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REGULAR PAPER

Long-term effects of grazing exclusion on aboveground and belowground plant species diversity in a steppe of the Loess Plateau, China

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Background and aims – Livestock grazing exclusion was widely used to manage degraded grassland ecosystems, but little is known on the effects of long-term grazing exclusion on aboveground and belowground species diversity of the steppe vegetation in China.
Material and methods – The species composition of the aboveground vegetation and the soil seed bank were examined on sites after a 25-year grazing exclusion in a typical steppe on the Loess Plateau, NW China.
Key results – Results showed that long-term grazing exclusion significantly improved vegetation cover, biomass and aboveground species evenness. Long-term grazing exclusion significantly increased species richness and seed density in the soil seed bank, but significantly decreased belowground species evenness. The seeds were mainly present in the litter and the topsoil (0–5 cm), accounting for about 76% of the total seed number.
Exclusion of grazing significantly decreased seed depletion in soil seed bank from April to July as compared to grazed sites. The Sørensen similarity index between aboveground and belowground species composition was low in the typical steppe, and long-term grazing exclusion did not significantly improve this similarity.
Conclusion – Our results suggest that long-term grazing exclusion can significantly improve both aboveground and belowground species diversity in the steppe vegetation of the Loess Plateau, but has little or no effect on the similarity in composition between the two compartments.

Key words – grazing, grazing exclusion, Loess Plateau, soil seed bank, steppe, vegetation.

INTRODUCTION

Grassland resource degradation has been considered one of the serious environmental problems on the Loess Plateau, mainly due to overgrazing, intensification of cultivation and other unreasonable land use (Zhang et al. 2004, Zhou et al. 2006). Restoration of degraded grassland on the Loess Plateau is critical for regional ecological reconstruction. In general, two simple restoration methods (plantation and disturbance exclusion) have been widely applied to solve this degradation problem. However, during the past years plantation measures gave poor results (Zhao et al. 2003a, 2003b). In recent years, some ecologists have proposed that the ecosystem restoration should depend on natural restoration rather than artificial disturbances (Bradshaw 2000). Natural restoration has become a research focus and is considered as an effective restoration approach for degraded grasslands (Wu et al. 2010).

Grassland management may significantly influence density and composition of the soil seed bank and its similarity with species composition of aboveground vegetation. For instance, grazing can reduce (McDonald et al. 1996), have no effect (Ortega et al. 1997, Meissner & Facelli 1999) or even increase (Russi et al. 1992, Bakoglu et al. 2009) seed density in the soil seed bank. Moreover, grazing can increase (Ungar & Woodell 1996), decrease (Jutila 1998) or have no effect on (Peco et al. 1998) the similarity between aboveground and belowground species composition in grassland ecosystems. Previous researches mainly focused on the effects of grazing exclusion on aboveground vegetation biomass, succession and community structure, or the effects of short-term grazing exclusion on soil seed bank (Spooner et al. 2002, Lunt et al. 2007, Jeddi & Chaieb 2010). However, to our knowledge, less information is available on the effects of long-term grazing exclusion on soil seed bank composition and density in a grassland ecosystem (Bakoglu et al. 2009), such as the steppe on the Loess Plateau. Understanding the effects of long-term grazing exclusion on both aboveground and belowground species diversity and composition is important for diversity conservation and vegetation restoration in this region.

Therefore, we conducted a comparative study to determine the effects of long-term (25 years) grazing exclusion on patterns of aboveground and belowground species composition and diversity, relative to grazing in semi-arid steppes of the Loess Plateau. Our working hypothesis was that long-term grazing exclusion can significantly improve both aboveground and belowground species diversity and density. We also examined the similarity between aboveground and belowground species composition, to test the hypothesis of a positive effect of long-term grazing exclusion and to better understand the role of the soil seed bank in community regeneration in the study area.

MATERIAL AND METHODS

Study area

This study was conducted in a typical steppe in Yunwu Mountain Pastoral Preservation Station (36°13'–36°19'N 106°24'–106°28'E) in Guyuan county, Ningxia Autonomous Region, located in the northwest of the Loess Plateau. The altitude ranges from 1,800 m to 2,100 m a.s.l. The region has a semiarid continental climate with an average temperature of 6.7°C, and an average annual evaporation of 1,400 mm. Mean annual precipitation is 400–450 mm with great inter-annual variability, and rainfall from July and September accounts for 65–85% of the annual precipitation. The study area's ≥ 10°C accumulated temperature is 2,259.7°C per year, and frost-free period is 112–140 days. The soils, developed on wind accumulated loess parent material, are thick with an average of 50 to 80 cm. The soil type of the study area is loessic with silt content ranging from 64 to 73% and clay content varying from 17 to 20%. The soil is weakly resistant to erosion. The vegetation in this area is dominated by *Stipa bungeana* Trin. ex Bunge, *S. grandis* P.A.Smirn., *Thymus mongolicus* (Ronniger) Ronn., *Artemisia frigida* Willd., and *Potentilla acaulis* L.

Experiment design and sampling

Grazing was the most frequent disturbance that induced serious grassland degradation and soil erosion in this area many years ago. In order to prevent further deterioration of the existing conditions, the reserve has been fenced by wire netting to completely exclude livestock grazing from 1982 to now, so it has been free of grazing for 25 years in 2007. In this area, we selected a grazing-excluded (GE) site. A grazed (G) site was selected in the neighborhood of the GE site (at c. 500 m of distance) as control. G site was not fenced by wire netting and was undergoing continuous sheep and cattle grazing.

Six 50 × 50 m^2 blocks were set up in each GE and G site using the line transect method at interval of 50 m. Three sampling quadrats (1 × 1 m) in each block were randomly established and separated by at least 15 m. Five soil cores were extracted with a 9-cm diameter soil auger to a depth of 15 cm by diagonal sampling in each quadrat in April 2007, which was after winter chilling but before any seedling emergence. Each soil sample was then divided into four layers: litter layer, 0–5 cm, 5–10 cm, 10–15 cm. The litter layer was included in this study because long-term grazing exclusion induced a large amount of litter and contained many seeds in this region. Subsamples of the same layer from the same quadrat were pooled and put in one plastic bag. We took soil samples again in July 2007 from the same areas in the same manner, which was the period that current-year seed germination has ceased and before any new seeds were dispersed. A total of 288 (2 sites × 6 blocks × 3 quadrats × 4 layers × 2 times) soil samples were taken back to laboratory and air dried and stored until germination experiment started.

Vegetation sampling was carried out in July 2007, which was the peak of the growing season. Near each soil sampling quadrat (at approximately 2 m of distance), we arranged another 1 × 1 m^2 quadrat to record aboveground vegetation. So, eighteen quadrats were set in each GE and G site. Species composition, vegetation cover and aboveground biomass were measured by point-intercept frequency in each quadrat.

Germination experiment

In this study, we applied the greenhouse seedling emergence method to estimate the germinable seed bank composition and density. The seedling emergence method is commonly used and considered more reliable than elutriation, although it needs large labor and long time (Gross 1990). The seedling emergence experiment was conducted in a greenhouse. The soil samples were evenly spread out to a depth of about 1 cm on 20 cm × 28 cm × 4 cm trays filled with sterilized sand. Five control trays filled with only sterilized sand were randomly placed in the greenhouse to detect for the potential contamination. No seedlings emerged from the control trays until the experiment ended. Temperature was not controlled and varied between 15 and 30°C. Each sample was handed-water to keep moist every day and emerging seedlings were labeled with small tags made of toothpicks to estimate their number at regular time intervals. Seedlings were identified at species level and then removed. Unidentifiable seedlings were planted and grown until they were identifiable. When there was no new emerging seedling for several days, soils were stirred by hand to stimulate germination, and then watered again. The germination experiment last about one year until no more new seedlings emerged.

Statistical analysis

Species were classified into four functional groups: annual forbs, perennial grasses, perennial forbs and shrubs; annual grasses were not detected in this study.

Although entropies such as the Shannon-Wiener and Gini-Simpson indices are commonly used as indices of diversity, they are not true diversity. In this study, we used Hill numbers to compute true diversity indexes. Hill numbers are interpreted as the 'effective number of species' or 'species equivalents' (Hill 1973, Jost 2006). Hill numbers were computed as follows:

$$^{q}D = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$$

Table 1 – Diversity indices of aboveground (vegetation) and belowground (soil seed bank) species in grazing-excluded (GE) and grazed (G) sites on the Loess Plateau.
Values are means (± SE) of 18 quadrats. Two-way ANOVA with block and management type showed significant differences between management types while differences between blocks and the interaction were not significant. Means followed by different letters are significantly different at $P < 0.05$.

Management type	Vegetation				
	^0D	^1D	^2D	$^1D/^0D$	$^2D/^0D$
GE site	18.1 ± 0.93a	11.11 ± 0.85a	8.61 ± 0.91a	0.61 ± 0.02a	0.48 ± 0.04a
G site	16.3 ± 0.62a	5.33 ± 0.58b	3.21 ± 0.34b	0.31 ± 0.02b	0.19 ± 0.02b
Management type	**Soil seed bank**				
	^0D	^1D	^2D	$^1D/^0D$	$^2D/^0D$
GE site	9.7 ± 0.40a	5.99 ± 0.45a	4.64 ± 0.43a	0.60 ± 0.03b	0.46 ± 0.03b
G site	7.8 ± 0.39b	5.44 ± 0.34a	4.46 ± 0.31a	0.70 ± 0.03a	0.58 ± 0.03a

where S is the number of species, p_i is the relative abundance of the i^{th} species and q is the 'order' of the diversity measure. The order of a diversity index determines its sensitivity to differences in species abundance. Hill numbers provide a unified framework for the three most popular groups of diversity measures, for q = 0, 1 and 2. Roughly, ^0D is completely insensitive to species abundances, ^1D measures the number of 'common' species in a community, and ^2D measures the number of 'very abundant' or dominant species in a community, and $^1D/^0D$ or $^2D/^0D$ measure species evenness in a community. The measure ^0D corresponds to species richness (total number of species present), ^1D corresponds to the exponential of Shannon entropy, and ^2D corresponds to the inverse of Simpson.

Similarity of the qualitative composition between grazing-excluded and grazed sites, as well as between seed bank and aboveground vegetation was computed as the binary Sørensen's index of similarity (IS) using the following equation:

$$IS = \left(\frac{2C}{A + B}\right) \times 100$$

where C is the number of species in common between two samples having A and B number of species, respectively.

We took two soil seed bank sampling times to analyze the seed bank depletion, according to the previous studies of Ortega et al. (1997), Funes et al. (2003) and Ma et al. (2010). The seed bank depletion was calculated as: (number of seeds per block in April - number of seeds per block in July) / number of seeds per block in April.

Two-way analysis of variance was performed to test the effects of the two management types and the six blocks on vegetation cover, biomass, species abundance of plant functional types, species diversity of the aboveground vegetation, and density, species diversity of the soil seed bank. To test for differences between blocks and soil depths in GE and G sites respectively, we also computed two-way analyses of variance. To meet the requirement of variance homogeneity, the data were logarithmically transformed prior to analysis. For all ANOVA analyses, results in which $P < 0.05$ are reported as significant. Untransformed mean values for sites of management types were obtained by averaging the values of the respective six blocks. All statistical analyses were performed using SPSS software, v.16.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Species composition and diversity of aboveground vegetation

In our vegetation survey, a total of 53 species were recorded, belonging to nineteen families. The dominant families were Poaceae, Rosaceae and Asteraceae. Forty-seven species were recorded in the GE site and 42 in the G site (electronic appendix). Species composition of aboveground vegetation in both sites was very similar, with 35 species in common. Perennial species are a major component of the aboveground vegetation in both sites. The results showed that long-term grazing exclusion significantly increased the species abundance of perennial grasses ($F = 7.859$, $P < 0.05$) and decreased the species abundance of annual forbs ($F = 17.971$, $P < 0.001$), but had little impacts on the shrubs and perennial forbs compared with G site (fig. 1A).

The two-way analyses of variance showed that there was significant differences in total vegetation cover between blocks ($F = 2.828$, $P < 0.05$), but no differences in aboveground biomass ($F = 2.319$, $P > 0.05$). Management types significantly affected total vegetation cover and aboveground biomass. The block × management type interaction was not significant in both total vegetation cover ($F = 1.078$, $P > 0.05$) and aboveground biomass ($F = 0.316$, $P > 0.05$). Long-term grazing exclusion significantly increased total vegetation cover (%) (82.33 ± 2.1 and 59.61 ± 2.7 for GE and G, $F = 64.990$, $P < 0.001$) and aboveground biomass (160.66 ± 9.43 and 77.29 ± 3.77 g/m^2 for GE and G, $F = 117.096$, $P < 0.001$) compared with G site.

Diversity indices of aboveground vegetation in GE and G sites based on ^qD for q = 0, 1 and 2 are shown in table 1. Two-way ANOVA revealed no significant differences in species diversity between blocks, but management type was a significant factor. Moreover, there were no interaction between management type and block. ^1D, ^2D, $^1D/^0D$ and $^2D/^0D$

in GE sites were significantly higher than that in G sites ($F = 36.411$, $P < 0.001$; $F = 54.365$, $P < 0.001$; $F = 50.611$, $P < 0.001$; $F = 31.717$, $P < 0.001$, respectively), but there was no significant difference in ^{0}D ($F = 2.893$, $P > 0.05$) between the GE and the G sites (table 1).

Species composition and diversity of soil seed bank

We recorded a total of 5141 seedlings in both sites, belonging to 37 species and sixteen families. The dominant families in the soil seed bank were Poaceae, Asteraceae, Ranunculaceae and Lamiaceae, and 80% of the species were perennials (electronic appendix). The results showed that there was little change in plant composition between GE and G sites (fig. 1B). Similarly to aboveground vegetation, we found no significant difference between blocks for diversity indices in soil seed bank. The block × management type interaction was not significant. Long-term grazing exclusion significantly increased ^{0}D ($F = 11.857$, $P < 0.05$), significantly decreased ^{1}D/^{0}D ($F = 6.286$, $P < 0.05$) and ^{2}D/^{0}D ($F = 7.337$, $P < 0.05$), but did not obviously change ^{1}D ($F = 0.463$, $P > 0.05$) and ^{2}D ($F = 0.016$, $P > 0.05$) compared with G sites (table 1).

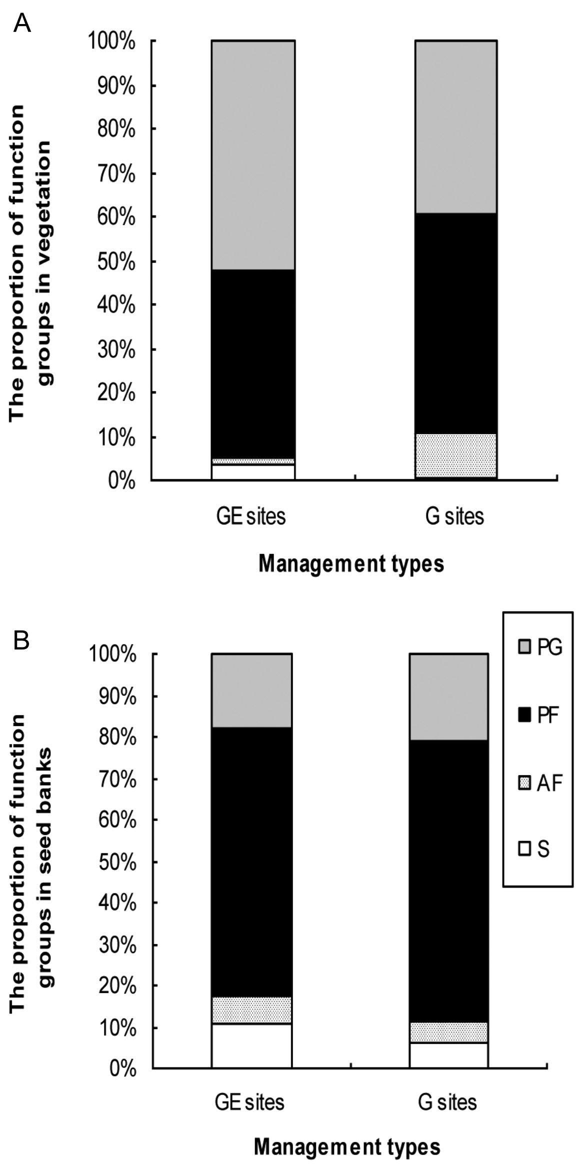

Figure 1 – Relative species abundance of four plant functional types in aboveground vegetation (A) and belowground soil seed bank (B) in grazing-excluded (GE) and grazed (G) sites. PG: perennial grasses; PF: perennial forbs; AF: annual forbs; S: shrubs.

Density of soil seed bank

The two-way analyses of variance showed that there were highly significant differences between management types ($F = 36.233$, $P < 0.001$), but no significant differences between blocks ($F = 2.187$, $P > 0.05$). The block × treatment interaction was not significant ($F = 0.826$, $P > 0.05$). Species density in sites with grazing exclusion (2876.6 ± 147.42 seeds m^{-2}) was significant higher than in G sites (1614.7 ± 159.35 seeds m^{-2}).

The soil seed density in different layers in both sites is shown in table 2. Two-way ANOVA with block and soil depth showed significant main effects for soil depth while differences between blocks and the interaction were not significant. Seed density was significantly different in different layers in GE sites ($F = 38.649$, $P < 0.001$) and G sites ($F = 34.481$, $P < 0.001$), respectively.

The soil seed proportions for the litter, 0–5, 5–10, 10–15 cm soil layers were 28.6%, 47.3%, 16.1%, and 8.0%, respectively. The soil seeds mainly existed in the litter and top 0–5 cm, which accounted for about 76% of the total seed number.

The depletion of soil seed bank from April to July in the GE site was significantly lower than that of the G site ($F = 11.868$, $P < 0.05$), and was mainly observed in the litter and the 0–5 cm top soil (51.8%).

Similarity between aboveground and belowground species composition

The average similarity between the aboveground vegetation and the soil seed bank species composition was low. Sørensen similarity index was slightly higher in GE than in G sites. Furthermore, the similarity of species composition for either aboveground or belowground vegetation between GE and G sites was high (table 3).

DISCUSSION

Effects of long-term grazing exclusion on the aboveground plant community

The results presented in this study demonstrated that the reduced disturbance in this typical steppe had a distinct and direct effect on vegetation cover, biomass, and species diversity. The significant increase of the total plant cover and aboveground biomass inside the grazing exclusion site is in agreement with the results of Jeddi & Chaieb (2010) and Wu et al. (2010). GE sites had higher diversity indices ^{1}D and ^{2}D in the aboveground vegetation than G sites, which indicated that long-term grazing exclusion increased the number of 'common' or 'very abundant' species in the aboveground

Table 2 – Seed density of the different layers in the soil seed bank in grazing-excluded (GE) and grazed (G) sites on the Loess Plateau.
Untransformed mean values (±se) for sites of each management type are given. Two-way ANOVA with block and layer showed significant differences among layers while differences between blocks and the interaction were not significant. Means in the same horizontal direction followed by different letters are significantly different at $P < 0.05$ tested with ANOVA and Tukey's test for post-hoc comparisons.

Management types	Layer			
	Litter layer	0–5 cm	5–10 cm	10–15 cm
GE site	979.0 ± 108.69a	1176.3 ± 72.70a	491.7 ± 30.37b	229.7 ± 24.37c
G site	501.3 ± 77.53b	758.9 ± 71.81a	234.0 ± 34.06c	120.5 ± 20.63d

Table 3 – Sørensen similarity index (%) between aboveground (vegetation) and belowground (soil seed bank) species composition for grazing-excluded (GE) and grazed (G) sites.
Mean values (±se) were obtained by averaging Sørensen index between blocks.

	Vegetation similarity		Soil seed bank similarity		Vegetation vs. soil seed bank similarity	
	G sites	GE sites	G sites	GE sites	G sites	GE sites
G site	-	66.5 ± 7.82	-	71.8 ± 9.52	28.5 ± 6.00	-
GE site	66.5 ± 7.82	-	71.8 ± 9.52	-	-	26.0 ± 5.21

vegetation. Moreover, we found that the GE site presented a higher species evenness ($^1D/^0D$ and $^2D/^0D$). However, there was no significant difference for species richness (^0D). Both sites shared a large proportion of common species, resulting in a high similarity between grazed and grazing-excluded blocks. These results indicated that long-term grazing exclusion led to minor changes in qualitative species composition of aboveground vegetation. Similar studies have reported that there was little change in plant composition associated with combinations of grazing exclusion and fertilizer applications in wet meadow restoration in eastern Washington (Beebe et al. 2002). Lunt et al. (2007) also proposed that grazing exclusion had minor impact on plant composition, and the composition between grazing-excluded and grazed sites did not become more different with grazing exclusion time increasing. This is strongly consistent with the results of this study.

The distinct and positive effect of the long-term grazing exclusion on vegetation cover, biomass, and species evenness may be attributed to the improvement of soil conditions (soil organic carbon and nitrogen storage, water infiltration rate and basal soil respiration, temperature, moisture) after grazing exclusion, which favours the regeneration and the development of herbaceous species (Jeddi & Chaieb 2010, Wu et al. 2010). An increase of the Shannon-Wiener species diversity index in protected sites was reported by Shaltout et al.(1996), Eweg et al. (1998), Shang et al. (2008), Mayer et al. (2009), Ma et al. (2009) and Jeddi & Chaieb (2010). However, the opposite was observed in the studies of Milchunas & Lauenroth (1993), Proulx & Mazumder (1998) and Dullinger et al. (2003). So far, there is no general agreement about species diversity response to grazing in grassland ecosystems. These effects could be either positive or negative. Why do effects differ? Zhang (1998) noted that change in plant species diversity in relation to grazing or grazing exclusion depended on resource partitioning and competitive patterns in vegetation. Olff & Ritchie (1998) also proposed this effect depends on regional variation in major habitat characteristics (soil fertility and water availability.

Effects of long-term grazing exclusion on soil seed bank

Long-term grazing exclusion significantly increased species richness (^0D) and density of the soil seed bank, but significantly decreased species evenness ($^1D/^0D$ and $^2D/^0D$), which suggests it could play an important role in steppe restoration. By contrast, continuous grazing resulted in less species richness and lower seed bank density. The finding of a marked impact of grazing exclusion and grazing regime on soil seed bank was also observed in other grasslands (Russi et al. 1992, McDonald et al. 1996, Jutila 1998, Liu et al. 2009). This increase could be explained by two reasons. First, livestock grazing can cause a massive reduction in seed production either by reducing allocation of plant resources for reproduction due to leaf harvesting or by the direct removal of flowers and seeds (Sternberg et al. 2003); therefore, the exclusion of livestock could ensure more seed import into the soil seed bank. Secondly, long-term grazing exclusion increased litter thickness and biomass. Cheng et al. (2006) found an increase of litter thickness up to 3.5 cm, and 51.3% of the seeds were included in the litter in typical steppe on Loess Plateau. Comins (1982) suggested that litter could provide the shelter for seeds to avoid being predated by livestock and washed away by rain. So the thick litter in grazing-excluded sites could explain the increase in species richness and density of the soil seed bank. As shown in our study, more seeds were included in the litter in the GE site than in the G site.

Our data suggest that long-term grazing exclusion has an important effect on species diversity of the soil seed bank, although no significant increase in ^1D and ^2D. The response of belowground diversity to grazing exclusion or grazing is complex. The exclusion of grazing in areas with a long history increased the common or very abundant species in the soil seed bank, and accordingly decreased the species evenness. However, some studies showed that grazing exclusion in an annual plant community had little or no effect on species diversity in the soil seed bank (Meissner & Facelli 1999). The contrasted results may be due to differences in the relative dominance of perennial plants in these study areas.

The depletion of soil seed bank from April to July was mainly induced by germination, predation by livestock and seed decay. In conditions of grazing exclusion, lower soil disturbance by livestock would lead to less opportunity for seeds to germinate and to be eaten (Edwards & Crawley 1999), thus explaining a lower depletion of seed bank from April to July in the grazing-excluded site. Furthermore, livestock mainly trampled the top soil layer and eaten the seeds in the top soil profile in grazed sites. While in the grazing-excluded situation thick litter provided the favorable water and heat conditions for seed germination, the depletion of seed bank mainly existed in the litter and top soil layer. Furthermore, the similarity index of soil seed bank between the GE and G sites was high. Long-term grazing exclusion did not significantly change the qualitative composition of seed bank, indicating that restoration of the grazed sites is not species-limited. A similar study by Ma et al. (2009) reported that the Sørensen index of similarity of soil seed banks was high (84.6%) between an enclosed and a degraded alpine meadow in the eastern Tibetan Plateau. Zhan et al. (2007) also reported that the grazed steppe and the enclosed steppe were relatively similar in soil seed bank composition, and that the dominant species were also the same. The high similarity between grazed and ungrazed sites may be due to low productivity in these regions. Mayer et al. (2009) proposed that the effect of grazing exclusion on the soil seed bank was productivity-dependent, after having reported a higher similarity between grazed and ungrazed subplots in the less productive grasslands.

Similarity between aboveground and belowground species composition

The similarity between soil seed bank and the vegetation was low in the typical steppe, which conformed to the relevant report by Edwards & Crawley (1999) in a mesic grassland in UK. To our knowledge, this dissimilarity is reported for the first time on the Loess Plateau. The main reason is probably owing to the dominance of perennial grasses in this steppe community. Similar results have been reported in other grasslands dominated by perennial species (Jutila 1998, Peco et al. 1998). In contrast, some studies concluded that there are relatively higher similarities between vegetation and seed bank in annual-dominated vegetation (Ungar & Woodell 1996, Chang et al. 2001). In perennial-dominated grassland, the dominant perennial species would choose vegetative reproduction and have a low seed production, so they make a minor contribution to the formation of seed banks.

Grazing exclusion or grazing can play a minimal role in the variation of the similarity between soil seed bank and the vegetation, as shown in our study, in which there was no statistically significant difference in seed bank – vegetation similarity between grazing-excluded and grazed sites. This is in agreement with the results of Osem et al. (2006) who found grazing did not affect similarity at low productivity. However, our results suggest that seed bank – vegetation similarity in the grazed site could be slightly higher than in the grazing-excluded site. The results of Milberg & Hanson (1993) also showed a higher similarity between seed bank and vegetation in disturbed and grazed sites. However, another study (Jutila 1998) reported that the dissimilarity between seed bank and vegetation was larger in grazed than in ungrazed sites. The recruitment in grazed sites could be more dependent on the soil seed bank. Wu et al. (2011) proposed that grazing increases sexual recruitment and decreases asexual recruitment.

We conclude that the main effects on seed bank – vegetation similarity depends on the dominance of annual or perennial plants. Management measures will have less effect on the similarity between soil seed bank and aboveground vegetation in perennial-dominated grasslands such as our study area. We can however expect that the development of the soil seed bank may be lagged behind increases in vegetation diversity with increasing grazing exclusion time. Long-term grazing exclusion is an effective restoration approach to protect species diversity and restore vegetation on the Loess Plateau, although this effect may take a long time. The potential to naturally restoring the degraded grasslands in this region by the exclusion of livestock could be substantial.

SUPPLEMENTRAY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of the following: species, families and plant functional types (PFT) of the taxa present in the aboveground and belowground plant community in grazing-excluded (GE) and grazed (G) sites on the Loess Plateau (pdf format).

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REFERENCES

Bakoglu A., Bagci E., Erkovan H.I., Koc A., Kocak A. (2009) Seed stocks of grazed and ungrazed rangelands on Palandoken Mountains of Eastern Anatolia. Journal of Food, Agriculture and Environment 7: 674–678.

Beebe J., Everett R., George S., Carl D. (2002) Effect of fertilizer applications and grazing exclusion on species composition and biomass in wet meadow restoration in eastern Washington. Res. Pap. PNW-RP-542. Portland, Oregon, Department of Agriculture, Forest Service, Pacific Northwest Research Station. [available at http://www.fs.fed.us/pnw/pubs/rp542.pdf]

Bradshaw A. (2000) The use of natural processes in reclamation advantages and difficulties. Landscape and Urban Planning 51: 89–100. doi:10.1016/S0169-2046(00)00099-2

Chang E.R., Jefferies R.L., Carleton T.J. (2001) Relationships between vegetation and soil seed banks in arctic coastal marsh. Journal of Ecology 89: 367–384. doi:10.1046/j.1365-2745.2001.00549.x

Cheng J.M., Wan H.E., Hu X.M. (2006) Soil seed bank and meadow renewal in the grassland on Loess Plateau. Acta Pedologica Sinica 43: 679–683. [in Chinese].

Comins H.N. (1982) Evolutionarily stable strategies for localized dispersal in two dimensions. Journal of Theoretical Biology 94: 579–606. doi:10.1016/0022-5193(82)90302-2

Dullinger S., Dirnböck T., Greimler J., Grabherr G. (2003) A resampling approach for evaluating effects of pasture abandonment on subalpine plant species diversity. Journal of Vegetation Science 14: 243–252. doi:10.1111/j.1654-1103.2003.tb02149.x

Edwards G.R., Crawley M.J. (1999) Herbivores, seed banks and seedling recruitment in mesic grassland. Journal of Ecology 87: 423–435. doi:10.1046/j.1365-2745.1999.00363.x

Eweg H.P.A., Van Lammeren R., Deurloo H., Woldu Z. (1998) Analysing degradation and rehabilitation for sustainable land management in the highlands of Ethiopia. Land Degradation and Development 9: 529–542. doi:10.1002/(SICI)1099-145X(199811/12)9:6<529::AID-LDR313>3.0.CO;2-O

Funes G., Basconcelo S., Díaz S., Cabido M. (2003) Seed bank dynamics in tall-tussock grasslands along an altitudinal gradient. Journal of Vegetation Science 14: 253–258. doi:10.1111/j.1654-1103.2003.tb02150.x

Gross K.L. (1990) A comparison of methods for estimating seed numbers in the soil. Journal of Ecology 78: 1079–1093. doi:10.2307/2260953

Jeddi K., Chaieb M. (2010) Changes in soil properties and vegetation following livestock grazing exclusion in degraded arid environments of South Tunisia. Flora 205: 184–189. doi:10.1016/j.flora.2009.03.002

Jost L. (2006) Entropy and diversity. Oikos 113: 363–375. doi:10.1111/j.2006.0030-1299.14714.x

Jutila H.M. (1998) Seed banks of grazed and ungrazed Baltic seashore meadows. Journal of Vegetation Science 9: 395–408. doi:10.2307/3237104

Hill M.O. (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427–432. doi:10.2307/1934352

Liu M.Z., Jiang G.M., Yu S.L., Li Y.G., Li G. (2009) The Role of Soil Seed Banks in Natural Restoration of the Degraded Hunshandak Sandlands, Northern China. Restoration Ecology 17: 127–136. doi:10.1111/j.1526-100X.2008.00366.x

Lunt I., Jansen A., Binns D., Kenny S. (2007) Long-term effects of exclusion of grazing stock on degraded herbaceous plant communities in a riparian Eucalyptus camaldulensis forest in southeastern Australia. Austral Ecology 32: 937–949. doi:10.1111/j.1442-9993.2007.01782.x

Ma M.J., Zhou X.H., Lv Z.W., Du G.Z. (2009) A comparison of the soil seed bank in an enclosed vs. a degraded alpine meadow in the eastern Tibetan Plateau. Acta Ecologica Sinica 29: 3658–3664. [in Chinese].

Ma M.J., Zhou X.H., Wang G., Ma Z., Du G.Z. (2010) Seasonal dynamics in alpine meadow seed banks along an altitudinal gradient on the Tibetan Plateau. Plant and Soil 336: 291–302. doi:10.1007/s11104-010-0480-5

Mayer R., Kaufmann R., Vorhauser K., Erschbamer B. (2009) Effects of grazing exclusion on species composition in high-altitude grasslands of the Central Alps. Basic and Applied Ecology 10: 447–455. doi:10.1016/j.baae.2008.10.004

McDonald A.W., Bakker J.P., Vegelin K. (1996) Seed bank classification and its importance for the restoration of species-rich flood-meadows. Journal of Vegetation Science 7: 156–164. doi:10.2307/3236315

Meissner R.A., Facelli J.M. (1999) Effects of sheep exclusion on the soil seed bank and annual vegetation in chenopod shrublands of South Australia. Journal of Arid Environment 42: 117–128. doi:10.1006/jare.1999.0515

Milberg P., Hanson M.L. (1993) Soil seed bank and species turnover in a limestone grassland. Journal of Vegetation Science 4: 35–42. doi:10.2307/3235635

Milchunas D.G., Lauenroth W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63: 327–366. doi:10.2307/2937150

Olff H., Ritchie M.E. (1998) Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13: 261–265. doi:10.1016/S0169-5347(98)01364-0

Ortega M., Levassor C., Peco B. (1997) Seasonal dynamics of Mediterranean pasture seed banks along environmental gradients. Journal of Biogeography 24: 177–195. doi:10.1046/j.1365-2699.1997.00080.x

Osem Y., Perevolotsky A., Kigel J. (2006) Similarity between seed bank and vegetation in a semi-arid annual plant community: the role of productivity and grazing. Journal of Vegetation Science 17: 29–36. doi:10.1111/j.1654-1103.2006.tb02420.x

Peco B., Ortega M., Levassor C. (1998) Similarity between seed bank and vegetation in Mediterranean grassland: a predictive model. Journal of Vegetation Science 9: 815–828. doi:10.2307/3237047

Proulx M., Mazumder A. (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79: 2581–2592. doi:10.2307/176502

Russi L., Cocks P.S., Roberts E.H. (1992) Seed bank dynamics in a Mediterranean grassland. Journal of Applied Ecology 29: 763–771. doi:10.2307/2404486

Shaltout K.H., El-Halawany E.F., El-Kady H.F. (1996) Consequences of protection from grazing on diversity and abundance of the coastal lowland vegetation in Eastern Saudi Arabia. Biodiversity and Conservation 5: 27–36. doi:10.1007/BF00056290

Shang Z.H., Ma Y.S., Long R.J., Ding L.M. (2008) Effect of grazing exclusion, artificial seeding and abandonment on vegetation composition and dynamics of 'black soil land' in the headwaters of the Yangtze and the Yellow Rivers. Land Degradation and Development 19: 554–563.

Spooner P., Lunt I., Robinson W. (2002) Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. Ecological Management & Restoration 3: 117–126. doi:10.1046/j.1442-8903.2002.00103.x

Sternberg M., Gutman M., Perevolotsky A., Jaime K. (2003) Effects of grazing on soil seed bank dynamics: an approach with functional groups. Journal of Vegetation Science 14: 375–386. doi:10.1111/j.1654-1103.2003.tb02163.x

Ungar I.A., Woodell S.R.J. (1996) Similarity of seed bank to above ground vegetation in grazed and ungrazed salt marsh communities on the Gower Peninsula, South Wales. International Journal of Plant Science 157: 746–749. [JSTOR: http://www.jstor.org/stable/2474888]

Wu Z.Y. (1995) Vegetation of China. Beijing, Science Press. [in Chinese].

Wu G.L., Liu Z.H., Zhang L., Chen J.M., Hu T.M. (2010) Long-term grazing exclusion improved soil properties and soil organic carbon storage in an alpine swamp meadow of western China. Plant and Soil 332: 331–337. doi:10.1007/s11104-010-0299-0

Wu G.L., Li W., Li X.P., Shi Z.H. (2011) Grazing as a mediator for maintenance of offspring diversity: Sexual and clonal recruitment in alpine grassland communities. Flora 206: 241–245. doi:10.1016/j.flora.2010.05.005

Zhan X., Li L., Cheng W. (2007) Restoration of Stipa kryloviisteppes in Inner Mongolia of China: assesment of seed banks and vegetation composition. Journal of Arid Environments 68: 298–307. doi:10.1016/j.jaridenv.2006.05.012

Zhang Q.J., Fu B.J., Chen L.D., Zhao W.W., Yang Q.K., Liu G.B. Gulinck H. (2004) Dynamics and driving factors of agricultural landscape in the semiarid hilly area of the Loess Plateau, China. Agriculture, Ecosystems and Environment 103: 535–543. doi:10.1016/j.agee.2003.11.007

Zhang W. (1998) Changes in species diversity and canopy cover in steppe vegetation in Inner Mongolia under protection from grazing. Biodiversity and Conservation 7: 1365–1381. doi:10.1023/A:1008852017493

Zhao J.B., Hou Y.J., Huang C.C. (2003a) Causes and countermeasures of soil drying under artificial forest on the Loess Plateau in northern Shaanxi. Journal of Desert Research 23: 612–615.

Zhao J.B., Zhou Q., Hou Y.J. (2003b) Effect of dried layer of soil ecological environmental reconstruction. Journal of Shaanxi Normal University 23: 93–109.

Zhou Z.C., Shangguan Z.P., Zhao D. (2006) Modeling vegetation coverage and soil erosion in the Loess Plateau Area of China. Ecological Modelling 198: 263–268. doi:10.1016/j.ecolmodel.2006.04.019

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