

Winter Grazing and Rainfall Synergistically Affect Soil Seed Bank in Semiarid Area[☆]

A. Hu, J. Zhang, X. Chen, S. Chang, F. Hou^{*}

State Key Laboratory of Grassland Agro-Ecosystems, Key Laboratory of Grassland Livestock Industry Innovation, Ministry of Agriculture and College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou, 730000, Gansu, China

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ABSTRACT

The soil seed bank is an important ecological component of grassland restoration and renewal. In semiarid regions, grassland restoration and renewal are highly affected by annual variations in precipitation and grazing activity because these variations can affect the composition, density, richness, and diversity of seeds in the soil. This study aimed to characterize and compare these parameters of the germinable seed bank under different stocking rates in a winter grazing system in a semiarid area of China in 2015 and 2016 (dry and near-average rainfall condition, respectively). The composition, density, richness, and diversity of seeds were determined by the method of seedling emergence. The results showed that a total of 18 species belonging to nine families germinated from the soil. Drought significantly reduced the density, richness, and diversity of the soil seed bank, but grazing was able to significantly increase the richness and diversity of the soil seed bank by increasing the richness and diversity of the aboveground vegetation. The similarity between the soil seed bank and aboveground vegetation was influenced by the rainfall conditions: in the dry year, it was higher at the lower stocking rates (0 and 0.4 animal unit months [AUM] ha⁻¹), and in the near-average rainfall condition year, it was higher at the higher stocking rates (0.8 and 1.3 AUM ha⁻¹).

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Introduction

The restoration of vegetation and grassland, as an important means to improve the ecological environment, has been the focus of many studies (Willems, 2001; Zhao et al., 2006; Wonkka et al., 2016; Link et al., 2017). To prevent the escalation of ecosystem degradation and to restore degraded vegetation within an ecosystem, it is necessary to study restoration ecology, of which the soil seed bank is an important component (Fourie, 2008). The soil seed bank represents the on-site natural seed source for the restoration process and places constraints on vegetation dynamics, which affect the anti-interference and recovery of the ecosystem (Gioria et al., 2014; Tessema et al., 2016). A detailed understanding of the soil seed bank is necessary for comprehensively understanding the ecological characteristics of the vegetation in a region (Thompson, 2000). The soil seed bank is the basis for population establishment, survival, reproduction, and expansion (Milberg and Hansson,

1994). The period during which seeds are stored in the soil seed bank (called the latent stage) is an important stage in the life history of the plant population (Thompson, 2000). This latent stage can reflect the history and current situation of the community and plays an important role in the restoration of a degraded grassland ecosystem (Kalamees et al., 2012). The composition of the status quo or species ratio and seed pool can indicate the quality of the system and can predict the development of vegetation dynamics. Soil seed bank research is an indispensable part of biodiversity research, as the soil seed bank represents the diversity of plant genes potentially available within the potential seed. The soil seed bank is thus of great importance for maintaining the ecological and genetic diversity of population and the community.

Climate and human influences are the two main factors that cause soil erosion, grassland degradation, and decline of biodiversity and vegetation productivity in semiarid areas (Altesor et al., 2005). Soil seed bank characteristics vary with rainfall patterns and livestock pressure (Dreber and Esler, 2011). Seed production is affected by the distribution of rainfall (O'Connor and Pickett, 1992), and seeds are released only after substantial rainfall (Guterman, 2012). The magnitude of the overall heterogeneity in soil seed banks is strongly influenced by livestock pressure through selective grazing and disturbance-related environmental changes (Kinloch and Friedel, 2005; Solomon et al., 2006; Kassahun et al., 2009). High livestock pressure favors annual plants,

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^{*} Correspondence: Professor F. Hou, Lanzhou University, Lanzhou, 730000, Gansu, China.

E-mail address: cyhoufj@lzu.edu.cn (F. Hou).

which tolerate intense grazing and trampling through various adaptations, such as prostrate growth and the production of small seeds that become easily buried (Navie and Rogers, 1997). Therefore, understanding the impact of environmental changes in relation to grazing on soil seed banks is important for conservation, grazing management, and restoration purposes (Osem et al., 2006; Kassahun et al., 2009).

The Loess Plateau in the arid and semiarid area of northern China is vulnerable to soil erosion and is one of the most fragile ecological environments in the world (Hu et al., 2015). It is an ecoregion of ~640 000 km² and spans seven provinces: Qinghai, Gansu, Henan, Shanxi, Shaanxi, Ningxia, and Inner Mongolia (Chen et al., 2017). Extreme weather and climatic events in recent decades have been a worldwide issue because of their potentially severe impacts on human lives, economies, and natural ecosystems (Zwiers et al., 2013). Owing to world climate change, the rainfall of the Loess Plateau has substantially decreased in the past 50 yr (Sun et al., 2016). The arid climate affects the production of local agriculture and animal husbandry. The decline in grassland productivity and agricultural production prompted us to ask how the drought affects the latent population phase as represented by the soil seed bank. Because grazing during anthesis of grasses can affect grass seed production, considerable effort has already been put into investigating the effect of summer grazing (Jacquelyn et al., 2011; Tessema et al., 2012; Yan et al., 2012) and yr-long grazing on the natural seed bank (Sternberg et al., 2003). The effect of winter grazing on the soil seed bank has, however, seldom been studied. Thus, we studied how different rainfall conditions in 2015 and 2016 affected the composition and distribution of the soil seed bank in the winter grazing system. Structural equation modeling (Fig. 5) was chosen to best quantify the influence of grazing and rainfall on the seed bank resulting from aboveground vegetation.

Materials and Methods

Site

This study is part of a larger long-term research project begun in 2001 (Chen et al., 2010; Chen et al., 2015). Briefly, the study site is located in Huan County, eastern Gansu Province, northwest China (37°07'N, 106°48'E, 1 700 m above sea level) and is identified as including semiagricultural and semipastoral areas belonging to the hilly terrain. The mean daily air temperature is 7.5°C, but there is a long cold winter (frost-free period, 125 d) and a hot summer (mean of 3 097 degree-d above 10°C). The average annual precipitation for 2000–2016 was 265 mm, ranging between 148 mm and 433 mm, and was highly variable among yrs (coefficient of variation [CV] = 25.6%). It was very dry in 2015, with annual rainfall of 148 mm, and in 2016 precipitation was close to average with 270 mm (Fig. 1). More than 70% of the precipitation was concentrated from July to September, which represents a typical continental monsoon climate, with 1 993 mm annual evaporation. The soil is classified as sandy, free-draining loess, and the

rangeland is a typical temperate steppe (Gong et al., 2007). The dominant species of plants are *Artemisia capillaris* Thunb., *Stipa bungeana* Trin., and *Lespedeza davurica* (Laxm.) Schindl.

Experimental Design

A long-term rotational grazing system was established in 2001 using 4-mo-old Tan wethers, a traditional sheep breed in the local region. A flatland area (4.5 ha) was selected for a winter pasture and divided into nine paddocks of the same size (50 × 100 m) for grazing. Each paddock has 2 smaller enclosures (each one is 4 × 4 m) within it, and 3 of the 18 were randomly selected for the no-grazing control in this trial. From the middle of November to the end of December or early January, a group of sheep—either 4 sheep, 8 sheep, or 13 sheep—grazed in each paddock, corresponding to stocking rates of 0.4, 0.8, and 1.3 animal unit months (AUM) ha⁻¹, respectively. In the first cycle (24 d), the sheep were moved every 8 d for three times, and then, for the second cycle (21 d), the sheep were moved every 7 d for three times, for a total of 45 d each yr.

Sampling

Aboveground Vegetation

To compare the soil seed bank species with the aboveground vegetation, the herbaceous species were assessed during the peak growth season (mid-August) in 2015 and 2016. Four quadrats (1 m²) were randomly selected from each of the nine grazing paddocks and due to the small area of the enclosure, so four small quadrats (0.25 m²) were selected from each of the three no-grazing plots, totaling 48 each yr. In every quadrat, the species and density were recorded, and vegetation were collected and dried to a constant weight at 65°C.

Soil Samples

All sampling occurred in the middle of November of 2015 and 2016, after seed production. The samples served as an indication of viable seeds not germinated in the soil over the season. Twelve cores (diameter, 9 cm) were selected from three lines (each line 10 m apart) in each grazing paddock, and each line had four samples 20 m apart. From the enclosed (no-grazing) plots, four squares were selected in each plot (two lines 2 m apart with two samples from each line 2 m apart). The soil samples were taken from depths of 0–5 cm and 5–10 cm (Liu et al., 2011; Tessema et al., 2012), and then the soil samples from the same soil layer from the same paddock were pooled and mixed. Finally, each of the 24 (samples from two soil depths from each of nine grazing paddocks, plus samples from two soil depths from each of three controls) composite soil samples were divided into two equal parts: one for the germination test and one for soil analysis. The soil samples for germination were two cores as subsamples, for a total of 48 samples. The samples were then placed outdoors for 2 mo to ensure that the seeds were subjected to freezing temperatures (for vernalization), and then they were taken back to the climate-controlled glasshouse for germination assays (Brock and Rogers, 1998).

Soil from the other half of each of the soil seed bank samples was used to measure the moisture of the soil at 105°C for 48 h.

Germination Test

The number of seedlings of different species emerging from the soil samples was used as a measure of the number of viable seeds and the composition of the soil seed bank. The emergence method is more appropriate than actual identification of the seed species (Espeland et al., 2010) because it determines the relative abundance of viable seeds that can germinate and excludes the nonviable seeds (Poiani and Johnson, 1988). Large stones and grass roots were removed from the soil samples after they were dried at room temperature, and the resulting soil block was crumbled to disperse and ensure the integrity

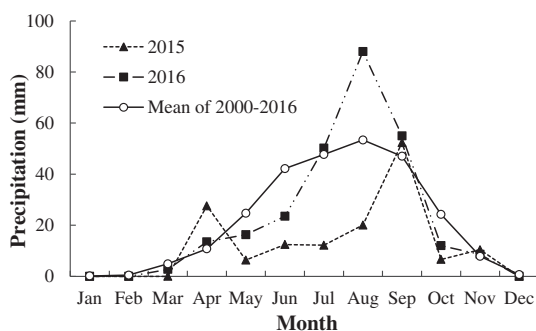


Figure 1. Monthly precipitation in 2015 and 2016, and the mean precipitation from 2000 to 2016.

of the seeds. The soil sample (2 cm thick) was placed on top of a 2-cm layer of (seed-free) sand in a germination tray (diameter, 20 cm). A total of 48 germination trays were placed under natural indoor light conditions at $20 \pm 5^\circ\text{C}$. The soil in the trays was kept moist. Seedlings started to emerge after 1 wk. During the entire growing period, emerging seedlings were identified as soon as possible, recorded, and removed. Those seedlings that were difficult to identify were counted but maintained until they were identified. Seeds in the samples were allowed to germinate for 3 mo (Thompson and Grime, 1979). No attempt was made to assess the number of ungerminated seeds potentially remaining in the samples.

Data Analysis

Following laboratory germination testing as outlined earlier, we have averaged the data of the subsamples before analysis and mixed the 0–5 cm and 5–10 cm layers of the data to analyze the effects of grazing and rainfall on soil seed banks. Density of seeds—number of emerged seedlings in each paddock (seeds m^{-2}), species richness—the number of species in each paddock (species m^{-2}), and species composition were recorded. Species diversity was calculated using the Shannon-Wiener diversity index (H):

$$(H) : H = \sum_{i=1}^S p_i \ln p_i \quad (1)$$

where p_i is the proportion of the i species of the total number of germinated seeds, and S is the total number of the species (Dougall and Dodd, 1997).

The Jaccard coefficient of similarity (Kalacska et al., 2004) was used to test for similarities in species composition between the soil seed bank and the aboveground vegetation for the different stocking rates.

$$\text{Jaccard similarity (J)} = a/b \quad (2)$$

where a represents the number of common species between the two treatments (the soil seed bank and aboveground vegetation at the same stocking rate), and b is the total number of species for the two treatments. The compositions of the soil seed bank and aboveground vegetation were compared between years by a nonmetric multidimensional scaling (NMDS) analysis (using R 3.42) using the Bray-Curtis

dissimilarity matrix, based on the relative density of the species in the 12 sample units (nine grazing paddocks and three control sites).

A goodness-of-fit test (Shapiro-Wilk test) indicated that data collected from this study were normally distributed. To test for differences in density, richness, and diversity of the soil seed bank, a general linear model was applied, with rainfall, stocking rates, and their interactions as independent factors. Differences in density, richness, and diversity of the soil seed bank between different stocking rates and years were verified by Tukey's post hoc test. All analyses were carried out using the software SAS 9.3 (SAS Institute Inc., Cary, NC).

We used structural equation modeling (SEM) to estimate the contributions of stocking rates and annual rainfall to responses of the aboveground vegetation (reproductive culms, richness, and diversity) and the soil seed bank (density, richness, and diversity) of the response. The primary advantage of SEM is its ability to evaluate complex causality between variables by translating the hypothesized causal relationships into a pattern of expected statistical relationships in the data (Grace, 2006). In the model, we assumed that stocking rates and rainfall had the potential to directly alter density, richness, and diversity of the soil seed bank, as well as indirectly through changing the reproductive culms, richness, and diversity of aboveground vegetation. We used the chi-square test to judge the fit of the model. The model has a good fit when $0 \leq \chi^2/\text{df} \leq 2$ and $0.05 < P \leq 1$. Here, a large P value (> 0.05) indicates that the covariance structure of the data does not differ significantly from the expected model (Grace, 2006). SEM analyses were performed using AMOS 21 (Arbuckle, 2010).

Results

Composition of the Soil Seed Bank

A total of 18 species germinated from seeds in the soil. These represented nine families (Asteraceae, Gramineae, Leguminosae, Rosaceae, Linaceae, Plantaginaceae, Chenopodiaceae, Brassicaceae, Boraginaceae), comprising 14 perennial and four annual species (Table 1). Thirteen and seventeen species were found in 2015 and 2016, respectively. *Ixeris chinensis* (Thunb.) Nakai, *Eragrostis pilosa* (Linn.) Beauv., *Potentilla multifida* Linn., *Plantago lanceolata* Linn., and *Torularia humilis* (C. A. Meyer) O. E. Schulz were found only in 2016, and *Salsola ruthenica* Iljin was found only in 2015. *Heteropappus altaicus* (Willd.) Novopokr., *Cleistogenes squarrosa* (Trin.) Keng, *Gueldenstaedtia verna* (Georgi)

Table 1
Germination density (mean \pm SE seed \cdot m^{-2}) of the various species in the soil seed bank at different stocking rates in 2015 and 2016.

Family	Species	Life form	2015				2016			
			0	0.4 AUM ha^{-1}	0.8 AUM ha^{-1}	1.3 AUM ha^{-1}	0	0.4 AUM ha^{-1}	0.8 AUM ha^{-1}	1.3 AUM ha^{-1}
Asteraceae	<i>Artemisia capillaris</i>	Perennial	105 \pm 43	157 \pm 64	184 \pm 57	79 \pm 37	1416 \pm 120	1075 \pm 120	944 \pm 164	603 \pm 69
	<i>Ixeris chinensis</i>	Perennial	–	–	–	–	–	–	–	26 \pm 21
	<i>Heteropappus altaicus</i>	Perennial	–	–	–	52 \pm 43	–	–	52 \pm 43	79 \pm 0
Gramineae	<i>Stipa bungeana</i>	Perennial	52 \pm 43	26 \pm 21	39 \pm 39	79 \pm 64	131 \pm 21	236 \pm 98	78 \pm 45	79 \pm 0
	<i>Eragrostis pilosa</i>	Annual	–	–	–	–	–	–	26 \pm 21	26 \pm 21
	<i>Cleistogenes squarrosa</i>	Perennial	–	–	–	26 \pm 21	–	–	52 \pm 21	26 \pm 21
	<i>Cleistogenes songorica</i> (Roshev.) Ohwi	Perennial	52 \pm 43	–	–	–	–	26 \pm 21	–	–
Leguminosae	<i>Lespedeza davurica</i>	Perennial	–	26 \pm 21	–	–	78 \pm 45	26 \pm 21	52 \pm 21	52 \pm 21
	<i>Gueldenstaedtia verna</i>	Perennial	–	–	–	26 \pm 21	–	26 \pm 21	–	–
	<i>Astragalus melilotoides</i> Pall.	Perennial	–	–	39 \pm 39	–	26 \pm 21	–	26 \pm 21	26 \pm 21
Rosaceae	<i>Potentilla bifurca</i> Linn.	Perennial	–	26 \pm 21	157 \pm 111	–	52 \pm 43	–	52 \pm 21	26 \pm 21
	<i>Potentilla multifida</i>	Perennial	–	–	–	–	105 \pm 86	–	52 \pm 21	79 \pm 0
Linaceae	<i>Linum perenne</i> Linn.	Perennial	–	26 \pm 21	–	–	26 \pm 21	–	26 \pm 21	78 \pm 78
Plantaginaceae	<i>Plantago lanceolata</i>	Perennial	–	–	–	–	–	–	26 \pm 21	–
Chenopodiaceae	<i>Salsola ruthenica</i>	Annual	–	–	–	105 \pm 105	–	–	–	–
	<i>Chenopodium glaucum</i>	Annual	–	–	39 \pm 39	–	–	26 \pm 21	–	–
Brassicaceae	<i>Torularia humilis</i>	Perennial	–	–	–	–	–	26 \pm 21	–	52 \pm 21
Boraginaceae	<i>Lappula deserticola</i> C. J. Wang	Annual	–	–	39 \pm 39	–	26 \pm 21	–	52 \pm 21	26 \pm 21

Note: "–" indicates species was not found in this stocking rate.

Boriss. subsp. multiflora (Bunge) Tsui, and *Chenopodium glaucum* Linn. were found only in grazing plots in both years, but all species found in the no-grazing plots were also found in the grazing plots. The dominant species, *A. capillaris* and *Stipa bungeana*, were found in all sample plots in both years, but *L. davurica* was mainly found in 2016. The density of *A. capillaris* was increased first and then decreased with the increased stocking rate in 2015, but it was decreased in 2016. The total densities of all species for both years at each stocking rate were consistent with the densities variation of *A. capillaris*. The density of *A. capillaris* contributed most to the total soil seed bank density (21.5%–59.9% and 51.1%–76.1% in 2015 and 2016, respectively), but in both years this contribution decreased with increased stocking rate. The annual species were found mainly in the grazing plots and seldom in the no-grazing plots.

Density of the Soil Seed Bank

Year and stocking rate had significant effects on the soil seed bank density ($P < 0.0001$, $P = 0.0058$). The interaction of them also had significant effects on the density ($P \leq 0.0001$; Table 2). The density of the soil seed bank in 2015 was significantly lower than that in 2016 ($P < 0.0001$; see Table 2). The density of the soil seed bank showed an opposite trend in 2 yr. The mean density first increased and then decreased with the increased stocking rate in 2015, with 175, 262, 665, and 367 seeds m^{-2} corresponding to the stocking rates 0, 0.4, 0.8, and 1.3 AUM ha^{-1} , respectively. The density of the soil seed bank decreased as the stocking rate increased in 2016; the densities were 1861, 1442, 1442, and 1180 seeds m^{-2} corresponding to the stocking rates 0, 0.4, 0.8, and 1.3 AUM ha^{-1} , respectively, and it was significantly higher at no-grazing plot than grazing plots ($P < 0.05$); but in 2015, it was significantly higher in 0.8 AUM ha^{-1} than 0 and 0.4 AUM ha^{-1} , and 1.3 AUM ha^{-1} had no significant difference with the other stocking rates ($P > 0.05$; Fig. 2).

The SEM explained 84% of the variation in density of the soil seed bank (Fig. 5A). Stocking rate had no significant indirect (through reproductive culms) or direct effect on seed density (standardized path coefficients of 0.03 and 0.14, respectively, both $P > 0.05$; see Fig. 5A). Rainfall was the main factor to affect the density of the soil seed bank, and both grazing and rainfall were also shown to influence soil moisture. The direct effect of rainfall on density was positive, but the indirect effect of stocking rate and annual rainfall (through soil moisture) were negative (standardized path coefficients of 0.95 and 0.86, $P < 0.001$ and $P < 0.01$, respectively; see Fig. 5A). Soil moisture had a negative influence on the density of the soil seed bank.

Richness of Soil Seed Bank

Yr and stocking rate both had significant effects on soil seed bank richness ($P < 0.0001$ and $P = 0.0001$), but their interaction had no influence on richness ($P = 0.1390$; see Table 2). The richness of the soil seed bank in 2015 was significantly lower than that in 2016 (see Table 2, Fig. 2). The richness of the soil seed bank was increased with the increased stocking rates in 2016, and 0.8 and 1.3 AUM ha^{-1} (7.3 and 7.7 species m^{-2}) were significantly higher than 0 and 0.8 AUM ha^{-1} (4.3 and 4.7 species m^{-2}), respectively, $P < 0.05$; see Fig. 2). It had a peak (5.0 species m^{-2}) at 0.8 AUM ha^{-1} in 2015, and it was significant higher than 0.4 and

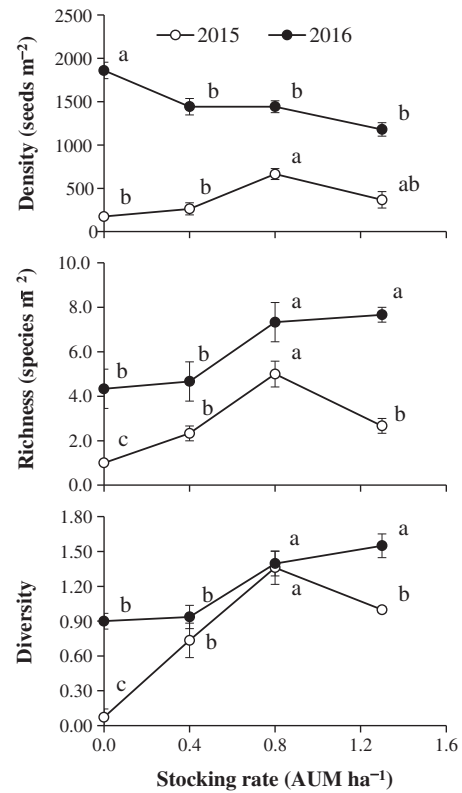


Figure 2. The density, richness, and diversity of the germinable soil seed bank at different stocking rates in 2015 and 2016. Different letters show significant differences at $P < 0.05$.

1.3 AUM ha^{-1} (2.3 and 2.7 species m^{-2}); it was lowest at no-grazing plots with 1.0 species m^{-2} (see Fig. 2).

The SEM explained 74% of the variation in richness of soil seed bank (Fig. 5B). The direct effects of the stocking rate and annual rainfall on the richness of the soil seed bank were not significant (0.22 and 0.32, both $P > 0.05$). However, they both had indirect effects through the richness of aboveground vegetation on the richness of the soil seed bank, as indicated by the standardized path coefficients of 0.29 ($P < 0.05$). And the rainfall cannot change the richness of the soil seed bank. The indirect effect of annual rainfall through soil moisture had no influence on the richness of the soil seed bank (0.30, $P > 0.05$; Fig. 5B), although annual rainfall and stocking rate had significant influence on the moisture (0.93 and 0.29, respectively, both $P < 0.001$).

Diversity of Soil Seed Bank

Yr and stocking rate both had significant effects on soil seed bank diversity ($P < 0.0001$), and their interaction also had a significant influence on the diversity ($P = 0.0063$) (see Table 2). The diversity of the soil seed bank showed the same rule with the richness. It was significantly lower in 2015 than that in 2016 ($P < 0.05$). Diversity increased with the increased stocking rate in 2016; it was significantly higher at 0.8 and 1.3 AUM ha^{-1} (1.40 and 1.55, respectively) than that in the no-grazing plots and at 0.4 AUM ha^{-1} (0.90 and 0.94, respectively). In 2015, it was highest at 0.8 AUM ha^{-1} with 1.36, and it was lowest at no-grazing plots with 0.07. There was no significant difference between 0.4 and 1.3 AUM ha^{-1} (0.73 and 1.00, respectively; see Fig. 2).

The SEM explained 78% of the variation in diversity of soil seed bank (Fig. 5C). The direct effects of the stocking rate and annual rainfall on the diversity of the soil seed bank were not significant (0.22 and 0.26, both $P > 0.05$). However, they both had indirect effects through diversity of aboveground vegetation on diversity of the soil seed bank, as indicated by the standardized path coefficients of 0.29 ($P < 0.05$). And the rainfall cannot change the diversity of the soil seed bank. The indirect effect of

Table 2 Effects of stocking rate and yr on the density, richness, and diversity of the germinable soil seed bank, with statistical results of the general linear model (F, P, R²_{adjusted}).

Variable	Density		Richness		Diversity	
	F	P	F	P	F	P
Year (Y)	424.55	< 0.0001	56.33	< 0.0001	30.83	< 0.0001
Stocking rate (SR)	6.09	0.0058	13.37	0.0001	32.19	< 0.0001
Y × SR	15.29	< 0.0001	2.11	0.1390	5.96	0.0063
R ² _{adjusted}	0.9682		0.8652		0.9008	

annual rainfall through soil moisture had no influence on the diversity of the soil seed bank (0.30 and 0.00, respectively, both $P > 0.05$; Fig. 5C), although annual rainfall and stocking rate had a significant influence on the moisture (0.93 and 0.29, respectively, both $P < 0.001$).

Similarity Analysis of Soil Seed Bank and Aboveground Vegetation

The NMDS showed that the species composition was significantly different between the soil seed bank and aboveground vegetation. The aboveground vegetation was clustered together in both yrs, and the soil seed banks were more heterogeneous: They were clustered in 2016 but more spread out along the two coordinates in 2015 (Fig. 3). This showed that drought had a great influence on the composition of the soil seed bank, but it had little influence on the composition of aboveground vegetation.

We next examined the similarity between the composition of the soil seed bank and the aboveground vegetation at different stocking rates. The Jaccard coefficients of similarity were all < 0.5 for both the grazing plots and no-grazing plots. In 2015, the similarity was at a medium level (Mendes et al., 2015) at the lower stocking rate (0.40 for no-grazing plots and 0.37 for 0.4 AUM ha⁻¹) and was significantly higher than that at the higher stocking rates of 0.8 and 1.3 AUM ha⁻¹ (0.16 and 0.33, $P < 0.05$, respectively). In 2016, the relationship was reversed, as a medium level of similarity occurred at the higher stocking rates of 0.8 and 1.3 AUM ha⁻¹ (0.42 and 0.47, respectively), which was significantly higher than that at the lower stocking rates (0.31 and 0.20 for the no-grazing plots and 0.4 AUM ha⁻¹, respectively, $P < 0.05$; Fig. 4).

Discussion

Density of Soil Seed Bank

Many studies have shown that grazing can affect the density and composition of the soil seed bank (Tessema et al., 2012; Frank et al., 2016), because livestock can reduce seed by consuming reproductive culms of plants, and it gets worse as stocking rates increase (Abule et al., 2005; Kassahun et al., 2008; Tessema et al., 2011). In this way, protection from grazing by enclosure fencing on the Loess Plateau can benefit the soil seed bank by increasing its density and richness (Zhao et al.,

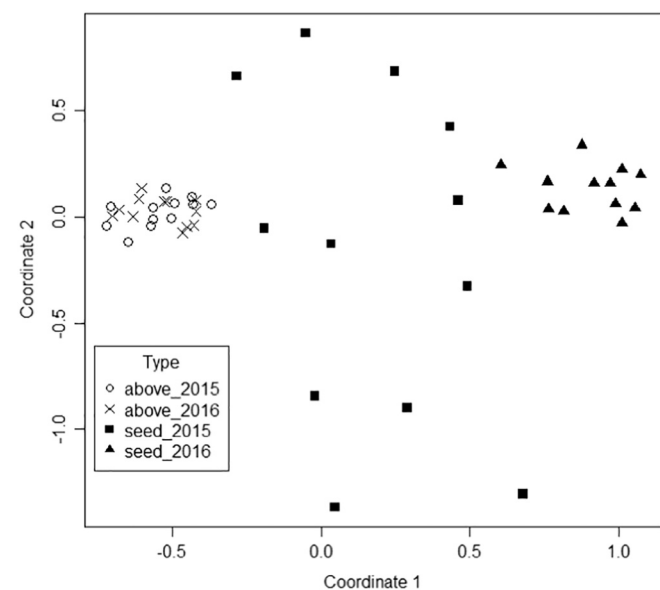


Figure 3. Ordination diagram of the 12 sampling sites for the density of soil seed bank and aboveground vegetation of 2 yr by NMDS. Above_2015 and above_2016 refer to the composition of aboveground vegetation in 2015 and 2016, respectively; seed_2015 and seed_2016 refer to the composition of the soil seed bank in 2015 and 2016, respectively.

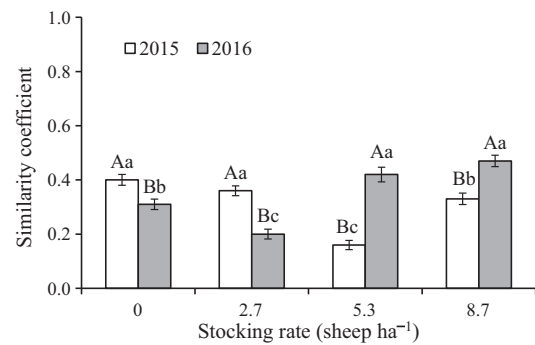


Figure 4. Jaccard coefficient of similarity for species composition comparing the soil seed bank and aboveground vegetation under different stocking rates in 2015 and 2016. Capital letters show significant differences between the 2 yr at $P < 0.05$, and lowercase letters show significant differences between different stocking rates at $P < 0.05$.

2008). Solomon et al. (2006) also observed more seedlings of grass species at lightly grazed areas compared with heavily grazed ones in semi-arid areas in Africa. This study showed that grazing had a significant effect on the density of the soil seed bank, but there were contrasting effects in 2 yr (see Fig. 1). In 2016, when there were near-average rainfall conditions, it showed the same rule with other studies (Abule et al., 2005; Kassahun et al., 2008; Tessema et al., 2011; Tessema et al., 2012). The density of the seed bank was decreased by the increased stocking rate, but in the dry yr in 2015 the density first increased and then decreased with the increased stocking rate. This result agrees with other studies, which showed that moderate grazing resulted in the highest soil seed bank density (Zhao et al., 2001; Dreber and Esler, 2011). Seeds may be more effectively stored in the soil as a result of sheep trampling, an effect that may last years, and thus grazing may lead to higher soil seed density relative to no-grazing plots (Willms and Quinton, 1995).

The rainfall was previously observed to affect the influence of stocking rate on soil seed bank density (Yan et al., 2012; Pol et al., 2014). Most studies on seed banks emphasize that the density of seed bank is higher during the rainy season, and the floristic composition is a function of this season (Mayor et al., 2003; Mendes et al., 2015). This was the reason that density in 2016 was significantly higher than in 2015. From the SEM (Fig. 5A), unlike summer grazing, when soil seed bank can be affected by livestock intake reproductive culms at or before flowering stage (Jacquemyn et al., 2011; Tessema et al., 2012; Yan et al., 2012), in winter grazing, the grassland was only disturbed by the livestock in winter, so it had no significant indirect (through reproductive culms) or direct effect on seed density. The rainfall was the main factor to affect the density of the soil seed bank. Both grazing and rainfall were also shown to influence soil moisture, and soil moisture had a negative influence on the density of the soil seed bank (Fig. 5A), most likely because it promoted seed germination, especially in autumn on the Loess Plateau, but higher annual rainfall can produce more seeds (O'Connor and Pickett, 1992). When the number of seeds produced is higher than the number of seeds germinated, rainfall has a positive impact on the density.

Richness and Diversity of the Soil Seed Bank

Grazing improves the richness of the soil seed bank (Harrison et al., 2003) because grazing can improve the richness of grassland species, thereby enhancing the richness of soil seed banks (Edwards et al., 2007; Báldi et al., 2013). Grazing also can increase the diversity of grassland vegetation (Stohlgren et al., 1999). Some studies showed that lightly grazing sites had a higher species diversity index in the soil seed banks compared with heavily grazed sites, indicating that heavy grazing has reduced the species diversity in not only the aboveground vegetation but also the soil seed banks (Snyman, 2004; Kinloch and

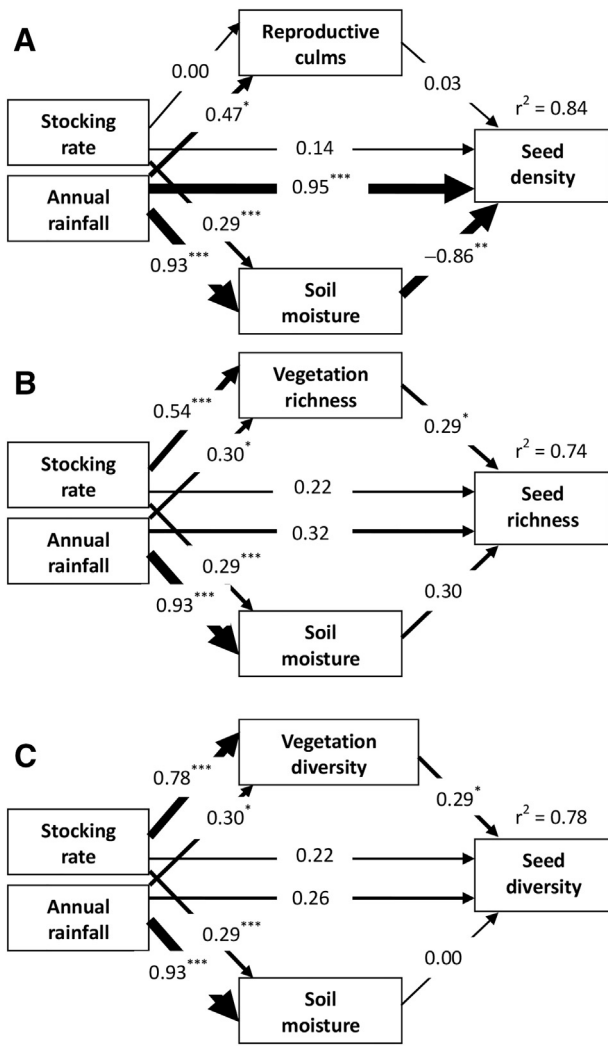


Figure 5. Structural equation models based on the data from soil and aboveground vegetation in this study. Models are shown for **A**, seed density, **B**, richness, and **C**, diversity. The *diagonal arrows* in the upper and lower halves of each model show the indirect effects of stocking rate and annual rainfall on the soil seed bank by way of aboveground vegetation (upper) and soil moisture (lower). The *horizontal arrows* show the direct effect of stocking rate and annual rainfall on the soil seed bank. Numbers on the arrows are standardized path coefficients, indicating the effect size of the relationship. Arrow width is proportional to the strength of the relationship. The proportion of variance explained is given as r^2 . * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Results of model fitting: **A**, $\chi^2 = 0.001$, $P = 1.000$, $df = 1$; **B**, $\chi^2 = 0.004$, $P = 0.998$, $df = 2$, **C**, $\chi^2 = 1.706$, $P = 0.426$, $df = 2$.

Friedel, 2005). Tessema et al. (2011) have reported that species richness in the seed bank was, however, not affected by grazing. In this study, the rainfall and stocking rate both had significant effects on the richness and diversity of the soil seed bank (see Table 2). In 2016, the near-average rainfall condition, the richness and diversity of were increased with increased stocking rate, but in 2015, both of them had a peak at 0.8 AUM ha⁻¹ (see Fig. 2). It confirmed that moderate grazing can keep higher richness and diversity of soil seed bank during dry yrs.

Limited seed dispersal has led researchers to believe that the richness of the vegetation is related to a species-rich soil seed bank (Lopez-Marino et al., 2000). So in the good rainfall yr, grazing can increase the richness and diversity of aboveground vegetation, which can increase the richness and diversity of seed banks, but in dry yrs, due to the higher pressure by livestock on the grassland, some species aboveground cannot bloom or fruit. Some studies emphasized that the richness of seed banks is higher during the rainy season, and the floristic composition is a function of this season (Mendes et al., 2015; Santos et

al., 2016). That can explain why the richness and diversity of seed banks were significantly higher in 2016 than in 2015 (see Fig. 2). The same effects of rainfall and stocking rate on richness and diversity of the soil seed bank also held true for summer grazing systems (Edwards et al., 2007; Báldi et al., 2013; see Fig. 5B and C). Richness and diversity of aboveground vegetation were higher under winter grazing, explaining the higher richness and diversity of the soil seed bank under winter grazing. Rainfall cannot change the richness and diversity of the soil seed bank in winter grazing system like it can in the summer grazing system (Lopez-Marino et al., 2000).

Similarity of Soil Seed Bank and Aboveground Vegetation

Many grassland studies have found a spatial pattern of seeds clustered around parent plants (Shaukat and Siddiqui, 2004). This suggests a trend whereby the similarity of the seed bank and aboveground species increases with the age of the system (Hopfensperger, 2007), because seeds disperse close to the parent plant. The soil seed bank also supports few species after a disturbance (e.g., grazing), and therefore over time aboveground and belowground species richness increases. Consequently, a short dispersal distance drives the high similarity between the soil seed bank and vegetation composition in grasslands (Bossuyt and Hermy, 2004). However, Sackfield et al. (2014) have reported a low similarity between the soil seed bank and aboveground vegetation. Milberg and Hansson (1994) reported that the similarity has a high correlation with the seed germination characteristics and that the species with high turnover in the community are higher in the soil. In this study, the Jaccard similarity values under winter grazing were all < 0.5 (see Fig. 4) similarly low compared with those reported under summer grazing (Sackfield et al., 2014). Previous studies (Thompson and Grime, 1979; Villiers et al., 2003) also reported poor correlations between species in the soil seed bank and aboveground vegetation. Others, however, report much higher similarity (Leck and Graveline, 1979; Levassor et al., 1990). But we found that the similarities under winter grazing were dependent on rainfall. Similarities were higher at the lower stocking rates (0 and 0.4 AUM ha⁻¹) in 2015 because the vegetation in dry yrs was more sensitive to disturbance by higher stocking rate (0.8 and 1.3 AUM ha⁻¹), and low stocking rates (0 and 0.4 AUM ha⁻¹) had less influence on vegetation. In addition, Parlak et al. (2011) have reported that soil seed banks are not disturbed by grazing because they are dormant in the soil, so the low stocking rate in the drought yr resulted in a higher similarity. Further, the similarity was higher at the higher stocking rates (0.8 and 1.3 AUM ha⁻¹; see Fig. 4) in 2016, consistent with the finding that, under near-average rainfall condition, the similarity between the soil seed bank and aboveground biomass is higher in grasslands that are often disturbed by animals (Fenner, 1985; Leck and Simpson, 1994).

Implications

Rainfall and stocking rate were important factors in regulation of the composition, density, richness, diversity, and similarities coefficient of the soil seed bank in winter grazing systems in semiarid rangelands of northwest China. Drought significantly reduced the density, richness, and diversity of the soil seed bank, but grazing can moderate this, so we found soil seed bank density of grazed plots was higher in the dry yr (2015) and the richness and diversity of the soil seed bank were significantly higher with higher stocking rates in both yrs. From our observations, it appears that long-term winter rotational grazing can improve grassland stability. This is particularly relevant in preparation for drought yrs. During drought, stocking rate can be 0.8 AUM ha⁻¹, resulting in maintenance of higher seed bank density, richness, and diversity. This will help to restore the grassland following better rainfall the next yr.

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