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Soil seed bank composition and distribution on eroded slopes in the hill-gully Loess Plateau region (China): influence on natural vegetation colonization

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Earth Surface Processes and Landforms

ABSTRACT: On the Chinese Loess Plateau, serious slope and gully erosion have caused a decrease in soil water capacity and fertility, which has resulted in vegetation degradation and a reduction in agricultural productivity. Great efforts have been made to restore vegetation to control soil erosion, but the efficiency of artificial revegetation is not satisfactory. Natural revegetation is an alternative. However, while soil seed banks are an essential source for natural revegetation, their composition and distribution on eroded slopes remains unknown. In addition, whether or not seed loss during soil erosion limits vegetation colonization is also unknown. In this work, soil seed bank composition and distribution were studied in three situations. Specifically, three main microsites were selected as sampling plots: fish-scale pits, as artificial deposited micro-topography; under tussocks, as trap microsites; and open areas, as eroded areas. Soil samples were collected at depths of 0–2 cm, 2–5 cm and 5–10 cm. The soil seed bank was identified using germination experiments, and a total of 34 species were identified. The dominant species in the soil seed bank were annual/biennial herbs with an average proportion more than 90% and density reaching 19,000 seeds m^{-2}. The pioneer species *Artemisia scoparia* was especially abundant. The dominant later successional species, such as *Lespedeza davurica*, *Artemisia giraldii*, *Artemisia gmelinii*, *Stipa bungeana* and *Bothriochloa ischcemum*, were present in the soil at a density that ranged from 38 to 1355 seeds m^{-2}. Compared with the eroded open areas, the fish-scale pits retained a higher density of seeds, and the tussocks retained a larger number of species. However, there was no serious reduction of the soil seed bank in the erosion areas. The present study indicates that, on these eroded slopes, the soil seed bank is not the key factor limiting the colonization of natural vegetation. Copyright © 2011 John Wiley & Sons, Ltd.

KEYWORDS: soil seed bank; soil erosion; seed distribution; vegetation colonization; Loess Plateau

Introduction

The Loess Plateau of China has suffered from serious soil erosion for a long time (Zhang *et al.*, 2004b; Wei *et al.*, 2006). The present rates of soil erosion on the Loess Plateau are due to both natural and human-induced factors and are approximately four times greater than those in the times before human activity (He *et al.*, 2006). With the increase in the Chinese population after the 1950s, more and more natural vegetation was destroyed, and part of the grassland was turned into farmland on the slope, aggravating soil erosion and ecological degradation (Zhang *et al.*, 2004a; Zheng, 2006; Zhou *et al.*, 2006). It is widely accepted that soil and water conservation are necessary to maintain and develop the national ecology (Zhang *et al.*, 2004b).

Numerous studies have shown that the presence of grass or trees can reduce runoff and conserve soil and water and, subsequently, stabilize the slope (Rey, 2004; Cammeraat *et al.*, 2005; Rey *et al.*, 2005; Blanco-Canqui *et al.*, 2006; Isselin-Nondedeu and Bédécarrats, 2007a). During the past few decades, great efforts have been made to restore vegetation to reduce soil erosion. In the late 1990s, the Chinese Central Government implemented the policy of ‘Replacing Farmland with Forest or Grass’ for soil erosion control on a large scale including the study region. However, the efficiency of vegetation restoration was not entirely satisfactory due to water shortages, and many of the planted trees died or grew poorly (Zhang *et al.*, 2005). Therefore, fish-scale pits were built on the slopes to collect runoff and sediment, thereby increasing the survival of the planted trees. These crescent-shaped pits are built on the slope in an alternating pattern similar to the arrangement of the scales of a fish, giving rise to their name (Figure 1). However, the fish-scale pits did not effectively resolve the problem because of their small capacity for runoff and sediment. Most of the fish-scale pits are filled up by sediment or destroyed by runoff within

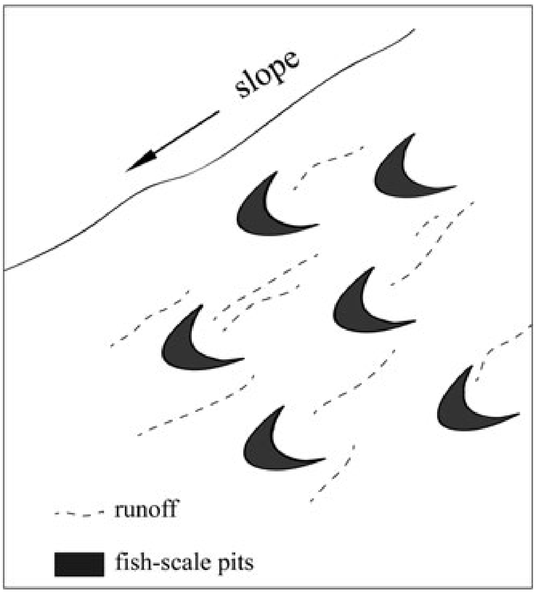

Figure 1. Sketch of fish-scale pits.

several years. Furthermore, the planted species may consume more of the soil water and can threaten long-term ecosystem sustainability in the Loess Plateau region (He *et al.*, 2003; Chen *et al.*, 2008; Wang *et al.*, 2008). Compared with an artificial plant community, a natural vegetation community has a higher potential for adaptability and stability (Montalvo *et al.*, 1997; Wang *et al.*, 2008) and can play a positive role in increasing species richness in a local area (Jiang *et al.*, 2003); thus, natural vegetation rehabilitation has been proposed to control soil erosion in the Loess Plateau region (Zhang, 2005; Jiao *et al.*, 2007). Potentially, soil seed banks can be used to accelerate the development of native vegetation and thus prevent soil erosion (Uhl *et al.*, 1981; Tekle and Bekele, 2000; Tischew and Kirmer, 2007).

It is well known that soil seed banks play an important role in assuring community regeneration after a disturbance (Harper, 1977; Bakker *et al.*, 1996; Tekle and Bekele, 2000). The seeds are dispersed from the surrounding parent plants and remain in the upper part of the soil profile until they germinate (Chambers and James, 1994). Post-dispersal movement of seeds is an important feature in severely disturbed ecosystems (Chambers, 2000); for example, splash and overland flow can carry away the seeds on the surface of the soil and in the soil seed bank (Seghieri *et al.*, 1997; Aerts *et al.*, 2006; Tíscar *et al.*, 2011). Furthermore, post-dispersal movement alters the primary seed-deposition pattern (García-Fayos *et al.*, 1995; Cerdà and García-Fayos, 2002) and thus affects the subsequent structure of plant communities (Nathan and Muller-Landau, 2000; Thompson and Katul, 2009; García-Fayos *et al.*, 2010). In addition, the current vegetation and ecogeomorphology of a site can influence the post-dispersal seed movement during the runoff process. Vegetation bands and patches are effective at trapping sediment (Cerdà, 1997; Abu-Zreig, 2001; Jones and Esler, 2004; Isselin-Nondedeu and Bédécarrats, 2007a) as well as seeds (Cerdà, 1997; Cerdà and García-Fayos, 1997; Isselin-Nondedeu and Bédécarrats, 2007b). Advection of seeds in runoff is likely to transport seeds into vegetation bands (Thompson and Katul, 2009) and depression topography, such as hoof prints, can trap seeds removed by runoff and strongly reduce the travelled distance of post-dispersal seeds (Isselin-Nondedeu *et al.*, 2006; Isselin-Nondedeu and Bédécarrats, 2007b). However, several studies have reported that shrubs do not trap seeds transported by overland flow (Aerts *et al.*, 2006) because microtopographic structures under the shrubs divert runoff water and concentrate flow into rills alongside the shrubs. In addition, slopes with many cracks can retain more seeds than pediments with a sedimentary layer and crust (Cerdà and García-Fayos, 1997).

Seed removal in runoff is influenced not only by environmental factors, such as slope angle, surface roughness (Cerdà and García-Fayos, 1997; Bochet and García-Fayos, 2004) and vegetation cover (Seghieri *et al.*, 1997), but also by seed morphological features such as shape, size (Chambers *et al.*, 1991; Cerdà and García-Fayos, 2002; García-Fayos *et al.*, 2010), mucilage secretion and the presence of appendices such as hairs or wings (García-Fayos and Cerdà, 1997; Chambers, 2000). Although the smallest seeds may be removed easily (Cerdà and García-Fayos, 2002), they are also more likely to be stored in cracks and hollows (Thompson *et al.*, 1993; Chambers and James, 1994); thus, rather small, compact and slightly heterometric seeds easily remain in the soil (Thompson *et al.*, 1993; Guàrdia *et al.*, 2000).

On the Chinese Loess Plateau, rapid overland flow usually occurs on the slopes where soils are crusted, vegetation is sparse and rainfall intensities are very high. On average, nearly 1 cm is lost from the top of the horizon every year due to soil erosion in this hill-gully region (Shi and Shao, 2000); thus, seeds in the topsoil profile are threatened by water erosion. Seed loss during soil erosion may be the limiting factor for the revegetation of eroded slopes (García-Fayos *et al.*, 2000; Jones and Esler, 2004). A number of rainfall-simulation experiments on slope-surface plots with added seeds have shown that seed loss during water erosion is low (García-Fayos *et al.*, 1995; Cerdà and García-Fayos, 1997, 2002; García-Fayos and Cerdà, 1997). Field measurements have shown that seed input from 'seed rain' is larger than output by erosion; hence, seed-loss rates should be tolerable for the maintenance of the soil seed bank (García-Fayos *et al.*, 1995; Cerdà and García-Fayos, 2002). These results indicate that seed removal by erosion is not the key factor that explains the lack of vegetation on badlands (García-Fayos *et al.*, 1995, 2000). There are other factors limiting vegetation colonization on the eroded slope besides the seeds. One important factor is the abiotic filters (or constraints). On the eroded slope, the very short duration of water availability and the spatial heterogeneity of available water in the soil influence the chances of germination and the subsequent survival of seedlings (García-Fayos *et al.*, 2000; Cipriotti *et al.*, 2008). In addition, the life-history strategies of different species also influence the colonisation of natural vegetation (Guerrero-Campo *et al.*, 2008).

There have been many studies on soil erosion on the slopes of the Chinese Loess Plateau, but little information can be found regarding seed redistribution by water erosion in this region. Whether seed removal by erosion is the key factor explaining the low cover of vegetation on eroded slopes is unknown. Therefore, the aim of this study was to evaluate the soil seed bank composition and distribution on eroded slopes in the hill-gully Loess Plateau region and analyse the factors limiting natural vegetation colonization. Our hypotheses were: (1) soil seed bank density and species richness are reduced in open areas on slopes, whereas tussocks and fish-scale pits retain more seeds; (2) species with different life-history strategies have different functions in the restoration process; and (3) the soil seed bank may be the key factor limiting natural vegetation colonization.

Materials and Methods

Study site

The study site, Zhifanggou watershed in Ansai, is located between 36°51′30″ N and 109°19′30″ E (Figure 2). The average

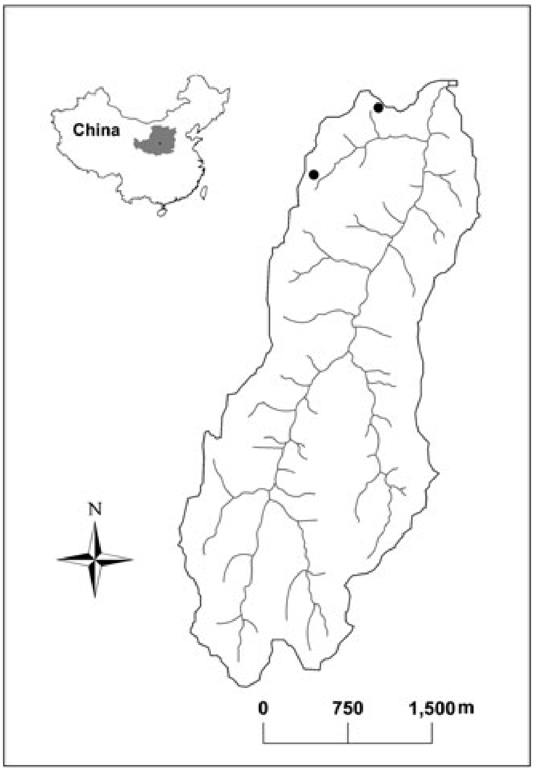

Figure 2. Location of the sites studied in the Zhifanggou watershed in the Loess Plateau region China: the two dots show the sampling slopes.

elevation above sea level is 1200m. The climate is within the transitional zone from a semi-humid warm climate to a semi-arid climate with an average annual precipitation of 504mm (1970–2006). More than 70% of the precipitation falls during the rainy season (June–September), usually in the form of storms. Annual evaporation is more than 1460mm, and the mean temperature is approximately 8.8°C (−11°C to 30°C), with a mean frost-free period of 160days. The landscape includes inter-gully slopes and gully slopes, and the land surface is fragmented by deeply incised and densely distributed gullies (gully density 8.06kmkm^{-2}). Soil erosion on loess slopes shows clear vertical zonation (Figure 3) comprising sheet zones, rill zones and ephemeral gully zones. Each erosion zone has its own characteristics of erosion and sediment yield. Loessial soil is the main soil type in this region and has a homogeneous texture, is poor in organic components and is susceptible to erosion.

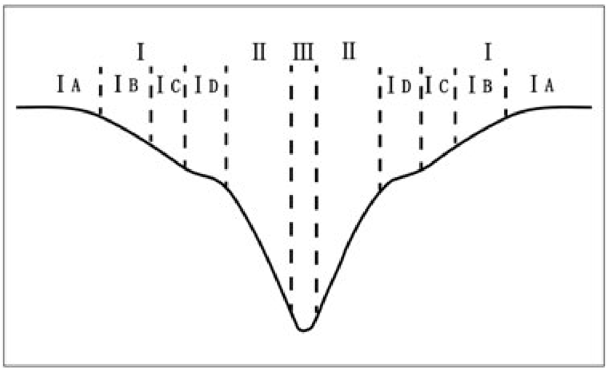

Figure 3. Vertical zonation of soil erosion on loess slopes. (I – Inter-gully water-erosion zone, IA – splash-erosion subzone, IB -- sheet- and rill-erosion subzone, IC – ephemeral-erosion subzone, ID – ephemeral- and gully-erosion subzone; II —gully-slope-water- and gravity-erosion zone; III – gullybottom-water-erosion zone).

Although this area is located in the forest-steppe region, natural forest is almost absent and has been replaced by typical steppe due to the disturbances caused by human activities. In the late 1990s, the slope farmland was gradually abandoned and vegetation began to restore naturally. The pioneer species is *Artemisia scoparia*, and after 5–10years the dominant species of the later successional stages, such as *Artemisia gmelinii, Artemisia giraldii, Lespedeza davurica, Stipa bungeana* and *Bothriochloa ischaemun*, and a few native shrubs, such as *Rosa xanthina, Sophora viciifolia, Syringa julianae* and *Ostryopsis davidiana*, gradually colonized the land according to the successional process (Du *et al.*, 2007; Jiao *et al.*, 2007).

Soil samples

A typical southern-aspect microcatchment with a short slope and a deep gully (Site 1) and an eastern-aspect microcatchment with a long slope and a shallow gully (Site 2) were selected as the sampling sites. Soil samples for the germination experiments were collected along the vertical-erosion zone of the slope. As shown in Figure 4, thirteen 5m × 5m plots were established on the slope ranging from the watershed to the bottom of the gully (Table I). Three microsites, including fish-scale pits (deposited micro-topography, 'A' in the following text), upslope position under vegetation canopy (tussock as a trap to intercept seeds removed by the runoff, 'B' in the following text) and open area (eroded areas, 'C' in the following text), were selected to collect soil core samples (diameter 4.8cm) in each plot (Figure 5). At each microsite, 24 soil cores were collected in the 0–2cm, 2–5cm and 5–10cm soil layers. In some plots, as another type of deposited micro-topography, soil samples were collected in the bottom of the ephemeral gully ('G' in the following text) in the 0–10-cm soil layer. The soil cores were collected from 1–4 April 2007, before seedling emergence. The 24 soil cores were mixed for germination tests.

Germination experiments

The soil seed bank was identified using the germination method. The air-dried soil samples were distributed over a 2-cm-deep coarse sand layer (pretreated at 115°C for 48 h to kill any seeds present in the sand) in 20cm × 28cm × 4cm plastic trays, and the soil-sample layer was kept to 1cm in this setup. Simultaneously, three trays with a coarse sand layer were put in different positions in the lab as a control to monitor any seeds dispersed through the air. During the experiments, the germination trays were illuminated daily from 08:00 to 17:00 and watered regularly; the temperature in the lab varied from 15 to 30°C, with a mean value of 23°C. The seedlings were identified and removed or replanted for later identification. When there was no seedling emergence within 2weeks after the peak of seedling emergence; the soil was dried and thoroughly stirred for the second germination period. After this period, the soil was dried and mixed again, and a gibberellin solution (1gL^{-1}) was applied to break the dormancy of the seeds. The germination experiment was concluded when there was no seedling emergence for 4weeks; the germination experiment continued for about 8months (5 May 2007 to 18 Jan 2008).

Under the experimental conditions, this germination method determines only the 'readily germinable' component of the soil seed bank; thus, it may not have detected all of the species present in the seed banks (Ter Heerdt *et al.*, 1996; Thompson, 2000). No attempt was made to assess the number of non-germinated seeds remaining in the samples. In

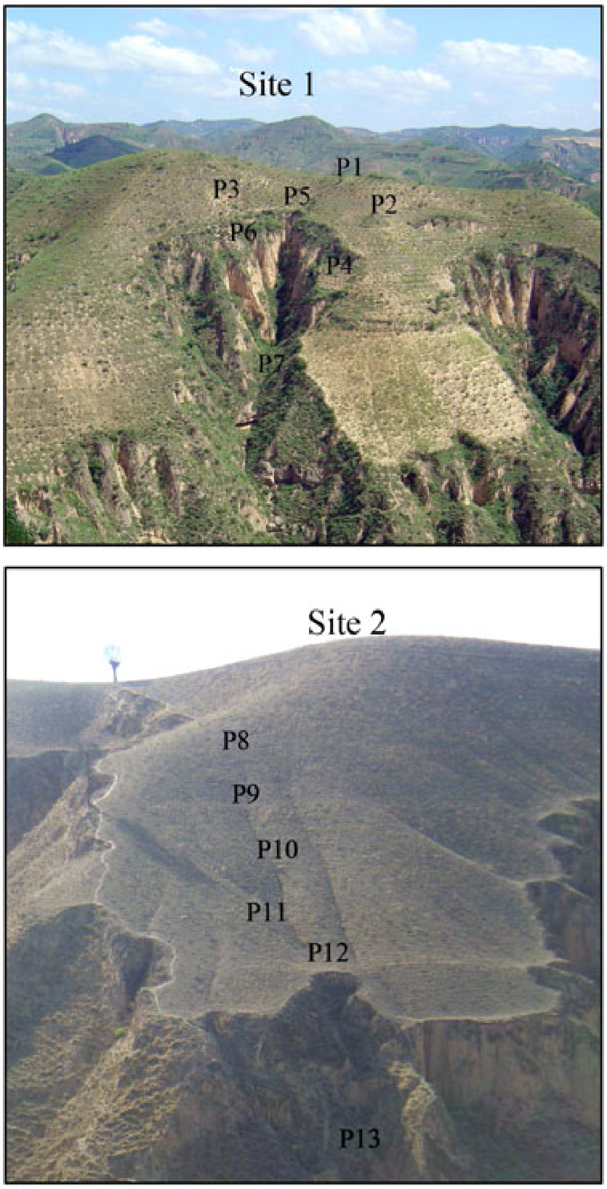

Figure 4. The positions of the sampling plots in the small catchment. Plots 1 to 7 were located on a catchment with a short slope and a deep gully (Site 1) and Plots 8 to 13 were located on a catchment with a long slope and an ephemeral gully (Site 2). This figure is available in colour online at wileyonlinelibrary.com/journal/espl

Figure 5. View of the fish-scale pits, tussocks and open areas. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

the wild, these 'readily germinable' seeds are most likely to determine the recruitment of vegetation after a disturbance (Davies and Waite, 1998).

Standing vegetation investigation and seed collection

The species composition, density, abundance and coverage of standing vegetation in the 13 plots were investigated in August 2007. Three quadrats (1 m × 1 m) were surveyed in

Table I. Characteristics of the sampling plots (* plots with soil samples collected in the gully)

Plot No.	Topography	Slope aspect (°)	Slope angle (°)	Erosion type	Dominant species	Vegetation cover (%)
Site 1						
1	Hill slope	SW30	13	Sheet	*H. altaicus, S. bungeana*	24
2	Hill slope	SW60	25	Sheet	*Leymus scalinus*	16
3	Hill slope	SW20	30	Sheet and rill	*A. scoparia*	14
4	Gully slope	SW58	30–35	Sheet and rill	*A. gmelinii*	12
5	Gully edge	SW45	25	Sheet and rill	*B. ischcemum. A. giraldii*	33
6	Gully slope	SE45	35–40	Sheet and rill	*A. giraldii, A. gmelinii*	28
7	Gully slope	SW35	35–40	Sheet and rill	*A. gmelinii, B. ischcemum*	31
Site 2						
8	Hill slope	NE10	23	Sheet	*A. scoparia*	15
9*	Hill slope	NE17	25	Ephemeral gully	*A. scoparia*	8
10*	Hill slope	NE25	25	Ephemeral gully	*A. scoparia*	11
11*	Hill slope	NE70	20–25	Ephemeral gully	*A. scoparia*	11
12*	Gully edge	NE18	15	Ephemeral gully	*A. scoparia, S. bungeana*	18
13*	Gully bottom	NE15	5	Rill	*A. giraldii, A. gmelinii*	41

every sampling plot. The mature seeds were collected in the experimental catchment and on adjacent slopes. After being air dried, the collected seeds were weighed, and their shapes observed.

Statistical analysis

Data on a range of attributes of each species were tabulated within the following categories: functional groups, reproductive form, soil seed bank density, seed characteristics and standing vegetation traits. The soil seed bank density was translated into seeds m^{-2} for the analyses. The differences in soil seed bank density and species richness among the various microsites and soil layers were analysed by nested ANOVA (seed density was transformed to log (x) to satisfy the homogeneity of variance assumption).

To analyse the difference of vegetation structure in the plots the importance value index (*Iv*) of standing vegetation was calculated as follows:

$$Iv = Dr + Pr + Fr \tag{1}$$

where *Dr* is the relative abundance, *Pr* is the relative dominance and *Fr* is the relative frequency.

The Sorenson index (*C*) was used to test the similarity of species in the soil seed bank and standing vegetation:

$$C = 2w/(a + b) \tag{2}$$

where w is the number of species found in both the soil seed bank and the standing vegetation, a is the number of species in the soil seed bank and b is the number of species in the standing vegetation.

Results

The species composition of the soil seed bank

Thirty-four species were identified in the germination experiments (Table II). They were divided into five groups: annual/biennial herbs, which included 13 species with soil seed bank densities ranging from 38 to 19 076 seeds m^{-2}; perennial forbs, which included 12 species with densities ranging from 38 to 765 seeds m^{-2}; graminoids, which included three species with densities ranging from 38 to 602 seeds m^{-2}; subshrubs, which included three species with densities ranging from 38 to 1355 seeds m^{-2}; and shrubs, which included three species with densities ranging from 38 to 602 seeds m^{-2}. The seeds of annual/biennial herbs occupied the largest proportion (>90%) of the soil seed bank, with the exception of six samples that were collected in the plots with vegetation at a later stage of restoration. Seeds belonging to other species comprised only small proportions of the seed banks: perennial forbs 0–17.9%, graminoids 0–28.6%, subshrubs 0–9.5% and shrubs with 0–29.4%.

Soil seed bank density and distribution in different microsites

The soil seed bank density varied among the different microsites and soil layers (Figure 6). In the 0–10 cm soil layer, the soil seed bank density ranged from 1580 to 21 585 seeds m^{-2} in the fish-scale pits (Microsite A), from 2170 to 10 736 seeds m^{-2} under the tussock (Microsite B), from 1129 to 11,301 seeds m^{-2} in the open area (Microsite C) and from 9984 to 17 157 seeds m^{-2} in the bottom of the ephemeral gully. The mean soil seed bank density in the four microsites was 11,322±1917 seeds m^{-2}, 5977±1301 seeds m^{-2}, 5554±769 seeds m^{-2} and 13 766±1167 seeds m^{-2}, respectively. The seed bank density in the depression microsites (fish-scale pits and the bottom of ephemeral gully) was approximately twice that of the open areas and 1.9-fold larger than the tussock microsite in the 0–10 cm soil layer.

Nearly 60% of the seeds were distributed in the 0–2 cm soil layer (57%, 58% and 64% in Microsites A, B and C, respectively), about 25% of the seeds were distributed in the 2–5 cm soil layer (28%, 26% and 23% in Microsites A, B and C, respectively), and only about 15% of the seeds were distributed in the 5–10 cm soil layer.

The mean soil seed bank density of the same soil layer also varied among the three microsites. There were significant differences among the three microsites (P=0.001). The soil seed-bank density in Microsite C was significantly smaller than that of Microsite A (P<0.001), but there was no significant difference between microsite A and B (P=0.134) and Microsite B and C (P=0.63). There were no significant differences (P=0.093) among the same soil layers in the same microsite.

The species richness of the soil seed bank in different microsites

The species richness changed with the soil layers and the sampled microsites (Table III). The species richness was significantly higher in the 0–2 cm soil layer than in the 2–5 cm (P=0.006) and 5–10 cm (P<0.001) soil layers, and the species richness in the 2–5 cm soil layer was significantly higher than in the 5–10 cm soil layer (P=0.017). Concurrently, species richness was significantly different among the three microsites (P=0.025). The highest degree of richness was identified in the tussock microsite, which was significantly higher than in the open areas (P=0.007), but there was no significant difference in species number between open areas and fish-scale pits (P=0.226).

The relationship between the soil seed bank and standing vegetation

In total, 51 species were observed in the standing vegetation in all plots, divided into six groups: annual/biennial herbs, perennial forbs, graminoids, subshrubs, shrubs and trees with 14, 23, 7, 2, 3 and 2 species belonging to each of the groups, respectively (Table II). The Sorenson index between the soil seed bank and the standing vegetation was low (Table IV). There were 26 species observed in both the soil seed bank and the standing vegetation, 25 species only in the standing vegetation and 9 species only in the soil seed bank.

The annual/biennial herbs comprised the largest proportion in the soil seed banks in all the sampling plots, whereas in the standing vegetation they were reduced during the restoration process. The perennial forbs, graminoids and subshrubs were relatively deficient in soil seed banks, but they were dominant in the standing vegetation in the later restoration stages. Some tree species were present in the vegetation, although no tree seeds were found in the soil seed bank (Figure 7).

Table II. The traits of seeds, the soil seed bank and the standing vegetation of all the observed species in the study plots (Rs - seed propagation; Rv - vegetative propagation)

Species	Reproductive form	Seed-bank density (seeds m^{-2})	Seed size (mg)	Seed shape	Vegetation importance value index (%)	Relative frequency in vegetation / seed bank (%)
annual/biennial herbs						
Androsace engleri	Rs	75–1,505	-	spherical	-	0/35
Artemisia annua	Rs	50–2,559	-	ellipsoid	-	0/61
Artemisia scoparia	Rs	151–19,076	0.020	ellipsoid	2.1–141.1	64/100
Bothriospermum secundum	Rs	50–151	-	ellipsoid	-	0/7
Dracocephalum moldavica	Rs	38–201	1.200	ellipsoid	7.2–8.7	8/20
Eragrostis pilosa	Rs	50–953	0.088	spherical	-	0/46
Euphorbia humifusa	Rs	50–1,957	-	spherical	2.0–29.0	49/41
Geranium wilfordii	Rs	-	9.031	prolate ellipsoid	2.1–4.5	8/0
Incarvillea sinensis	Rs	-	0.576	flat	4.3–7.9	10/0
Ixeris denticulata	Rs	-	0.568	ellipsoid	6.6–9.3	8/0
Ixeris sonchifolia	Rs	38–301	0.054	ellipsoid	0–2.0	3/20
Kochia scoparia	Rs	50–75	2.008	spherical	0–4.3	3/4
Linum stelleroides	Rs	-	0.849	ellipsoid	2.0–13.4	5/0
Panicum miliaceum	Rs	0–50	-	spherical	0–7.9	3/4
Salsola collina Pall	Rs	0–50	1.334	spherical	3.6–12.9	8/2
Serratula centauroides	Rs	-	-	prolate ellipsoid	0–2.0	3/0
Setaria viridis	Rs	38–903	0.659	spherical	4.1–12.9	23/70
Stenosolenium saxatile	Rs	38–301	2.000	spherical	0–7.9	3/7
perennial forbs						
Artemisia capillaris Thunb	Rs/v	38–226	-	spherical	-	0/7
Artemisia giraldii	Rs/v	38–263	0.061	spherical	15.9–62.8	33/13
Artemisia mongolica	Rs/v	38–151	0.193	ellipsoid	0–33.7	3/9
Astragalus scaberrimus	Rs	-	1.664	ellipsoid	2.0–20.1	13/0
Circium segetum Bunge	Rs/v	-	2.512	ellipsoid	1.8–21.4	33/0
Convolvulus arvensis	Rs/v	-	-	ellipsoid	0–2.1	3/0
Galium aparine var. echinospermum	Rs/v	-	9.674	spherical	0–3.6	3/0
Gentiana macrophylla	Rs	38–301	-	prolate ellipsoid	-	0/13
Glycyrrhiza uralensis	Rs/v	-	7.474	ellipsoid	1.8–23.0	5/0
Gueldenstaedtia stenophylla	Rs	0–75	-	ellipsoid	3.8–19.7	54/2
Heteropappus altaicus	Rs/v	50–151	0.388	ellipsoid	4.1–127.1	72/17
Ixeris chinensis	Rs/v	50–301	-	prolate ellipsoid	7.2–32.2	56/15
Iris tenuifolia	Rs/v	-	-	prolate ellipsoid	0–3.6	3/0
Leontopdium leontopodioides	Rs/v	-	-	prolate ellipsoid	0–2.1	3/0
Medicago sativa	Rs	0–75	2.156	ellipsoid	-	0/2
Oxytropis discolor	Rs	-	1.340	ellipsoid	0–8.0	3/0
Patrinia heterophylla	Rs/v	0–38	0.810	flat	5.4–56.0	5/2
Polygala tenuifolia	Rs	-	2.722	spherical	2.0–21.1	23/0
Potentilla bifurca	Rs/v	0–301	-	spherical	3.8–8.2	5/2
Potentilla tanacetifolia	Rs	50–765	0.233	spherical	2.0–14.3	26/15
Scorzonera austriaca	Rs	-	-	prolate ellipsoid	2.0–3.1	5/0
Scorzonera divaricata	Rs	-	-	prolate ellipsoid	1.8–5.7	5/0
Speranskia cantonensis	Rs	-	-	spherical	0–8.2	5/0
Taraxacum mongolicum	Rs	-	0.790	ellipsoid	2.4–9.0	13/0
Viola dissecta	Rs/v	38–301	-	ellipsoid	0–9.4	5/9
Viola philippica	Rs	-	-	ellipsoid	0–5.3	3/0
Graminoids						
Bothriochloa ischcemum	Rs/v	38–602	0.432	prolate ellipsoid	3.8–33.9	26/20
Cleistogenes caespitosa	Rs/v	-		prolate ellipsoid	0–2.5	3/0
Cleistogenes chinensis	Rs/v	38–301	-	prolate ellipsoid	4.0–70.6	41/17
Cleistogenes squarrosa	Rs/v	-	-	prolate ellipsoid	1.8–28.8	10/0
Leymus scalinus	Rs/v	-	-	prolate ellipsoid	12.9–101.6	31/0
Poa sphondylodes	Rs/v	-		prolate ellipsoid	2.0–7.7	13/0
Stipa bungeana	Rs/v	75–151	1.682	prolate ellipsoid	6.0–44.6	51/9
Subshrubs						
Artemisia gmelinii	Rs/v	75–602	0.085	ellipsoid	2.0–89.6	38/33
Lespedeza davurica	Rs	38–1,355	2.129	ellipsoid	12.1–59.2	79/41
Lespedeza juncea	Rs	0–151	1.624	ellipsoid	-	0/2
Shrubs						
Buddleya alternifolia	Rs	38–602	0.05	flat	-	0/20
Clematis fruticosa	Rs	0–38	3.284	flat	0–6.6	3/2
Periploca sepium	Rs	0–151	5.506	prolate ellipsoid	4.0–10.6	8/0
Sophora viciifolia	Rs	-	23.769	spherical	11.1–47.2	8/0
Trees						
Ulmus pumila	Rs	-	-	flat	0–3.8	3/0
Ailanthusaltissima	Rs/v	-	10.702	ellipsoid	0–41.0	5/0

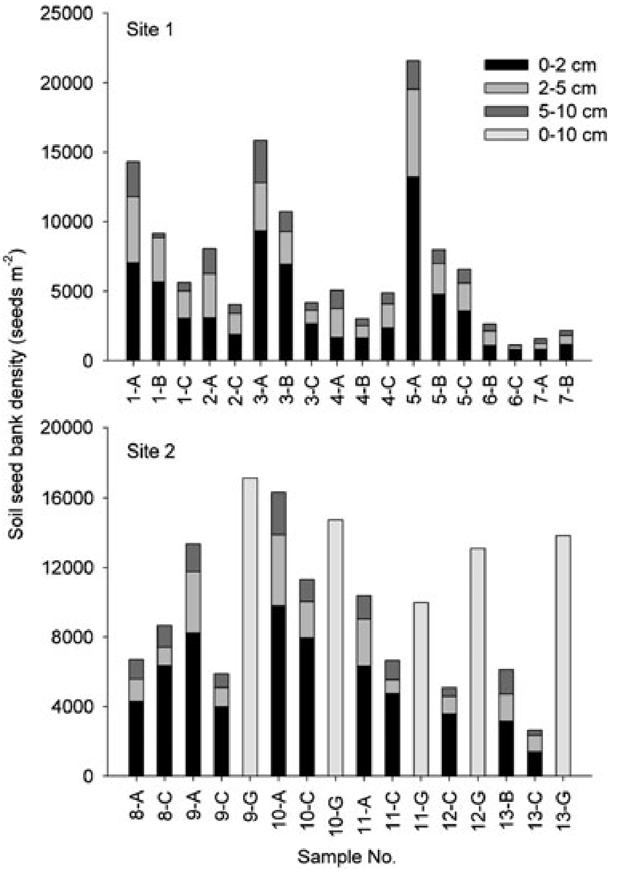

Figure 6. Soil seed bank densities in different microsites. In the sample labels, the numbers are the plot numbers and the letters indicate the microsite (A, the deposited microtopography; B, under tussock; C, open area; and G, the bottom of the ephemeral gully). 0–2 cm, 2–5 cm, 5–10 cm and 0–10 cm are the sampled soil layers.

Discussion

Soil seed bank composition and distribution in different microsites on eroded slopes

In the present study, the mean soil seed bank density in the 0–10 cm soil layer was 11 322±1917 seeds m^{-2} in fish-scale pits, 5977±1301 seeds m^{-2} under tussocks, 5554±769 seeds m^{-2} in open areas and 13 766±1167 seeds m^{-2} in the bottom of the ephemeral gully. These numbers are of the same order of magnitude as those reported in previous studies in the Loess Plateau region (Zhao *et al.*, 2008; Bai *et al.*, 2010; Wang *et al.*, 2010).

The numbers of germinable seeds in depression microsites were approximately twice that of the open areas and 1.9-fold larger than the tussock microsite in the 0–10 cm soil layer. Furthermore, the species richness under the tussock was higher than in the open areas. These results support our first hypothesis, i.e. that soil seed bank density and species richness are reduced in open areas on slopes, whereas tussock and fish-scale pits retain more seeds. Seghieri *et al.* (1997) found an average of 9000 seeds m^{-2} at the core of a thicket and 50 seeds m^{-2} at the centre of a bare zone. Studies on alpine ski trails have found that hoof prints can trap seeds relocated by runoff effectively (Isselin-Nondedeu *et al.*, 2006; Isselin-Nondedeu and Bédécarrats, 2007b), and Tíscar *et al.* (2011) found that soil seed density was highly variable between slopes (ranging from 78 to 2023 seeds m^{-2}), with the lowest values found in the most eroded slopes. In the present study, the depression microsites present a larger number of seeds, but there was no serious reduction of the seed bank in the eroded areas as was found in previous studies. Additionally, some field studies show that seed input from seed rain is larger than output by erosion (García-Fayos *et al.*, 1995; Cerdà and García-Fayos, 2002), and therefore, seed-loss rates should be tolerable for the maintenance of the soil seed bank.

More seeds are retained in the depression microsite and under the tussock, but the process of seed trapping is unclear. Therefore, more studies will be necessary to elucidate what proportion of seeds in the depression microsites are deposited by seed relocation due to runoff and sediment transportation versus the proportion deposited from the initial seed dispersal (seed rain).

The role of annual/biennial species in the restoration of eroded slopes

The soil seed bank was dominated by the annual/biennial species; in particular, the pioneer species *A. scoparia* comprised 87% and 76% of the soil seed bank in the initial and later

Table III. The mean soil seed bank density and species composition in the different microsites and soil layers (A, the deposited microtopography; B, under tussock; C, open area; and G, bottom of the ephemeral gully)

Microsite	Soil layer (cm)	Mean Soil seed bank density (seeds m^{-2})	Species ($^{\triangledown}$frequency > 30%, * proportion in the seed bank > 1%)
A	0–2	6,407±1,249	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ag, Ac, Am, Ld*$^{\triangledown *}$, *Eh*$^{\triangledown}$, *Dm, Pt, Ss, Ae*$^{\triangledown *}$, *Gm, Sv, Ep*$^{\triangledown}$, *Bi, Cc,*
	2–5	3,155±536	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ic, Ha, Ld*$^{\triangledown}$, *Eh**, *Dm, Pt, Ae*$^{\triangledown *}$, *Vd, Sv*$^{\triangledown *}$, *Ep*$^{\triangledown *}$, *Cc, Ks, Bs*
	5–10	1,725±250	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ic, Is, Ha, Ae**, *Ba, Sv*$^{\triangledown *}$, *Ep, Cc**, *Pm*
B	0–2	3,583±884	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ag*$^{\triangledown *}$, *Agi*$^{\triangledown}$, *Ic, Ha, Ac, Ld, Ms, Eh*$^{\triangledown}$, *Ph, Dm*$^{\triangledown *}$, *Cf, Ba*$^{\triangledown}$, *Sv*$^{\triangledown *}$, *Ep*$^{\triangledown *}$, *Bi*$^{\triangledown *}$, *Cc*$^{\triangledown *}$, *Sb, Vd, Pt**, *Gm*
	2–5	1,699±350	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ag, Agi*$^{\triangledown *}$, *Ic, Is*$^{\triangledown *}$, *Am, Eh*$^{\triangledown *}$, *Scp, Dm*$^{\triangledown}$, *Bs, Ba*$^{\triangledown}$,*Sv*$^{\triangledown *}$, *Ep*$^{\triangledown *}$, *Cc, Pt, Vd, Gm, Sc*
	5–10	781±187	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ag, Agi*$^{\triangledown *}$, *Ae, Ba*$^{\triangledown *}$, *Sv*$^{\triangledown *}$, *Ep*$^{\triangledown *}$, *Bi*$^{\triangledown *}$, *Pt**, *Gm*
C	0–2	3,531±591	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ag*$^{\triangledown}$, *Is, Ha, Ac, Am, Ld*$^{\triangledown *}$, *Eh*$^{\triangledown *}$, *Dm, Pt, Ae*$^{\triangledown *}$, *Vd, Ba, Sv*$^{\triangledown}$, *Ep*$^{\triangledown *}$, *Cc, Gs, Agi*
	2–5	1,283±164	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ag**, *Ha, Ld**, *Eh**, *Dm, Ae, Gm, Sv*$^{\triangledown *}$, *Ep*$^{\triangledown *}$, *Bi, Sb*
	5–10	736±108	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Is, Ld, Eh, Pt, Ae**, *Ba**, *Sv*$^{\triangledown *}$, *Ep*$^{\triangledown *}$, *Pm*
G	0–10	13,245±1,197	*As*$^{\triangledown *}$, *Aa*$^{\triangledown *}$, *Ag*$^{\triangledown *}$, *Ha, Bs, Is, Sb*$^{\triangledown *}$,*Ld*$^{\triangledown *}$,*Eh*$^{\triangledown *}$, *Pb, Av*$^{\triangledown *}$, *Ss, Ep, Pt, Vd, Gm, Ic, Ae*$^{\triangledown *}$, *Dm, Ba*

As, Artemisia scoparia; Aa, Artemisia annua; Ag, Artemisia gmelinii; Agi, Artemisia giraldii; Ic, Ixeris Chinensis; Is, Ixeris sonchifolia; Ha, Heteropappus altaicus; Ac, Artemisia capillaris Thunb; Am, Artemisia mongolica; Ld, Lespedeza davurica; Ms, Medicago sativa; Eh, Euphorbia humifusa; Scp, Salsola collina Pall; Ph, Patrinia heterophylla; Dm, Dracocephalum moldavica; Bs, Bothriospermum secundum; Ae, Androsace engleri; Cf, Clematis fruticosa; Ba, Buddleya alternifolia; Sv, Setaria viridis; Ep, Eragrostis pilosa; Bi, Bothriochloa ischcemum; Cc, Cleistogenes chinensis; Sb, Stipa bungeana; Pt, Potentilla tanacetifolia; Vd, Viola dissecta; Gm, Gentiana macrophylla; Sc, Speranskia cantonensis; Ss, Stenosolenium saxatile; Ks, Kochia scoparia; Pm, Panicum miliaceum; Gs, Gueldenstaedtia stenophylla.

Table IV. Species similarity index between soil seed bank and standing vegetation (A, the deposited microtopography; B, under tussock; C, open area; and G, bottom of ephemeral gully).

	Plot No.												
Microsite	1	2	3	4	5	6	7	8	9	10	11	12	13
A	0.17	0.38	0.29	0.3	0.31	-	0.26	0.27	0.38	0.32	0.2	-	-
B	0.08	-	0.32	0.1	0.5	0.38	0.32	-	-	-	-	-	0.46
C	0.08	0.29	0.31	0.22	0.43	0.21	-	0.17	0.31	0.4	0.33	0.4	-
G	-	-	-	-	-	-	-	-	0.54	0.32	0.17	0.1	0.3

restoration stages, respectively. The annual/biennial species always produce seeds with a small and spherical shape (Table II), which are easily buried in the soil and form a persistent soil seed bank (Thompson *et al.*, 1993). Although studies have shown that seeds that weigh less than 10 mg are easily removed by runoff (Cerdà and García-Fayos, 2002), they are also likely to be stored deeply in cracks and hollows (Chambers *et al.*, 1991; Thompson *et al.*, 1993; Chambers and James, 1994). In addition, some of the species can produce seeds with a mucilage secretion that can fix seeds in the soil, such as *A. scoparia* and *D. moldavica*; thus, many seeds of the annual/biennial species persist in the soil profile.

A large soil seed bank of annual/biennial species is important for the restoration of eroded slopes after a disturbance. The erosion process reduces the amount of fertile topsoil and the water capacity and subsequently stresses the regeneration of vegetation (Pimentel and Kounang, 1998; Guerrero-Campo and Montserrat-Martí, 2000; Bochet *et al.*, 2009). Because of the harsh conditions after a disturbance on eroded slopes, microsites are important for seed storage and germination (Jones and del Moral, 2005). Moreover, seed limitation tends to occur more commonly in early successional habitats and species (Turnbull *et al.*, 2000); thus, the annual/biennial species with a large seed production and soil seed banks have a greater opportunity to reach suitable microsites (Tsuyuzaki and del Moral, 1995; Guo *et al.*, 2000) and produce more seedlings, after which seedling pressure increases the establishment rates (Pacala and Rees, 1998; Paiaro *et al.*, 2007). In the study region, the pioneer species *A. scoparia* could colonize bare land due to its large seed production, persistent soil seed bank and large seedling bank. Moreover, the *A. scoparia* population could make modified microsites for the later successional species. This species will be replaced by later successional dominant species, such as *L. scalinus, H. altaicus, L. davurica, A. gmelinii, A. giraldii, S. bungeana* and *B. ischcemum*, approximately 10 or more years after the restoration (Du *et al.*, 2007; Jiao *et al.*, 2007).

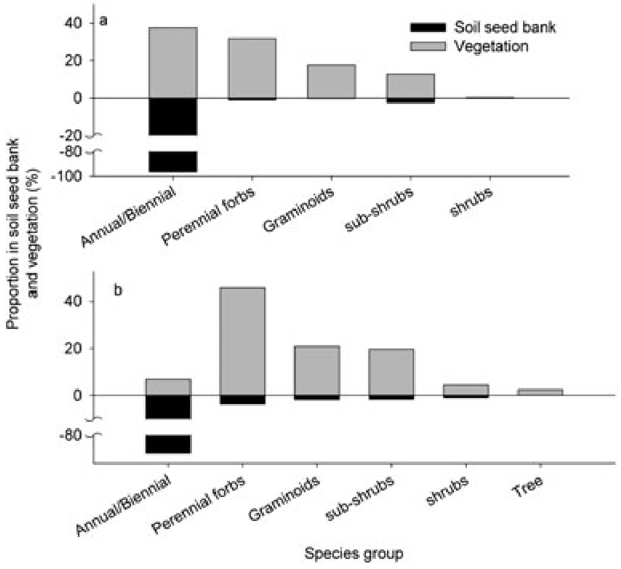

Figure 7. Relative densities of the soil seed banks and relative importance values of standing vegetation in different species groups ('a' indicates the plots in the initial restoration stages, 'b' the plots in the later restoration stages).

Function of perennial species in community succession

Although most of the seed densities of the dominant perennial species, such as *L. davurica, A. gmelinii, A. giraldii, S. bungeana, B. ischcemum* and *C. chinensis*, that germinated in the seed banks were small, they could potentially develop a vegetative cover once established and contribute to reducing soil erosion (Du *et al.*, 2007; Jiao *et al.*, 2007). Additionally, these species should accelerate the rehabilitation of an ecosystem by facilitating the establishment of additional native species (Aronson *et al.*, 1993). The established vegetation plays important roles in trapping seeds (Seghieri *et al.*, 1997; Isselin-Nondedeu *et al.*, 2006; Thompson and Katul, 2009) and providing safe sites for seedlings to emerge and become established (Maestre *et al.*, 2003; Padilla and Pugnaire, 2006; Cipriotti *et al.*, 2008). Established vegetation can improve the chemical and physical properties of the soil in the surrounding microenvironment, including increasing soil water and fertility capacity (Bochet *et al.*, 1999, 2000). Shade provided by the canopies of large plants may protect seedlings and smaller plants from temperature extremes, reduce water loss and photoinhibition during stomatal closure (Callaway, 1995; Maestre *et al.*, 2001). In this study region, previous studies have suggested that vegetation restoration can improve the physicochemical and microbiological properties of the soil during natural succession (Wang and Liu, 2009; Zhu *et al.*, 2010).

Factors limiting plant colonization

In the study region, many vegetation restoration efforts aim to reintroduce native vegetation and re-create functional communities on the abandoned slope farmland. Annual/biennial species dominate the soil seed bank with a large number of seeds, and this could overcome the problem of seed limitation in the early successional stage. However, the persistence of annual/biennial species depends solely on seeds (Caballero *et al.*, 2008). Seed germination and emergence and seedling establishment are susceptible to environmental conditions (Harper, 1977; Fenner, 2000). In addition, the erosion environment is harsh toward seedling establishment. Eroded slopes with sparse vegetation are characterized by intense radiation at the soil surface, which results in extreme fluctuations in the soil temperature and rapid drying of the surface soils. Simultaneously, rapid overland flow usually occurs on the slopes, and the precipitation cannot infiltrate on site. On the study slope, the soil water content (average in the top 20cm of soil) ranged from 2.2% to 15.0% from April to October in 2007 (unpublished data), and the surface soil is always desiccated. The main factor limiting plant colonization in the badland is the very short duration of available water in the soil (García-Fayos *et al.*, 2000; Cipriotti *et al.*, 2008). In addition, the spatial heterogeneity of soil water, soil nutrients and soil texture also influence the vegetation colonization and distribution in this region (Jiao *et al.*, 2007).

Compared with annual species, perennials can survive for many years once established, and many perennials can regenerate by vegetative propagation, such as rhizome (e.g. *H. altaicus, A. giraldii, A. gmelinii*) and tiller (e.g. *B. ischcemum, C. chinensis, S. bungeana*); thus, they can continuously expand once established (Zhan *et al.*, 2007). According to a study by Guerrero-Campo *et al.* (2008), soil erosion favours the frequency of species with the ability to reproduce vegetatively over those that can only reproduce by seedling, such as annual/biennial species. But the seed dispersal of later-successional-stage species consistently limits target species colonization (Bakker *et al.*, 1996). In the study region, however, the particular mosaic landscape formed by patches of remnant vegetation, abandoned farmland and reforested land can improve the connectivity between these seed sources and the soil seed bank at the restoration sites (Wang *et al.*, 2010). This improved connectivity can help the dispersal of seeds belonging to the species of later successional stages.

Conclusions

In the present study, 34 species were identified, and the dominant species in the soil seed bank were annual/biennial herbs with a density reaching 19 000 seeds m^{-2}. The pioneer species *A. scoparia* was especially abundant. The later successional dominant species, such as *L. davurica*, *A. giraldii*, *A. gmelinii*, *S. bungeana* and *B. ischcemum*, presented in the soil with density that ranged from 38 to 1355 seeds m^{-2}. The results suggest that, even on an eroded slope, a large soil seed bank can be formed. Moreover, microsites such as fish-scale pits and tussocks can retain seeds effectively, and the seed-loss on eroded areas is tolerable for maintenance of the soil seed bank.

The dominant species in the soil seed banks are annual/biennial species. The high density of the seed bank indicates an opportunity to gain suitable microsites for seedling establishment in the harsh conditions. Additionally, perennial species do not propagate only from seeds; they can survive for many years by continuous vegetative propagation after being established. Thus, the results indicate that the soil seed bank is not the key factor limiting natural vegetation colonization on eroded slopes in this study region. Under the eroded condition, the short duration of available water in the topsoil is the major factor limiting vegetation colonization, especially in the seedling stage.

In the study region, the dry, poor topsoil restricts seed germination, seedling survival and establishment. Therefore, the speed of natural vegetation colonization is low. More research should be done to elucidate the factors limiting vegetation colonization and to find approaches to facilitate vegetation colonization on eroded slopes.

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