectives of this study were to quantify the influence of degradation processes on plant communities, vegetation production, and topsoil physical variables, with particular emphasis on soil water content and water-holding capacity. In accordance with previous alpine studies (Wang et al. 2008; Li et al. 2012), we hypothesized that: (1) plant community diversity changed little along degradation gradients, mainly because of significant compensatory effects among plant functional groups and individual species in the ecosystem with higher species richness and (2) soil water content decreased while retention capacity increased along the degradation gradients. We determined whether equilibrium or non-equilibrium paradigms (Suding et al. 2004; Sasaki et al. 2008) better explained vegetation dynamics caused by degradation in the alpine *Kobresia* meadow in order to facilitate development of future restoration strategies. Additionally, there is generally a positive association between soil organic matter (SOM) and grassland ecosystem health (Whitford et al. 1998; Asner et al. 2004), but whether this observation is applicable to alpine meadows remains a point of contention as higher SOM hinders the release of soil nutrients in alpine meadows (Wang and Fu 2004).

Materials and methods

Site description and experimental design

The study was performed in August 2012 near the Haibei National Field Research Station of Alpine Grassland Ecosystem (101°19'E, 37°37'N, 3200 m above sea level), which is located in the northeastern region of the QTP. The mean annual air temperature in this region is -1.70°C with yearly precipitation of 570 mm, 80 % of which falls between May and September (Chen et al. 2008). The dominant species in the alpine *Kobresia* meadow include *Kobresia humilis* (C. A. Mey.) Serg., *Elymus nutans* Griseb., *Stipa aliena* Keng, *Taraxacum dissectum* (Ledeb) Ledeb, *Anaphalis lactea* Maxim, and *Potentilla anserina* L. Sp. Pl. The soil at this site is clay loam that is high in organic matter (7 %, 0–10 cm) and is classified as Mat Cry-gelic Cambisols (Institute of Soil Science 2001).

We selected four homogeneous winter pasture sites along the grazing gradients. The criteria for site selection were based on clear decline in the coverage of palatable (all sedges and graminoids and some legumes and little forbs) grasses (Whitford et al. 1998). As in other studies (Medina-Roldán et al. 2007), we defined absolute abundance of palatable grasses as <20, 20–70, 70–90, and >90 % with the corresponding degradation condition categories being poor, fair, good, and excellent, respectively. Since collapse of over-growth ME takes a long time, the range of palatable species coverage was much greater in fair plots. More sheep and fewer yaks grazed the studied sites during winter and spring, and the corresponding grazing intensity was relatively stable for one decade at approximately 0.5, 11.5, 8.5 and 3.5 sheep/hm², respectively. It should be noted that the lowest grazing intensity at poor sites was not because of grazing enclosure and could be attributed primarily to the presence of unpalatable species. Therefore, grazing management could be considered to be the primary factor influencing variations in degradation status (Li et al. 2012). The maximum distance among sites was not more than 30 km, and the four sites could be classified as climatically homogeneous sites, as radiation, rainfall, and wind were similar along the gradients. Detailed information about the four sites is provided in Table 1. Based on our field investigation, the soils at the four sites were classified as Mat Cry-gelic Cambisols and were homogeneous in texture.

Data collection

During the flourishing vegetation growing season in August, we selected a flat and homogeneous area of about 1000 m² (100 m × 10 m) in each of the four gra-

Table 1 Geographic and plant characteristics of the four study sites along the degradation gradients in an alpine meadow

	Meadow degradation gradients			
	Excellent	Good	Fair	Poor
Location and elevation	101°18.798'E 37°36.666'N 3200 m	101°2.698'E 37°52.189'N 3527 m	101°10.620'E 37°40.054'N 3239 m	101°18.237'E 37°36.676'N 3189 m
Grazing management	Light 1 ± 1.0 ^b	Light 8.4 ± 2.6	Moderate 34.0 ± 2.5	None ^a 21.8 ± 5.9
Exposed soil coverage (%)	102.8 ± 8.03	76.7 ± 7.54	64.0 ± 8.96	6.0 ± 2.08
Palatable species absolute coverage (%)	183.6 ± 42.48	42.4 ± 4.88	41.6 ± 7.24	4.4 ± 2.2
Palatable species aboveground biomass (gm ⁻²)	132.0 ± 24.66	56.4 ± 10.84	63.3 ± 8.19	95.7 ± 2.19
Inedible species absolute coverage (%)	126.8 ± 33.28	23.2 ± 0.6	101.2 ± 18.04	182.8 ± 41.24
Inedible species aboveground biomass (gm ⁻²)				
Dominant species composition and plant community description	Two-layer canopy Upper canopy: <i>Stipa aliena</i> , <i>Helictotrichon tibeticum</i> , <i>Elymus nutans</i> ; Lower canopy: <i>Kobresia humilis</i> , <i>Scirpus distigmaticus</i> , <i>Poa crymophila</i> , <i>Dracocephalum heterophyllum</i> Benth	One-layer canopy <i>Stipa aliena</i> , <i>Poa crymophila</i> , <i>Kobresia humilis</i> , toxic species: <i>Oxytropis kansuensis</i> , <i>Leontopodium hastioides</i> , <i>Morina chinensis</i>	Shorter vegetation canopy: <i>Kobresia pygmaea</i> , <i>Saussurea superba</i> , <i>Gentiana straminea</i> , <i>Oxytropis kansuensis</i> , <i>Leontopodium hastioides</i>	<i>Elsholtzia calycocarpa</i> , <i>Ajania tenuifolia</i> , <i>Polygonum sibiricum</i> , <i>Ligularia virgaurea</i> , <i>Potentilla anserina</i>

^aNo grazing management in poor plots does not indicate grazing enclosure. Because of few palatable grasses, poor plots could not support many livestock (0.5 sheep/hm²)

^bMean value ± standard error, the same below

dient sites. Ten plots, each with the dimensions of 10 m × 10 m, were uniformly established in each study area, and were numbered plot 1 to plot 10 from east to west. To minimize pseudo-replication, we surveyed the abiotic and biotic variables in different plots.

In plots 1, 3, and 5, plant relative coverage (PC) and vegetation height (VH) were estimated first by visual observation then measured using a ruler by the same expert. Following this, the plant community was surveyed via a grid method of 5 × 5 cm (frame of 50 × 50 cm, total of 100 points). Absolute coverage was defined by occurrence within the 100 points, and aboveground biomass (AGB) of each species was obtained by standard harvesting method. Species diversity was measured based on relative AGB of each plant species in the same quadrat. Species richness (SR, Eq. 1), Shannon–Weaver index (SW, Eq. 2), and species evenness (Pielou index, P, Eq. 3) were calculated according to the following equations:

$$SR = S \quad (1)$$

$$SW = - \sum_{i=1}^s P_i \ln(P_i) \quad (2)$$

$$P = \frac{SW}{\ln(S)} \quad (3)$$

where S is the sum of species number in the frame, and P_i is the relative AGB of species i . Meanwhile, four plant functional groups were also identified: sedges, graminoids, legumes, and forbs.

In plots 2, 4, 6, 8, and 10, 50 cm × 50 cm quadrats were used to harvest the vegetation AGB. Following this, we sampled six soil cores at depths of 0–10, 10–20, 20–30, and 30–50 cm using a soil sampler with a diameter of 6 cm in each of the five quadrats mentioned above. Finally, we mixed the three soil cores from the same depth to acquire belowground biomass (BGB) and utilized the other three soil cores for SOM analysis. Samples for determination of BGB and SOM had five replicates. Samples for determining AGB and BGB were oven-dried at 65 °C for 48 and 72 h, respectively, before weighing. SOM was measured using a TOC analyzer (TOC-5000, Shimadzu, Japan). The volumetric ratio of root/soil (R/S) was defined as the ratio of root volume and soil volume at the same depth and. R/S was surveyed using a root-sampler with a diameter of 1.5 cm with five replicates and measured using a volumetric flask in the laboratory (Li et al. 2012).

In plots 5, 7, and 9, soil bulk density (BD) and water retention capacity samples were acquired with a 100 cm³ cutting ring (5 cm in diameter) from the soil profile at depths of 0–10, 10–20, 20–30, and 30–50 cm with three replicates in each plot. The volumetric soil water content at different depths was measured using a portable Time Domain Reflectometer (TDR) with five replicates. BD was determined using an oven-dry weighing method. Based on the standard method of soaking the ring sampler with in situ turf and soil, soil water retention was determined by weighing, oven drying and calculat-

ing after immersing for 24 h in a pan of water in the laboratory and then draining on a grate for 0 h for saturation soil water capacity (SWC) and 24 h for field soil water capacity (FWC), respectively (Zhang et al. 1999). Volumetric soil water content was transformed to mass soil water content (MSWC) using the corresponding BD to facilitate comparison with water-holding capacity. ME was clearly visually different from substratum, and its depth was measured in the soil vertical profile using a ruler.

In plots 5, 7, and 9, the soil surface infiltration rate (IR) was measured using a soil ring sampler with three replicates in each plot. The soil ring sampler was pressed vertically into the soil surface at a depth of 0.8 cm and 50 mL of water was slowly poured into the ring sampler. IR was calculated as the ratio of the time taken for the water to completely infiltrate the soil surface over 50 mL (Li et al. 2012).

Statistical methods

The Kolmogorov–Smirnov test was first conducted and the results showed that variables were normally distributed ($0.22 < P < 0.73$) without transformation. One-way ANOVA (analysis of variance) and LSD (least significant difference) tests were performed for multiple comparisons of biotic factors, edaphic factors, and water-holding capacity along degradation gradients using SPSS 15.0 software (SPSS Inc, USA). Stepwise regression was adopted to identify relatively important variables. For comprehensive analysis of the degradation

processes within the plant community, we used PC-ORD 4.2 (MjM Software, USA) for non-metric multidimensional scaling (NMDS), which is one of the most powerful ordination methods (Clarke 1993). We performed the ordination of the matrix (61×12) of 53 species, absolute abundance of four functional groups and AGB $\times 4$ gradients with three replicates. In the NMDS set-up, the autopilot mode (slow and thorough) was applied, and Sorensen (Bray–Curtis) was chosen for measuring distance. Because the replicates of environmental factors were different, PC, VH, AGB, ME, IR, BGB, NSWC, SWC, SOM, BD, and R/S, were averaged by degradation gradients and then treated as a second matrix (11×12) for exploring their influence on community variations.

Results

Response of abiotic and biotic variables

Significant differences among AGB, ME, and IR were observed along the degradation gradients (Table 2). AGB and IR demonstrated U-shaped variations, and their minima occurred in fair plots. ME, which exhibited a unimodal pattern, was the highest in fair plots and increased by 125 % in comparison with that in excellent plots, and then decreased by 215 % in poor plots. Stepwise regression analysis showed that ME was the overriding driving factor on IR, and further analysis revealed a negative exponential relationship ($r^2 = 0.88$, $P < 0.001$, $N = 9$). Notably, the biodiversity indices

Table 2 The mean (one-way analysis of variance) and multiple (least significant difference) comparisons of biotic and edaphic factors along the degradation gradients in an alpine meadow

	Meadow degradation gradients			
	Excellent	Good	Fair	Poor
Plant coverage (PC, %)	99.0 \pm 1.0 ^{Aa}	91.6 \pm 2.6 ^{Aa}	66.0 \pm 2.5 ^{Bb}	78.2 \pm 5.9 ^{Bc}
Vegetation height (VH, cm)	23.6 \pm 1.07 ^{Aa}	2.3 \pm 0.53 ^{Cc}	2.2 \pm 0.35 ^{Cc}	6.7 \pm 0.65 ^{Bb}
Species richness (R)	27 \pm 1 ^{Aa}	15 \pm 4 ^{Bb}	19 \pm 3 ^{Bb}	18 \pm 2 ^{Bb}
Shannon–Weaver index (SW)	3.5 \pm 0.13 ^{Aa}	2.6 \pm 0.16 ^{Bc}	3.2 \pm 0.15 ^{ABb}	3.2 \pm 0.07 ^{ABab}
Pielou index (P)	1.1 \pm 0.03 ^{Aa}	1.0 \pm 0.10 ^{Aa}	1.1 \pm 0.03 ^{Aa}	1.1 \pm 0.03 ^{Aa}
Aboveground biomass (AGB, g m ⁻²)	331.1 \pm 15.2 ^{Aa}	166.1 \pm 27.8 ^{Cc}	101.3 \pm 3.6 ^{Dd}	218.7 \pm 17.2 ^{Bb}
0–10 cm Belowground biomass (BGB, g m ⁻²)	1690.2 \pm 318.5 ^{Bb}	1962.4 \pm 297.3 ^{Bb}	4289.6 \pm 343.8 ^{Aa}	980.2 \pm 193.7 ^{Cc}
0–10 cm Soil organic matter (SOM, % _{op})	66.5 \pm 6.5 ^{Bb}	78.3 \pm 3.1 ^{Bb}	134.8 \pm 7.9 ^{Aa}	46.1 \pm 4.8 ^{Cc}
0–10 cm Soil bulk density (BD, g cm ⁻³)	0.73 \pm 0.07 ^{Aab}	0.68 \pm 0.03 ^{Aab}	0.64 \pm 0.03 ^{Ab}	0.76 \pm 0.02 ^{Aa}
0–10 cm Volumetric ratio of root/soil (R/S)	0.5 \pm 0.2 ^{Cc}	0.7 \pm 0.4 ^{Bb}	1.4 \pm 0.5 ^{Aa}	0.3 \pm 0.2 ^{Cc}
Mattic epipedon (ME, cm)	2.0 \pm 0.4 ^{Cc}	3.1 \pm 0.2 ^{Bb}	4.5 \pm 0.3 ^{Aa}	0.2 \pm 0.1 ^{Dd}
Infiltration rate (IR, mm min ⁻¹)	29.8 \pm 4.9 ^{Bb}	2.0 \pm 0.3 ^{Cc}	0.9 \pm 0.1 ^{Dd}	52.9 \pm 7.5 ^{Aa}
Function type biomass (g m ⁻²)				
Sedges	29.3 \pm 4.57 ^{ABab}	157.7 \pm 15.54 ^{Aa}	20.2 \pm 1.64 ^{Bb}	1.5 \pm 1.52 ^{Cc}
Graminoids	97.0 \pm 22.13 ^{Aa}	11.5 \pm 4.00 ^{Bb}	19.1 \pm 5.40 ^{Bb}	2.8 \pm 0.74 ^{Bb}
Legumes	21.7 \pm 4.51 ^{Aa}	11.8 \pm 7.82 ^{Bb}	7.6 \pm 2.51 ^{Bb}	0.6 \pm 0.54 ^{Bb}
Forbs	129.4 \pm 35.72 ^{ABa}	80.4 \pm 8.93 ^{Bb}	96.0 \pm 18.81 ^{ABab}	182.2 \pm 41.10 ^{Aa}
Function type absolute cover (%)				
Sedges	24.0 \pm 6.1 ^{Bbc}	72.3 \pm 7.2 ^{Aa}	42.3 \pm 12.8 ^{ABb}	0.7 \pm 0.7 ^{Cc}
Graminoids	52.7 \pm 12.7 ^{Aa}	4.3 \pm 0.9 ^{Bb}	19.7 \pm 7.3 ^{Bb}	5.0 \pm 2.5 ^{Bb}
Legumes	24.3 \pm 14.3 ^{Aa}	3.7 \pm 1.9 ^{Aa}	3.7 \pm 0.9 ^{Aa}	0.7 \pm 0.3 ^{Ab}
Forbs	153.0 \pm 13.8 ^{Aa}	52.7 \pm 12.1 ^{Bc}	61.7 \pm 8.4 ^{Bbc}	96.3 \pm 2.3 ^{Bb}

The different uppercase and lowercase letters indicate significant differences with $P < 0.01$ and $P < 0.05$, respectively

(*SR*, *SW*, and *P*) changed little along the degradation gradients, mainly because of the emergence of exotic or rare species. The final stress and final instability in NMDS were 7.96 and 0, respectively, for this two-dimensional solution (Fig. 1), suggesting an appropriate ordination with high reliability (Clarke 1993). The variability explained by the first and second axes was 56.2 and 34.4 %, respectively, and revealed clear separation of plant communities along degradation gradients (Fig. 1). The first axis combined the positive effect of *VH* and *AGB*, while the second axis illustrated the impact of topsoil *BD*, *BGB*, *IR*, and *ME* (Table 3). Except for poor plots, all plots were above the first axis (Fig. 1). These results suggest that there is a threshold of plant community transition along the degradation gradient and that occurs in the periods between fair plots and poor plots, together with dramatic simultaneous changes in ecological variables such as *BGB*, *SOM*, *R/S*, *ME*, and *IR*.

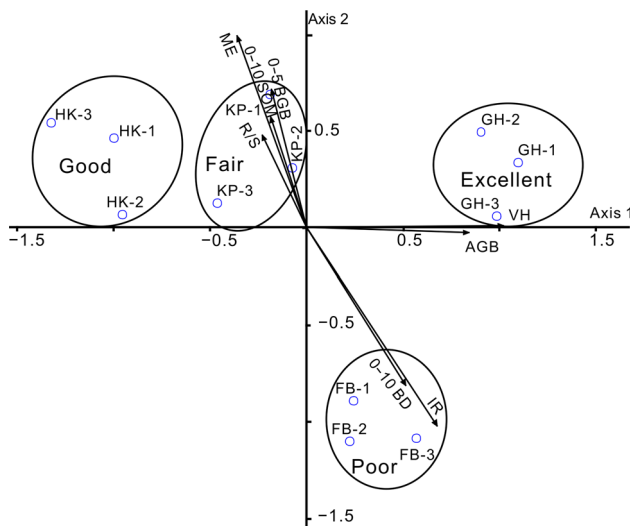


Fig. 1 Results of non-metric multidimensional scaling analysis of the alpine plant community along the degradation gradients. GH, KP, HK, and FB indicate excellent, good, fair, and poor plots, respectively. “–1,” “–2,” and “–3” are ordinal quadrats. The direction of vector arrows represents positive and negative effects and their lengths represent the magnitude of the effects of environmental factors on ordination axes

Table 3 Correlation coefficients between environmental factors and the two nonmetric multidimensional scaling axes

Environmental factors	Axis 1	Axis 2
Plant coverage (PC)	0.23	0.20
Vegetation height (VH)	0.83	0.07
Aboveground biomass (AGB)	0.75	–0.15
Mattic epipedon (ME)	–0.48	0.82
Infiltration rate (IR)	0.67	–0.83
0–5 cm Belowground biomass (0–5 BGB)	–0.34	0.69
0–10 cm Soil water content (0–10 NSWC)	0.21	0.27
0–10 cm Saturation water content (0–10 SWC)	0.10	0.26
0–10 cm Soil organic matter (0–10 SOM)	–0.35	0.62
0–10 cm Soil bulk density (0–10 BD)	0.58	–0.74
0–10 cm Volumetric ratio of root/soil (R/S)	–0.38	0.57

Surprisingly, the topsoil *BD* changed significantly only between fair and poor plots. This finding might be because of coarser soil texture and higher topsoil root biomass in alpine meadow, which is indicative of an environment that was not very sensitive to animal hooves. Additionally, the similar unimodal trend of *R/S* and *SOM* also coincided with the topsoil *BD* pattern along the degradation gradients from excellent to poor (Table 2), and *R/S* and *SOM* were negatively correlated with *BD* ($r^2 > 0.93$, $P < 0.05$, $N = 9$).

Soil water-holding capacity

Rangeland degradation was accompanied by significantly less topsoil water content, except in poor plots (Fig. 2). The pattern of topsoil water content along the degradation gradients (from excellent to poor) was depicted by a quadratic function ($r^2 = 0.76$, $P < 0.01$, $N = 9$). The difference in soil water content at other depths was undetectable only between fair and poor plots (Fig. 2), which suggested that topsoil moisture was more sensitive to degradation processes. *FWC* and *SWC* exhibited similar variation along the degradation gradients, and their maxima both occurred in fair plots and were much greater than that of shallow soil layers (depth < 20 cm). Stepwise regression analysis showed that *PC* and *R/S* were the dominant factors in variations in topsoil water content and retention capacity along the degradation gradients, respectively.

It is worth noting that the minimum soil water content and the maximum water holding capacity were both observed in fair plots, indicating that soil water content and retention were asynchronous during degradation processes and their highest difference occurred in fair plots in the alpine meadow. *IR*, which is related to soil water recharge, might be a contributing factor to this pattern. Furthermore, over-growth of *ME* decreased *IR* (Table 2), which resulted in more surface runoff from rainfall.

Discussion

Vegetation dynamics

Along the degradation gradients, *AGB* and *PC* of the vegetation exhibited U-shaped patterns while *SOM* showed unimodal variation (Table 2), contrary to previously reported results (Snyman 2000; Swemmer et al. 2007). One potential explanation involves the specific properties of *Kobresia* species in alpine meadow. *K. pygmaea* is a xerophile and has a very high root/shoot ratio and formed extremely firm *ME* easily under heavy grazing pressure (Miehe et al. 2008). *ME* enhanced topsoil organic matter, blocked the ecosystem nutrient cycle and impeded the colonization of most competitor plant species. Over-growth of *ME* reduced the soil water recruitment by hindering rainfall infiltration and re-

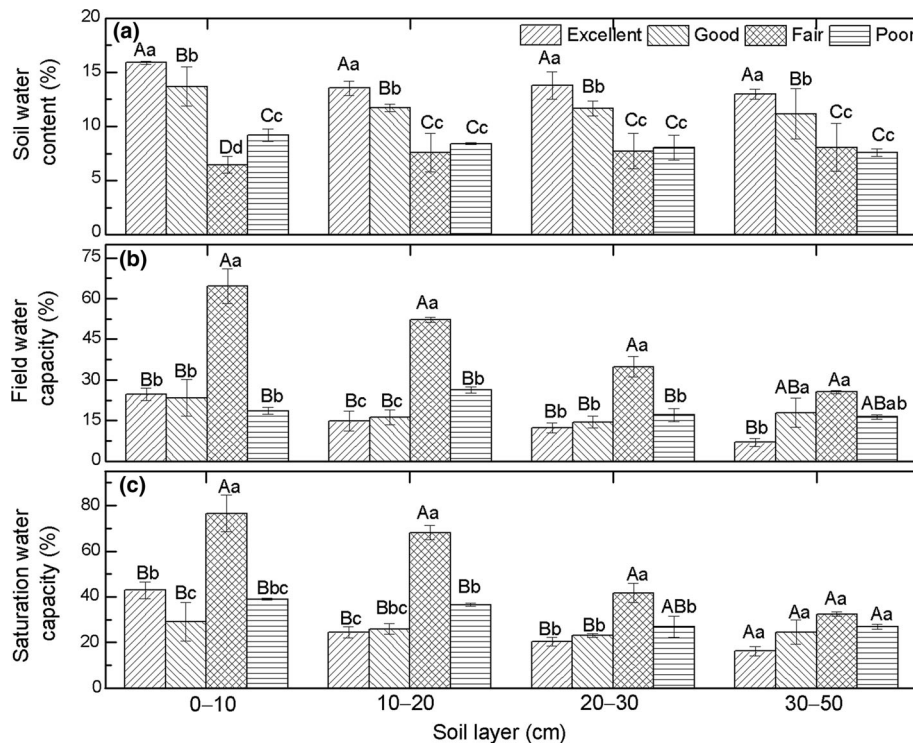


Fig. 2 The mean (one-way analysis of variance) and multiple (least significant difference) comparisons of soil water content (a), field water capacity (b), and saturation water capacity (c) along the degradation gradients in the alpine meadow. The different

uppercase and lowercase letters indicate significant differences with $P < 0.01$ and $P < 0.05$, respectively. Error bars indicate standard error (SE)

sulted in serious physiological desiccation, even for *K. pygmaea* (Miehe et al. 2008). Consequently, the center turf of ME was dead and the lowest AGB and PC in vegetation occurred in fair plots, which provide suitable habitat and food for plateau pikas (Kang et al. 2007). Collapse of ME induced by rodent infestation and soil gelification resulted in a higher proportion of dicotyledonous weedy species (Table 1), which clearly promoted aboveground plant production in poor meadows while degrading grassland health status (Wang et al. 2006). It should be noted that transition of ME from overgrowth phase to a complete collapse phase takes several decades (Li et al. 2012).

Plant species diversity fluctuated little with degradation gradients, which was in good agreement with the notion that biodiversity might not be an appropriate criterion for assessing ecosystem quality (Perevolotsky and Seligman 1998; Whitford et al. 1998). As grazing pressure increases, undesirable exotic disturbance-tolerant species invade and outcompete palatable and less-resistant species, potentially resulting in stable species richness in the ecosystem (Milton et al. 1994). Thus, compensatory effects among plant species and functional groups (i.e. sedges vs. graminoids between excellent plots and fair plots, Table 2) mainly resulted in insignificant diversity variations. Additionally, this area has one of the highest small-scale species richness globally (Chen et al. 2008).

Ordination revealed good separation of health status based on degradation gradients but did not follow a linear or gradual transition (Fig. 1), highlighting the presence of discontinuity in vegetation changes along grazing gradients (Wang et al. 2006; Sasaki et al. 2008). This finding supported the non-equilibrium theory of the response of the plant community to degradation (Suding et al. 2004) and a threshold in vegetation transition might occur from fair plots to poor plots (Fig. 1). This means that vegetation transition should be irreversible if alpine meadow have crossed the threshold and vice versa. A succession experiment within a grazing enclosure demonstrated reversible vegetation dynamics among excellent, good, and fair sites (Miehe et al. 2008), also supporting the presence of a threshold between fair and poor plots. Topsoil quality (SOM, BGB, ME, and IR) changed dramatically from fair to poor plots (Table 2), indicating that the soil properties might have degraded in this transition. These results partially confirmed the hypothesis that irreversible soil degradation resulted in catastrophic vegetation shifts (van de Koppel et al. 1997; Perevolotsky and Seligman 1998). Our finding of non-equilibrium vegetation dynamics is important for future efforts to rehabilitate degraded alpine meadows. For example, reduction in grazing intensity or enclosure could be prescribed to less degraded meadows. Artificial seeding and controlling of the rodent population is recommended to restore meadows that have

crossed the threshold and are severely degraded, like black soil beaches.

Soil water content and holding capacity

Water reapportionment is considered to be the first manifestation of the degradation process (Cheng et al. 2008; Wang et al. 2008). Soil water content declined significantly along the gradient from excellent to good, then fair (or poor) plots (Fig. 2), mainly because of a combination of increased surface evapotranspiration induced by overgrazing and subsequent enhancement of sensible heat (Cheng et al. 2008), and decreased moisture recruitment caused by changes in rainfall IR (Table 2). The mean difference in topsoil water content among the gradient plots was 32.6 %, which was much greater than the 20.7 % water content of the other soil layers. Consequently, the effect of degradation on water content was the largest in the topsoil layer. This is consistent with the fact that the grazing effect is usually limited to the upper 50–150 mm of soil (Greenwood and McKenzie 2001), which has a disproportionately large effect on soil water and nutrient supply (Mills and Fey 2003).

The water-holding capacity of the fair plots was the highest (Fig. 2), mainly because they had the highest SOM, which corresponded to more stable aggregates and water storage (Valentini et al. 1999; Neary et al. 2000). Significant positive relationships ($r^2 > 0.90$, $P < 0.05$, $N = 9$) were found between topsoil water retention and SOM. Other studies have shown that root adsorption had a greater contribution to water retention than soil capillary action in alpine meadows (Cao et al. 2001; Li et al. 2012). In our study, the highest BGB existed in fair plots (Table 2). Therefore, the observed pattern of soil water retention could be the result of synergistic influences from vegetation and soil in alpine meadows (Wang et al. 2008). The maximum topsoil water retention and minimum water content were both found in fair plots, suggesting that a strong asynchronous pattern exists between topsoil water content and holding capacity along degradation gradients in alpine meadow with the largest difference occurring in fair plots. This might also explain the non-equilibrium vegetation transition by severe physiological desiccation (Miehe et al. 2008) and low nutrient availability (Wang and Fu 2004) previously observed in *Kobresia* meadow.

Soil condition is the cornerstone of rangeland health, and degradation triggers a positive feedback loop of reduced water and nutrient availability (van de Koppel et al. 1997; Medina-Roldán et al. 2007). Surprisingly, neither topsoil water content ($P = 0.57$, $N = 9$) nor ecosystem health status were positively correlated with SOM along the degradation gradients in alpine meadow (Table 2). This is in contrast to the general conclusion that greater organic matter content is positively related to soil water content (Milton et al. 1994) and grassland conditions (Whitford et al. 1998; Asner et al. 2004). A

possible reason for this discrepancy is that higher SOM is mainly caused by overgrowth of ME, which decreases rainfall infiltration and reduces water recruitment (Miehe et al. 2008). In addition, higher SOM also means greater soil heat capacity, which generally inhibits soil temperature increase and decreases microbial mineralization (Wang and Fu 2004) since the alpine region is a nutrient-limited ecosystem and the available nutrients are regulated by thermal conditions (Wang et al. 2007). Therefore, we constructed a threshold-based management hypothesis in which the optimal topsoil organic matter ranges from 6.6 % (excellent plots) to 10.6 % (mean value of good and fair plots), with a corresponding ME of 3.8 cm (mean value of good and fair plots) in alpine meadows over the northeastern QTP. Topsoil with appropriate water retention capacity has better heat insulation characteristics in the alpine region, which are beneficial for vegetation growth and ecosystem stability (Cheng et al. 2008).

Conclusion

Our results highlight how changes in species dominance and soil hydrology are triggered by different grazing intensities under similar climatic and edaphic conditions in alpine *Kobresia* meadow in the northeastern QTP. Along the degradation gradients, the absolute abundance of palatable plants declined significantly. AGB and IR exhibited a U-shaped pattern, while ME, BGB, and topsoil SOM demonstrated unimodal variations. Plant community biodiversity and topsoil BD showed little fluctuation, mainly because of the high local species richness and coarse soil texture, respectively. NMDS on plant community variations along degradation gradients indicated that the vegetation variation processes were consistent with non-equilibrium theory in the alpine *Kobresia* meadow and that the threshold existed between fair and poor plots. The relationship of topsoil (<10 cm) water content to degradation gradients was represented by a quadratic function with a minimum in fair plots and PC as the dominant driving factor. The topsoil field and saturation water capacity showed a unimodal pattern with peaks in fair plots, which were ascribed to highest R/S because much more soil moisture was adsorbed by roots rather than by soil capillaries. In addition, the maximum soil water content and maximum holding capacity occurred in excellent and fair plots, respectively. This indicated that soil water content and retention were asynchronous along degradation gradients. This resulted in serious physiological desiccation and was an important driving factor in non-equilibrium vegetation transition. Topsoil organic matter and ME are appropriate internal and external indicators for threshold-based management and their optimal values are 10.6 % (7.83–13.5 %) and 3.8 cm (3.1–4.5 cm), respectively, for the alpine *Kobresia* meadow in the northeastern QTP.

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