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Effects of different habitats on *Achnatherum inebrians* (Hance) Keng ex Tzvelev (drunken horse grass) soil seed banks and aboveground vegetation

Saimilakezi Taiwaikuli[1], Guili Jin[1], Shazhou An[1], Yiqing Dong[1], Peng Wei[2]*

[1]College of Grassland and Environmental Sciences, Xinjiang Agricultural University, Key Laboratory of Grassland Resources and Ecology of Xinjiang, Urumqi Xinjiang, P.R. China
[2]Pratacultural Research Institute of Xin Jiang Academy of Animal Sciences, Urumqi Xinjiang, P.R. China

**Corresponding author: jguili@126.com*

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Abstract: The soil seed bank, as a potential source of ground vegetation renewal, plays an important role in the natural recovery and succession of vegetation as well as in the construction of ecosystems. To clarify the characteristics of the soil seed bank of *Achnatherum inebrians* and its relationship with the aboveground vegetation, the soil seed bank density, species composition and aboveground vegetation of three different grassland types, namely, desert, steppe and meadow, were investigated by means of field survey sampling and indoor germination experiments. The results showed that the seed bank densities of the three habitats were ranked as desert (1 422.22 seeds/m^2), steppe (2 077.78 seeds/m^2) and meadow (3 722.22 seeds/m^2). The numbers of species were 16, 11 and 17, respectively. With respect to the vertical allocation, the soil seed banks in each habitat were shallow, and the seeds were mainly concentrated in the soil surface layer (0–5 cm). The species richness of the soil seed banks in the three habitats was higher than that of the aboveground vegetation, but there were some differences in richness, evenness and dominance. The species richness and diversity of soil seed banks and aboveground vegetation in meadow habitats were higher than those in desert and steppe habitats, indicating that the soil seed banks and aboveground vegetation in meadow habitats had higher stability. There was a significant positive correlation between the density of temporary soil seed banks and the density of aboveground plant communities in grassland habitats. The results may provide some reference for the prevention and control of *Achnatherum inebrians* in the three habitats.

Keywords: invasive plants; poisonous plant; poisonous grass; heterogeneous habitats

The influence of alien invasive species on communities is basically manifested in the change in species composition and ecosystem structure through competition with and exclusion of native species, which finally leads to the deterioration of the ecosystem and the ecological environment. Biological invasion usually leads to the loss of community diversity (Wilcove et al. 1998, Enserink 1999). Previous studies have shown that alien plant invasion in native plant communities will reduce aboveground biodiversity and improve invasive species dominance (Rusterholz et al. 2017). In addition, alien plant invasion also influences community lighting and the soil environment, such as the nitrogen (N) and organic carbon (C) contents (Zubek et al. 2016). To date, the impact of invasive alien plant species on plant communities

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has been mostly examined with respect to changes in aboveground vegetation (Gaertner et al. 2009, Gioria and Osborne 2010). By comparison, the impact on the soil seed bank (hereafter seed bank) has received relatively less attention (Krinke et al. 2005, Gioria et al. 2014), which may be due to practical difficulties associated with seed bank assessment (Thompson et al. 1997, Gioria and Osborne 2009a).

The soil seed bank is an important part of the plant community and plays an important role in the process of vegetation renewal and recovery. The soil seed bank is not only the source of vegetation renewal but also a mechanism to maintain vegetation species diversity (Zhao et al. 2003). In general, seeds are better than adult plants at escaping interference, disease and predation damage (Bakker et al. 1996), enabling plants to survive adverse periods and being one of the important plant reproductive strategies (Grime et al. 2010). The storage and replenishment of seeds are prerequisites for plant reproduction (Bekker et al. 1997), and the soil seed bank undertakes the replenishment and storage of seeds, which plays an important role in vegetation recovery. Therefore, the study of soil seed banks is also highly valued. As a reservoir of propagators, the soil seed bank will germinate rapidly and occupy habitats once conditions are suitable, thus changing the original vegetation landscape, which is called the subpopulation stage. In disturbed environments, seed regeneration is the primary condition of *in situ* regeneration or migration to a new habitat (Bruun and Ejrnaes 2006). Under the stress of adverse conditions, the dynamics of the soil seed bank are the manifestation of plant ecological adaptation. An increasing number of human activities interfere with nature, resulting in soil seed banks playing a more important role in the process of ecosystem reconstruction (Yan et al. 2005, Jin 2009). The study of the relationship between the soil seed bank and aboveground vegetation and ecological factors is helpful to understand the response of the soil seed bank to aboveground vegetation and ecological factors in the process of wetland degradation and to manage better and protect degraded wetlands, which has important theoretical and practical significance for the restoration of degraded wetlands and the protection of biodiversity.

Seed banks have been classified into transient or persistent depending on how long seeds of a species can retain their viability in the soil, with the viability of less than 1 year typically being considered transient (Thompson et al. 1997). This distinction is very important in invasive ecology because it indicates how long invasive species can survive in the receiving community after eradication attempts and without further introduction from nearby sources (Gioria et al. 2012). In addition, it improves our ability to estimate the size of seed banks that invasive species accumulate over time, which can eventually germinate under specific environmental conditions (Gioria and Pyšek 2016). In view of these functions, seed banks affect the resistance and resilience of ecosystems (Pugnaire and Lázaro 2000). Therefore, in addition to the invasiveness and restoration potential of recipient communities, seed banks may greatly promote the naturalisation and invasion potential (invasiveness) of alien species (Gioria et al. 2012, 2014, 2018, Gioria and Pyšek 2016, 2017). Invasive plants are divided into narrow expansion and broad expansion. The broad expansion includes the expansion of native species and the expansion of alien species. *Achnatherum inebrians* (drunken horse grass) belong to grassland species, if it spreads in the grassland, it belongs to local expansion, and to deserts and meadows belong to local invasion.

Achnatherum inebrians is the main toxic weed in natural grasslands and is distributed in Xinjiang, Gansu, Inner Mongolia, Qinghai and other provinces in China. Hitchcock first recorded the toxicity of *Achnatherum inebrians* in 1922 and officially listed it as a poisonous plant (Hitchcock 1922). Due to its advantages of resistance to cold and drought, wide distribution and strong adaptability, it presents a competitive advantage in degraded grassland, which leads to increased density and increasingly serious spreading in degraded grassland, exacerbating the trend of grassland degradation. In recent decades, with the aggravation of grassland degradation, the harm caused by *Achnatherum inebrians* to livestock has gradually attracted attention (Ren 1954). Scholars have conducted a large number of studies on its botanical characteristics (Sahedula 1992, Ji 2009), ecological-biological characteristics (Ren 1954, Gao 2001) and other aspects. In 1984, Zhang Youjie and Zhu Ziqing isolated ergometrine and isoergometrine from *Achnatherum inebrians*, and a number of scholars successively conducted experiments on the feeding of *Achnatherum inebrians* to domestic animals and found a poisoning phenomenon (Zhang and Zhu 1982, Dai 2010, Li et al. 2018, Wang et al. 2018). In 1954, Ren Jizhou took the lead in research on burning and eliminating *Achnatherum inebrians*. Subsequently, many scholars proposed

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various methods for the prevention and control of *Achnatherum inebrians* (Li et al. 2008, 2016, Yang et al. 2015). Although predecessors have performed much work on the botanical characteristics, control and removal of *Achnatherum inebrians*, there is no report on the seed bank of poisonous weeds in the soil. Therefore, in this study, the effects of different habitats on *Achnatherum inebrians* soil seed banks and aboveground vegetation characteristics were analysed with desert, steppe and meadow as objects to reveal the succession and renewal of *Achnatherum inebrians*. This study can provide an important theoretical basis for vegetation recovery and species diversity protection of degraded wetlands in these areas.

MATERIAL AND METHODS

Study site. The studied areas are located in Heijiagou and Xiejiagou of in Urumqi city, Xinjiang, China. Among them, Heijiagou is located in the low hills of the shallow mountain belt in the middle of the northern slope of Tianshan Mountain. The annual average precipitation is 221.3 mm, the annual average evaporation is 1 765.4 mm, the annual average temperature is 4.3 °C, the annual frost-free period is approximately 129 days, and the soil is mountain brown desert soil. Xiejiagou is located in the middle and low mountain zone of the northern slope of Tianshan Mountain, with an annual average precipitation of 388.7–535.9 mm, an annual average evaporation of 1 141.7–1 564.9 mm, an annual average temperature of 2.1–3.3 °C and a frost-free period of 100–113 days. The soil types are mountain chestnut soil and mountain chernozem. The area is an important spring and autumn pasture for local livestock. The specific coordinates of the Heijiagou Desert habitat are 43°39'N, 87°23'E, and 1 353 m a.s.l.; the specific coordinates of the Xiejiagou steppe habitat are 43°31'N, 87°01'E, and 1 660 m a.s.l.; and the specific coordinates of the Xiejiagou meadow habitat are 43°28'N, 87°02'E, and 2 180 m a.s.l. Three grassland types constitute three different environmental sample areas, which are typical areas invaded by *Achnatherum inebrians*, where this species has become the dominant species in the community (Figure 1).

Research methods

Soil seed bank sampling. In late October 2019 (temporary soil seed bank), soil seed bank sampling was conducted in the three habitats. First, 3 sample belts with the same length (60 m) were selected, and the spacing between them was approximately 10 m. Within the sample belt along the diagonal direction, "Z" – shaped sampling was conducted: five 1 m × 1 m sampling areas were established along the sample belt, repeated three times in each soil layer, spaced 20 m apart, using homemade soil seed banks for all samplers (10 cm long × 10 cm width × 5 cm high) in the vertical direction based on a stratified sampling method (0–5, 5–10, 10–15 and 15–20 cm).

Sample processing and testing. There are two methods of species identification commonly used in soil seed banks: physical separation and seed germination (Harper 1977, Grime 1989). This study used the seed germination method to detect the plant species and effective seed number of the *Achnatherum inebrians* soil seed bank. After the soil sample was retrieved, large roots and gravel were picked up and then screened with a fine sieve with an aperture of 0.2 mm. Then, a flowerpot (15 cm × 30 cm × 7 cm) was used to fill the retrieved soil sample at a depth of approximately 3 cm and to mark it. The samples were placed in a greenhouse at an average temperature of 25 °C and were watered daily to keep the soil moist in the germination basin. The species and number of seedlings in the pot were recorded daily, and the seedlings were removed after germination to carry out species identification. The seedlings that could not be identified were transplanted into new pots and grown until they could be identified (Zhang et al. 2018). This experiment lasted for 21 days and no seedlings appeared for 2 consecutive weeks. The experiment ended.

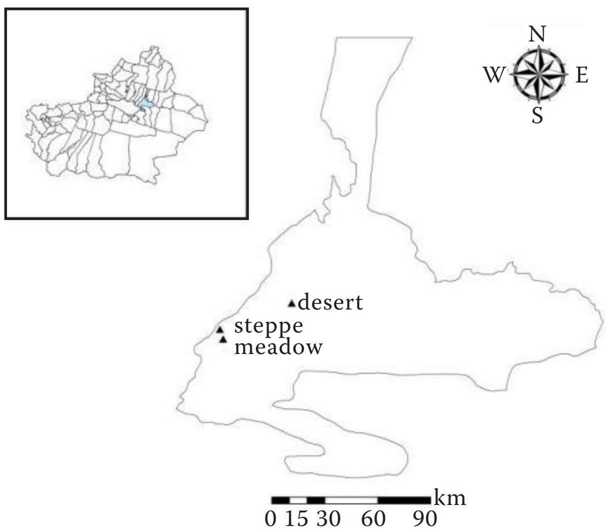

Figure 1. Location of the study sites

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Soil seed bank determination. The density of a soil seed bank is expressed by the number of seeds contained in a unit area, namely, the number of germinated seeds in the sampling area is converted to the number of seeds within 1 m^2 (Zhang et al. 2003). After the seed germination test, plant species were identified according to "The Flora of China" (2004), and the plants were divided into three life forms: shrub, perennial herb and annual herb. The proportion of each type in all plants' total soil seed bank was calculated.

Data analyses. With the help of Excel to input and calculate the data measured in the experiment, the relevant data were analysed by SPSS 17.0 software, and the single factor analysis of variance was used to compare the number of species in the soil seed bank of different habitats and the differences between different soil layers of inebrians. The regression analysis method was used to reveal the relationship between seed banks and aboveground vegetation under different treatments. The drawing was completed in Origin 2019b. The data in the charts are presented in the form of mean ± standard error.

RESULTS

Species composition of the transient soil seed bank in different habitats. It can be seen from Table 1 that in the 0–20 cm soil layer, the species composition and seed density of the soil seed bank of plant communities in different habitats were different, and the seed density of the same species in the soil seed bank of different plant communities was also different. A total of 31 species of plants belonging to 28 genera and 14 families appeared in the transient soil seed banks in the 3 habitats. Among them, 7 species of annual plants or biennial plants, 8 species of perennial plants and 1 species of semishrubs were found in desert habitats. There was 1 species of annual plants or biennial plants, 9 species of perennial plants and 1 species of semishrubs in the steppe habitat. There was 1 species of annual or biennial plants and 16 species of perennial plants in the meadow habitat. Perennial plants, annual plants or biennial plants and semishrubs accounted for 90.31, 9.31 and 0.38%, respectively, of the total soil seed bank, and the number of perennial plants was the highest. The proportion of *Achnatherum inebrians* transient seed banks in desert habitats was 11.61%, compared with 17.31% in the steppe habitat and 26.00% in the meadow habitat.

Vertical distribution characteristics of the soil seed bank. As seen from Table 2, the distribution of the soil seed banks varies with different habitats. Specifically, the *Achnatherum inebrians* seed distribution in meadows was the largest, and the plant growth was also good, while the seed distribution in desert habitats was the smallest, and that of plants was the lowest. At the vertical distribution level of desert habitats, *Achnatherum inebrians* seeds in the 0 to 5 cm soil layer accounted for 50% of the total, the seeds in the 5 to 10 cm soil layer accounted for 60.49%, and the seeds in the 10 to 15 cm soil layer accounted for 71.43% of the total, but no seeds were distributed in the 15 to 20 cm soil layer. In steppe habitats, *Achnatherum inebrians* seeds in the 0 to 5 cm soil layer accounted for 56.60% of the total, seeds in the 5 to 10 cm soil layer accounted for 58.56%, seeds in the 10 to 15 cm soil layer accounted for 78.43%, and seeds in the 15 to 20 cm soil layer were not distributed. In the meadow habitat, *Achnatherum inebrians* seeds in the 0 to 5 cm soil layer accounted for 41.80%, seeds in the 5 to 10 cm soil layer accounted for 45.50%, seeds in the 10 to 15 cm soil layer accounted for 55.24%, and seeds in the 15 to 20 cm soil layer accounted for 100%.

Relationship between soil seed bank and aboveground vegetation. It can be seen from Figure 2, that there is a significant positive correlation between the aboveground vegetation density of the steppe habitat and the density of the transient soil seed bank ($P < 0.05$). At the same time, there is no significant correlation between the aboveground vegetation community of desert and meadow grassland habitat and the density of transient soil seed bank ($P > 0.05$). The results showed that the aboveground vegetation density of grassland habitat increased significantly with the increase of seed density of the transient soil seed bank, while there was no significant relationship between the aboveground vegetation density of other habitats and the density of the soil seed bank.

DISCUSSION

The life form is an ecological classification unit of plants and a plant community with similar morphological and structural features (Niu et al. 2015). The species composition of soil seed banks in different plant communities and different stages of vegetation succession is very different (Zhang et al. 2013, Gioria et al. 2014). Chen et al. (2014) and Zhao et al. (2018) analysed the correlation between different

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Table 1. Species composition and density (seeds/m^2) of the soil seed bank in different habitats

Life form	Family	Genus	Generic name	Desert	Steppe	Meadow
Perennia plants	Compositae	*Achillea* Linn.	*Achillea millefolium*			27.78
	Compositae	*Heteropappus* Less.	*Heteropappus altaicus*	55.56	50.00	
	Compositae	*Taraxacum* F. H. Wigg.	*Taraxacum mongolicum*	5.56	227.78	222.22
	Leguminosae	*Astragalus* Linn.	*Astragalus membranaceus*	5.56		
	Leguminosae	*Medicago* Linn.	*Medicago sativa*			94.44
	Leguminosae	*Oxytropis* DC.	*Oxytropis* sp.		27.78	27.78
	Gramineae	*Achnatherum* Beauv.	*Achnatherum inebrians*	838.8	1 250.00	1877.78
	Gramineae	*Achnatherum* Beauv.	*Achnatherum splendens*	16.67		
	Gramineae	*Bromus* Linn.	Bromus inermis		16.67	11.11
	Gramineae	*Elytrigia* Desv.	*Elytrigia repens*			5.56
	Gramineae	*Poa* Linn.	*Poa angustifolia*			5.56
	Rubiaceae	*Rubia* Linn.	*Rubia* sp.			55.56
	Rubiaceae	*Galium* Linn.	*Galium* sp.		55.56	
	Cyperaceae	*Carex* Linn.	*Carex turkestanica*	55.56	238.89	138.89
	Labiatae	*Phlomis* Linn.	*Phlomis pratensis*			61.112
	Rosaceae	*Fragaria* Linn.	*Fragaria vesca*			11.11
	Rosaceae	*Potentilla* Linn.	*Potentilla bifurca*		27.78	438.89
	Rosaceae	*Potentilla* Linn.	*Potentilla multifida*	16.67	150.00	111.11
	Geraniaceae	*Geranium* Linn.	*Geranium pratense*			44.44
	Plantaginaceae	*Plantago* Linn.	*Plantago asiatica*			327.78
	Zygophyllaceae	*Peganum* Linn.	*Peganum harmala*	22.22		
Total				1 016.67	2 044.44	3 461.11
Annuals plants or biennial plants	Leguminosae	*Trigonella* Linn.	*Trigonella arcuata*	61.11		
	Gramineae	*Eremopyrum* (Ledeb.) Jaub. et Spach	*Eremopyrum triticeum*	5.56		
	Brassicaceae	*Lepidium* Linn.	*Lepidium apetalum*	183.33		
	Compositae	*Lappula* Moench	*Lappula* sp.	61.11	11.11	0.00
	Amaranthaceaeae	*Ceratocarpus* Linn.	*Ceratocarpus arenarius*	33.33		
	Amaranthaceaae	*Petrosimonia* Bunge	*Petrosimonia sibirica*	27.78		
	Polygonaceae	*Polygonum* Linn.	*Polygonum aviculare*	27.78		
	Primulaceae	*Androsace* Linn.	*Androsace* sp.			261.11
Total				400.00	11.11	261.11
Semi-shrub plant	Compositae	*Seriphidium* (Besser ex Less.) Fourr.	*Seriphidium borotalense*		22.22	
	Compositae	*Seriphidium* (Besser ex Less.) Fourr.	*Seriphidium transiliense*	5.56		
Total				5.56	22.22	
Total density				1 422.22[b]	2 077.78[b]	3 722.22[a]

Different lowercase letters indicate significant differences at the 0.05 level. The same is below

life types of species and soil, and the results showed that the utilisation of soil and other resources was different among species with different life forms, promoting species' coexistence. In this study, perennial plants were most common in the transient soil seed banks of the three habitats, followed by annual or biennial plant seeds, which is related to the fact that the aboveground vegetation in the

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Table 2. Vertical distribution characteristics (seeds/m^2) of the soil seed bank in different habitats

Habitat	0–5 cm		5–10 cm		10–15 cm		15–20 cm	
	Achnatherum inebrians	other plant	*Achnatherum inebrians*	other plant	*Achnatherum inebrians*	other plant	*Achnatherum inebrians*	other plant
Desert	511.11^{Ab}	311.11	272.22^{Bb}	177.78	138.89^{Cc}	55.56	0.00^{Db}	0.00
Steppe	666.67^{Aa}	511.11	361.11^{Bb}	255.56	222.22^{Cb}	61.11	0.00^{Db}	0.00
Meadow	674.44^{Aa}	938.89	477.78^{Ba}	572.22	411.44^{Ba}	333.33	294.44^{Ca}	0.00

Different lowercase letters indicate that the *Achnatherum inebrians* seed number differed significantly in the same soil layer in different habitats and the same soil components in different habitats (P < 0.05), and different uppercase letters indicate that the *Achnatherum inebrians* seed number in different soil layers in the same habitat was significantly different (P < 0.05)

study area is mostly perennial and annual plants or biennial plants; the steppe and meadow habitats are dominated by perennial plants, while annual plants or biennial plants dominate the desert habitats in terms of survival, growth and reproduction. The number of seeds in meadow habitats was higher than that in desert and steppe habitats, which was related to the change in the soil seed bank quantity and seed output (germination, feeding, decay) and input (seed rain).

Soil seed banks have an obvious vertical distribution pattern, which affects the germination and retention of seeds in soil seed banks and then affects the succession of vegetation in the future (Li et al. 2009). In this study, in the soil seed bank, the number of *Achnatherum inebrians* seeds in the meadow habitat was the largest, while that in the desert habitat was the lowest. In the three habitats, the proportion of *Achnatherum inebrians* seeds in the soil seed bank in the 0–5 cm soil layer was the highest, mainly because the vegetation produced seeds that fell on the soil surface, and it was difficult for the seeds to reach lower depths. With the deepening of the soil layer, the number of *Achnatherum inebrians* seeds and species in the soil seed banks in the three habitats showed a decreasing trend, and the number of seeds decreased significantly, which is consistent with the research results of Dong et al. (2016), Chen et al. (2017), and Tan et al. (2019) for the vertical distribution of soil seed banks.

Some studies believe that the density of soil seed banks in grassland is positively correlated with the density and coverage of the aboveground vegetation community (Li et al. 2019). The results of this study showed that the density of temporary soil seed banks in grassland habitats showed a significant positive correlation with the density of aboveground plant community, while the density of temporary soil seed banks and permanent soil seed banks in desert and meadow habitats showed an increasing trend with the increase of aboveground vegetation density, but the difference was not significant, which was compared with Harper (1977), Thompson and Grime (1979), Coffin and Lauenroth (1989) and other researchers think that there is no obvious correlation between the grassland aboveground vegetation density and the soil seed bank density. The results are similar. The significant differences in research results are mainly due to differences in grassland type, sampling time, and interference methods.

In conclusion, the species composition of the plant community in the soil seed bank of the three habitats was mainly dominated by perennial species, and the

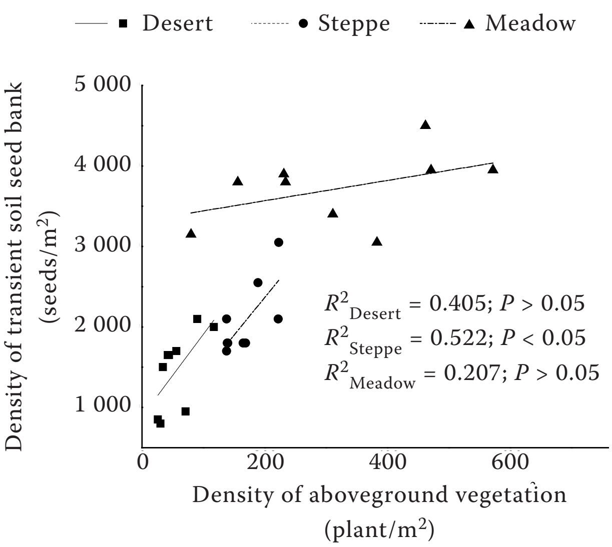

Figure 2. The relationship of density between transient soil seed bank and above-ground plants

proportion of *Achnatherum inebrians* in the soil seed bank was the highest in the meadow habitat.

The results of the α diversity analysis showed that the diversity of the soil seed bank and aboveground vegetation in the meadow habitat was higher than that in the desert and steppe habitats. There were some differences between soil seed banks and aboveground vegetation in terms of richness, evenness and ecological dominance. The similarity between seed banks and aboveground vegetation was generally high. Comparatively speaking, the similarity between the soil seed banks and aboveground vegetation was highest in the desert habitat.

The density of *Achnatherum inebrians* seeds in the transient soil seed banks in the three habitats showed a decreasing trend with the deepening of the soil layer, and the seed density in different soil layers was 0–5 cm > 5–10 cm > 10–15 cm > 15–20 cm, generally concentrated in the 0–5 cm soil layer, which is conducive to the rapid germination of the soil seed bank with limited rainwater. There is a significant positive correlation between soil seed banks and grassland vegetation.

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