Seed Science Research (2011) **21**, 295–304 doi:10.1017/S0960258511000195

Seed persistence in the soil on eroded slopes in the hilly-gullied Loess Plateau region, China

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(Received 9 May 2011; accepted after revision 22 June 2011; first published online 5 August 2011)

Abstract

The soil seed-bank is an important component of vegetation dynamics. Its presence affects both ecosystem resistance and resilience. A persistent seed-bank is especially important in disturbed habitats and harsh environments. In the hilly-gullied Loess Plateau region, serious soil erosion causes decreases in soil water capacity and constrains vegetation recolonization. A stable and long-term persistent soil seed-bank is necessary for natural vegetation recolonization. We used an integrated measure of the depth distribution of seeds in the soil and the seasonal dynamics of soil seed-banks to analyse the persistence of seeds in soil and to investigate the correlation of seed longevity with seed size/shape and the species' life history. The results showed a significant tendency for small seeds and seeds of annuals/biennials to persist longer in soil than large seeds and seeds of perennials. However, seed shape was not related to persistence. The main dominant species *Artemisia scoparia*, *Lespedeza davurica*, *Heteropappus altaicus*, *Stipa bungeana*, *Artemisia gmelinii*, and *Bothriochloa ischaemun* in the different successional stages in this region can form a persistent and stable soil seed-bank. The pioneer species *A. scoparia* is especially significant because it can form a large, long-term, persistent seed-bank. These species can play a role in the recolonization of the eroded abandoned slope lands by vegetation.

Keywords: hilly-gullied Loess Plateau, seed mass, seed persistence, seed shape, soil erosion, vegetation recolonization

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Introduction

The soil seed-bank is an important component of vegetation dynamics. Its presence affects both ecosystem resistance and resilience (Thompson, 1987; Davies and Waite, 1998; Bakker and Berendse, 1999; Funes *et al.*, 2001). Seed-bank floristic composition is both a product of the species composition of the current vegetation and a record of the long-term substitution of species (Falińska, 1999). Furthermore, the seeds dispersed from nearby populations persist in the soil and may serve to predict successional tendencies (Major and Pyott, 1966; Soons and Bullock, 2008). Seed-bank composition and density vary among seasons as well as years (Thompson and Grime, 1979; Ortega *et al.*, 1997; Gutiérrez and Meserve, 2003). Information about the types and dynamics of seed banks is needed to assess the role of seed banks in vegetation recolonization and in community restoration (Luzuriaga *et al.*, 2005).

Seeds disperse from the mature plants and are deposited on the soil, where they experience different fates (Chambers and MacMahon, 1994). The seeds deposited on the soil may germinate immediately, may be removed by water flow or wind, may die from biotic or abiotic causes, or may be buried and persist in the soil, to germinate in the future under suitable conditions. Based on seed longevity in the soil, soil seed-banks are divided into two types: transient and persistent (Thompson and Grime, 1979). Seed size and shape have been proposed as indicators for predicting seed persistence in the soil for British herbaceous plant species (Thompson *et al.*, 1993). In general, small, round and compact seeds are always buried easily in the soil and can persist for a long time (Thompson, 1987; Thompson *et al.*, 1993; Bekker *et al.*, 1998; Funes *et al.*, 1999; Zhao *et al.*, 2011). In addition, gradients of habitat disturbance accompanied by parallel shifts in population composition influence the longevity of seeds in the soil. The species having persistent diaspores are more common in frequently disturbed habitats and are annuals or biennials (Thompson *et al.*, 1993; Bakker *et al.*, 1996; Ortega *et al.*, 1997; Kleyer, 1999).

The reappearance of plant species may depend on their persistence in the soil seed-bank as a 'memory' of the original plant community (Bakker *et al.*, 1996). In today's increasingly fragmented environments, knowledge of seed reservoirs in the soils of natural communities should provide useful tools for conservation and restoration efforts (Bekker *et al.*, 1998; Bakker and Berendse, 1999). The semi-arid, hilly-gullied Loess Plateau region in north-western China has suffered serious soil erosion for a long time (Zhang *et al.*, 2004b; Wei *et al.*, 2006). The increase in Chinese population after the 1950s had particularly severe consequences for the region. More natural vegetation was destroyed, and part of the slope grassland was turned into farmland. These changes aggravated soil erosion and ecological degradation (Zhang *et al.*, 2004a; Zheng, 2006; Zhou *et al.*, 2006). In the late 1990s, the Chinese Central Government implemented the policy of 'Replacing Farmland with Forest or Grass' for the control of soil erosion and large-scale ecological–environmental restoration. However, these afforestation efforts have not been entirely satisfactory. Owing to water shortages, many of the trees that were planted died or did not grow well (Zhang, 2005; Cao *et al.*, 2009). As a result, many slopes are still suffering intensive erosion and support only sparse vegetation. Natural re-vegetation is an alternative (Kirmer and Mahn, 2001). Soil seed-banks could potentially 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).

Harsh environmental conditions are expected to favour persistent seed-banks (Bakker *et al.*, 1996; Thompson *et al.*, 1998; Thompson, 2000). In the study region, eroded slopes with sparse vegetation are exposed to intense solar radiation at the soil surface. This exposure produces extreme fluctuations in soil temperature and a rapid drying of surface soils (Chen, 2003). Additionally, the precipitation is heterogeneous in time, such that drought conditions persist in the topsoil. The main factor limiting plant colonization in badland areas is that soil water is available only over very short time spans (García-Fayos *et al.*, 2000; Cipriotti *et al.*, 2008). For this reason, a persistent soil seed-bank is very important to support vegetation recruitment during periods when soil water is available. The aim of this study was to identify the species that can form persistent soil seed-banks in the eroded habitat and to investigate the relationship of seed-bank persistence to the seed size/shape and life history of individual species. To achieve this aim, an integrated measure of the depth distribution of the soil seed-bank and the seasonal dynamics of seed banks were used to analyse the persistence of the soil seed-bank.

Materials and methods

Study site

Zhifanggou watershed is located in An'sai county, in the Loess Plateau region (109°19′30″E, 36°51′30″N) at 1010–1431 m above sea level. The watershed has a semi-arid climate with an average annual precipitation of 504 mm (1970–2006). Over 60% of the precipitation falls during the rainy season (July–September), usually in the form of storms. The annual evaporation is over 1460 mm, and the mean temperature is approximately 8.8°C (−11°C to 30°C). Within the study region, the landscape includes inter-gully slopes and gully slopes, and the land surface is fragmented by deeply incised and densely distributed gullies (gully density 8.06 km km^{-2}). Loessial soil is the main soil type in this region. It has a homogeneous texture, is poor in organic components and is susceptible to erosion. Although this area is located in the forest–steppe region, natural forest is almost absent and has been replaced by typical steppe as a result of long-term human activity. The main native species in the different successional stages and landscapes include *Artemisia scoparia*, *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*.

Soil samples

The soil samples prepared for the germination experiments were collected in two different habitats. Twenty-one plots, each 5 m × 5 m, were located on abandoned slopes in a relatively early successional stage (habitat 1) with vegetation coverage ranging from 10 to 40%. In this habitat, the dominant herbaceous species were the pioneer species *A. scoparia* and the succession species *Heteropappus altaicus, S. bungeana, L. davurica, A. gmelinii* and *B. ischaemun.* Twelve 5 m × 5 m plots were located on gully slopes without farm activity and with better native vegetation (habitat 2), where vegetation coverage ranged from 40 to 70%. The dominant species in this habitat were the perennial herbs *A. gmelinii* and *A. giraldii* and the shrubs *Sophora davidii* and *Periploca sepium*. At each plot, 20 soil cores (diameter 4.8 cm) were collected in the 0–2-cm, 2–5-cm and 5–10-cm soil layers. The soil samples were collected in April, July and October in 2008 and in 2009. In the study region, *Artemisia* species constitute a large proportion of the standing vegetation. Seeds of these species and of some grasses are always released during the late autumn and winter. The soil samples collected in April, before the seeds germinated, included the fresh seeds of these species.

Moreover, the precipitation in the study region generally occurs from July through September, and seedling emergence is always related to the timing of the precipitation in arid and semi-arid regions (Schwinning and Sala, 2004). Most of the seeds found in the soil samples collected in July are therefore like those found in the April samples. In addition, the July samples contain fresh seeds released during the spring and summer. The soil collected in October, after the period of seedling emergence, include the constituents of the main persistent seed-banks and some fresh seeds released during the autumn.

Germination experiments

The soil seed-bank was identified using the germination method. TerHeerdt *et al.* (1996) reported that concentrating soil samples by washing and sieving improved the germination of most species. Concentrating soil samples can also save emergence time and space. Accordingly, the air-dried soil samples were sieved using a pore size of 0.15 mm. The size of the sieve was determined by passing the soil through a size-graded series of sieves, from large to small, and then germinating the soil passed through each sieve. The smallest sieve that passed soil without seedling emergence was chosen for use. The germination experiment was conducted in a greenhouse with controlled illumination, temperature and moisture. The concentrated soil samples were distributed over a 2-cm-deep perlite layer in 24 × 15 × 5-cm plastic trays and the soil-sample layer was kept to 0.5 cm of this set-up. Simultaneously, six trays with a perlite layer were put in different positions in the greenhouse as a control to monitor any seeds dispersed through the air. During the experiments, the germination trays were watered regularly. The temperature in the greenhouse varied from 11 to 35°C, with a mean value of 25°C. The seedlings were identified and removed or replanted for later identification. If no seedlings emerged within 2 weeks after the peak of seedling emergence, the soil was then dried and thoroughly stirred for the second germination period, and a gibberellin solution ($1\,g\,l^{-1}$) was applied to break the dormancy of the seeds. The germination experiment was terminated when there was no seedling emergence for 4 weeks, and the germination continued for approximately 4 months (15 March to 15 July in 2009 and 2010, respectively). Although sieved soil samples can improve the germination of most species, the germination method determines only the ‘readily germinable’ component of the soil seed-bank and thus may not detect all of the species present in the seed banks (TerHeerdt *et al.*, 1996; Thompson, 2000). In the wild, these ‘readily germinable’ seeds are most likely to determine the recruitment of vegetation after a disturbance (Davies and Waite, 1998). No attempt was made to assess the number of non-germinated seeds remaining in the samples.

Standing vegetation investigation and seed collection

The standing vegetation was investigated in July of each study year. Three 1 m × 1 m quadrats were surveyed in each sampling plot. The species composition was studied by recording the species that grew in the quadrat or that had shoots present in the quadrat. The density of a given species was calculated as the number of that species per square metre. The coverage of the vegetation was recorded by measuring the ratio of the area shaded by a given species to the total area of the quadrat. Two expert researchers performed this measurement jointly. The mature seeds were collected in the experimental watershed. After being air dried, the collected seeds were weighed and their shapes were observed.

Seed longevity index

Thompson *et al.* (1993) classified the seeds in the soil into three classes: transient, persisting in the soil for less than 1 year; short-term persistent, persisting for more than 1 but less than 5 years; and long-term persistent, persisting for at least 5 years. It is difficult to distinguish between short-term persistent and long-term persistent categories. We, therefore, distinguished only between ‘transient’ and ‘persistent’ (including both short-term persistent and long-term persistent). The persistence of seeds was estimated using an integrated measure of the depth distribution of seeds [viable seeds deep in the soil are older than those nearer the surface (Bekker *et al.* (1998)], the dynamics of soil seed-banks in different seasons and the vegetation composition. The species that had small seed-banks or that were rarely found in the soil samples were excluded. The species with significant seed-banks but little or no standing vegetation were classified as having persistent seeds. The species having relatively high-standing vegetation cover but no seeds or few seeds in the soil were considered to have transient seeds. The longevity index was calculated using the following formula:

$$\text{Longevity index (L)} = (P)/(T + P),$$

where P represent the total number of persistent records and T the total number of transient records. The longevity index ranges from 0 (strictly transient) to 1 (strictly persistent) (Bekker *et al.*, 1998). Species that were rare in the seed bank and in the standing vegetation were not classified.

Seed attributes

The seed dimensions and mass were used as seed attributes and measured after the seeds were air dried. Seed mass was defined as the average of 100 seeds per species unless the seeds were large (>100 mg). The average of ten seeds was used to determine seed mass for these larger seeds. Simultaneously, seed length, width and height were measured (to micrometer precision using Vernier calipers) on 10 seeds/species. Seed dimension variance was then calculated following the methods of Thompson *et al.* (1993). The variance of seed length, width and height were calculated after first transforming all values so that length is unity. The seed dimension variance of a perfectly spherical seed would be zero, the minimum value possible. Needle-shaped and disc-shaped seeds would have larger values.

Importance value index (I_v) of standing vegetation

To compare individual species between standing vegetation and the soil seed-bank, and to contrast the vegetation structure in the different habitats, the importance value index (I_v) of the individual species in standing vegetation was calculated as follows:

$$I_v = D_r + P_r + F_r,$$

where D_r is the relative density index (density of a particular species/the summed density of all species), P_r is the relative coverage index (coverage of a particular species/the summed coverage of all species), and F_r is the relative frequency index (frequency of a particular species/the summed frequency of all species).

Statistical analysis

The dynamics of the soil seed-bank density and species richness over the different sampling times within years were analysed using ANOVA. The data were obtained by averaging of 2 years, and seed density was transformed using log $(x + 1)$ to satisfy the homogeneity of variance assumption. The dominant species in the soil seed-bank and the standing vegetation were species with a relatively high density and frequency in the seed bank and a relatively large importance value index in the vegetation. The dynamics of the soil seed-bank density [transformed to log $(x + 1)$] of individual dominant species were also analysed using ANOVA. The Pearson correlation of seed longevity with seed attributes and vegetation life history attributes was analysed. The life history attributes considered were vegetation longevity (annuals/biennials or perennials) and propagation traits (with or without vegetative propagation). In this analysis, annuals/biennials were indicated by the value 0, and perennials were indicated by 1; species without vegetative propagation were indicated by 0, and species with vegetative propagation were indicated by 1.

Results

Soil seed-bank dynamics

The seedlings emerging in the germination experiment belonged to 76 species (Table 1). Both species richness and seed-bank density varied across the sampling times (Fig. 1). Most of the seeds (more than 50%) were found in the 0–2-cm soil layer. This layer, the most active portion of the soil seed-bank, showed significant seasonal variation. The largest seed-banks were present in April, after the dispersal of many species' seeds during winter and before seedling germination. After the germination that occurred during the rainy season (July to September), the smallest seed-banks were found in the October samples.

The density of individual species also exhibited varying patterns within the year (Table 1). The dynamics of the soil seed-bank density of individual dominant species were analysed (16 species: *A. scoparia*, *Artemisia hedinii*, *Setaria viridis*, *Dracocephalum moldavica*, *Eragrostis pilosa*, *L. davurica*, *H. altaicus*, *S. bungeana*, *Ixeridium chinense*, *Ixeris sonchifolia*, *Potentilla tanacetifolia*, *A. gmelinii*, *Poa sphondylodes*, *Cleistogenes chinensis*, *A. giraldii*, *B. ischaemun*). On the abandoned slope (habitat 1), *A. scoparia* was the most common species found in the seed bank and exhibited significant changes across different seasons, especially in the 0–2-cm soil layer ($P < 0.001$). However, on the slope with better native vegetation cover (habitat 2) the density of *A. scoparia* was lower and did not change significantly across different seasons. The seed-bank density of other species was relatively small. Only *L. davurica* and *A. gmelinii* in habitat 1 and *A. gmelinii* and *P. sphondylodes* in habitat 2 had significant seasonal changes ($P < 0.05$) in the 0–2-cm soil layer.

Relationships between seed persistence and seed attributes/vegetation species attributes

A total of 102 species were found in the study area. Of these species, 76 were recorded in seed banks, 85 in standing vegetation, and 60 in both seed banks and vegetation. At least 29 species had persistent seed-banks, and 34 species had transient seed-banks. The status of the other species was not clear because little standing vegetation or few seeds were present in the study plots (Table 1).

The mean seed mass ranged from 0.020 to 357.43 mg, the mean seed dimensions ranged from

Table 1. The traits of seeds, the soil seed-bank and the standing vegetation of all the observed species in the study plots (P, persistent seed-bank; T, transient seed-bank; '–', species was not defined due to it is rarity in the soil seed-bank and standing vegetation; '*', species capable of vegetative propagation)

		Vegetation I_v (%)		Soil seed-bank density (seeds m^{-2})						Seed attributes	
				H1			H2				
Species	Persistence	H1	H2	Apr	Jul	Oct	Apr	Jul	Oct	Dimension variance	Mass (mg)
Annuals and biennials											
Androsace septentrionalis	P	0.1		616	558	380		32	55		
Artemisia hedinii	P	2.8		278	162	291	515	614	512		
Artemisia scoparia	P	52.5	1.1	11 264	8194	5187	1962	1716	1380	0.124	0.020
Bothriospermum secundum	P			14	41	14	41	78	138	0.109	12.68
Chenopodium serotinum	P	0.3		41	28		28	27	28	0.076	0.444
Digitaria sanguinalis	–			28					14		
Dracocephalum moldavica	P	2.4	1.2	69	62	71	59	64	18	0.100	1.200
Eragrostis pilosa	P	0.1		371	347	250	67	156	39	0.044	0.088
Euphorbia humifusa	P	6.2	0.4	85	77	89	31	64	97	0.032	0.35
Galium aparine var. *echinospermum*	T		1.0							0.075	9.674
Hypecoum erectum	–				99	28	14				
Incarvillea sinensis	T	2.6								0.197	0.576
Ixeris polycephala	–	1.1	0.6	28	14			41			
Kochia scoparia	P	0.3		58	69	62		14			
Leonurus artemisia	–						28	104		0.102	1.080
Linum usitatissimum	T	1.1	0.9	1188	83		55	69	152	0.145	0.849
Lithospermum arvense	–					14					
Panicum miliaceum L.	–					14					
Salsola collina	T	1.1	0.4	14		78		14	41	0.081	1.334
Saussurea japonica	–	0.2	0.2	14						0.142	1.612
Setaria viridis	P	1.8		184	218	176	111	162	123	0.091	0.659
Siphonostegia chinensis	–		0.2							0.118	0.064
Sonchus oleraceus	–					14	14			0.189	0.568
Swertia bimaculata	P			14			341	279	270	0.024	0.07
Torilis scabra	–			14				14	28		
Torularia humilis	P		0.2	14			926	422	187		
Trigonotis peduncularis	–	0.1							14		
Perennials											
Adenophora lobophylla	T		1.3							0.152	0.105
Androsace henryi	–								41		
*Artemisia giraldii**	P	21.4	32.8	54	78		204	147	82	0.112	0.061
*Artemisia mongolica**	T	2.1	1.1							0.166	0.193
*Arundinella anomala**	–		0.2								
Astragalus adsurgens	–				83		14			0.129	1.452
*Astragalus scaberrimus**	T	4.5	1.4		14					0.264	1.664
*Bothriochloa ischaemun**	P	2.5	9.7	41	14	157	74	163	117	0.165	0.432
*Bupleurum scorzonerifolium**	–		0.3				14	28		0.157	0.664
*Calamagrostis epigeios**	–	1.5									
*Carex lanciflia**	–		5.0				145		41		
*Cirsium setosum**	T	10.3		28	14					0.146	2.512
*Cleistogenes chinensis**	P	4.0	19.3	65	80	78	254	203	382	0.229	0.32
*Cleistogenes hancei**	T		0.9					41		0.260	0.303
*Cleistogenes squarrosa**	T	1.0									
*Convolvulus arvensis**	–	0.8	0.3								
*Cynanchum thesioides**	–	0.0	0.5							0.193	7.288
*Dendranthema indicum**	T		17.4				28	41	41		
*Elymus dahuricus**	–		0.8								
Geranium wilfordii	T	3.6		14			14			0.223	9.031
*Glycyrrhiza uralensis**	T	6.4								0.066	7.474

Table 1. *Continued*

Species	Persistence	Vegetation I_v (%)		Soil seed-bank density (seeds m^{-2})						Seed attributes	
				H1			H2				
		H1	H2	Apr	Jul	Oct	Apr	Jul	Oct	Dimension variance	Mass (mg)
Gueldenstaedtia stenophylla	T	7.3	2.2	35		14					
*Helictotrichon schellianum**	–		0.4					28			
*Heteropappus altaicus**	P	38.6	4.8	222	110	120	76	117	74	0.135	0.388
Ixeridium chinense	P	13.6	3.0	110	133	66	82	119	99	0.206	0.40
Ixeris sonchifolia	P	0.3	4.5	28	14	41	138	160	110	0.208	0.054
*Koeleria cristata**	T		2.5								
*Leontopodium leontopodioides**	T		1.8						14		
Lespedeza davurica	P	37.8	26.1	159	59	101	147	48	81	0.109	2.129
*Leymus secalinus**	T	10.0	2.6		14	14		14	28		
*Melica scabrosa**	P		1.7				55	175	64	0.136	0.329
Melica scabrosa var. *puberula**	–							64	90	0.136	0.329
*Melilotus albus**	T	1.2	1.9	55	138			34	14	0.067	2.28
Oxytropis discolor	T	0.3	1.1	14	21				41	0.111	1.340
*Patrinia scabiosaefolia**	P		13.3				74	55	83	0.082	0.810
*Phragmites australis**	–	3.3	0.2								
Plantago asiatica	–							41			
*Poa sphondylodes**	P	0.9	5.0	14	61	23	610	1035	233		
Polygala tenuifolia	P	4.5	9.7	14		55	69	14	14	0.066	2.722
*Potentilla bifurca**	T	5.7	0.9								
*Potentilla sericea**	–								14		
Potentilla tanacetifolia	P	4.1	0.9	325	488	248	207	199	246	0.105	0.233
*Roegneria kamoji**	T	0.6	1.8					14	14	0.252	3.284
*Rubia cordifolia**	–		0.3		28		14			0.075	9.674
*Scorzonera austriaca**	–	0.2	0.3								
*Scorzonera divaricata**	T	1.7									
Scutellavia scordifolia Fisch	–		0.3								
Speranskia tuberculata	–		0.3				14	14			
*Sphaerophysa salsula**	–						28				
Stenosolenium saxatile	–	0.1		14	14	55	28	41		0.014	2.000
*Stipa bungeana**	P	19.2	15.5	104	174	67	99	149	62	0.242	1.682
*Stipa grandis**	T		0.9							0.292	8.080
Taraxacum mongolicum	–		0.3		21			14		0.175	0.790
Thalictrum aquilegifolium var. *sibiricum*	–				28					0.189	1.382
*Vicia sepium**	T	0.2	9.0							0.019	12.216
Viola dissecta	P		3.8				80	96	75		
Viola philippica	–	0.7		55	14	14	28			0.062	0.38
Shrubs and trees											
*Ailanthus altissima**	T		1.1							0.129	10.702
*Ampelopsis glandulosa**	T		3.2								
*Artemisia gmelinii**	P	12.8	54.0	132	54	47	445	270	153	0.132	0.085
Berberis purdomii	–		0.2							0.128	7.858
Buddleja alternifolia	P		4.3	84	71	114	253	133	142	0.098	0.050
Clematis aethusifolia	–		0.3		14					0.135	2.674
Clematis fruticosa	P	0.5	3.7	138	28				55	0.172	3.284
*Lespedeza cuneata**	T		6.0	28			14			0.124	1.624
*Lespedeza floribunda**	T		5.0								
*Periploca sepium**	T		3.0							0.237	5.506
Prinsepia uniflora	T		3.0		83					0.053	151.36
*Robinia psendoacacia**	T	9.0				28		41		0.199	14.108
*Rubus piluliferus**	–		0.3								
Sophora davidii	T	5.6	13.9			14	41	28	83	0.035	23.769

Table 1. *Continued*

Species	Persistence	Vegetation I_v (%)		Soil seed-bank density (seeds m^{-2})						Seed attributes	
				H1			H2				
		H1	H2	Apr	Jul	Oct	Apr	Jul	Oct	Dimension variance	Mass (mg)
Spiraea pubescens	–						14			0.136	0.876
*Syringa oblata**	T		6.0					35	41	0.228	4.530
Ulmus pumila	–	0.3				14					
Ziziphus jujube var. *spinosa**	T		0.6							0.002	357.428

0.193 to 19.9 mm, and the seed dimension variance ranged from 0.002 to 0.292 (Table 1). The relationship of seed persistence and seed attributes is shown in Fig. 2. The persistent seeds were mainly small and had a mass of less than 1 mg. Seed longevity and seed mass showed a significant negative correlation ($R = -0.334$, $P = 0.005$), but no significant correlation was found between seed longevity and seed dimension variance ($R = -0.116$, $P = 0.453$). There was a significant negative correlation between seed longevity and vegetation longevity ($R = -0.406$, $P = 0.006$) and between seed longevity and vegetative propagation ($R = -0.400$, $P = 0.007$). These results indicated that the perennials and the species capable of vegetative propagation produced more transient seed banks.

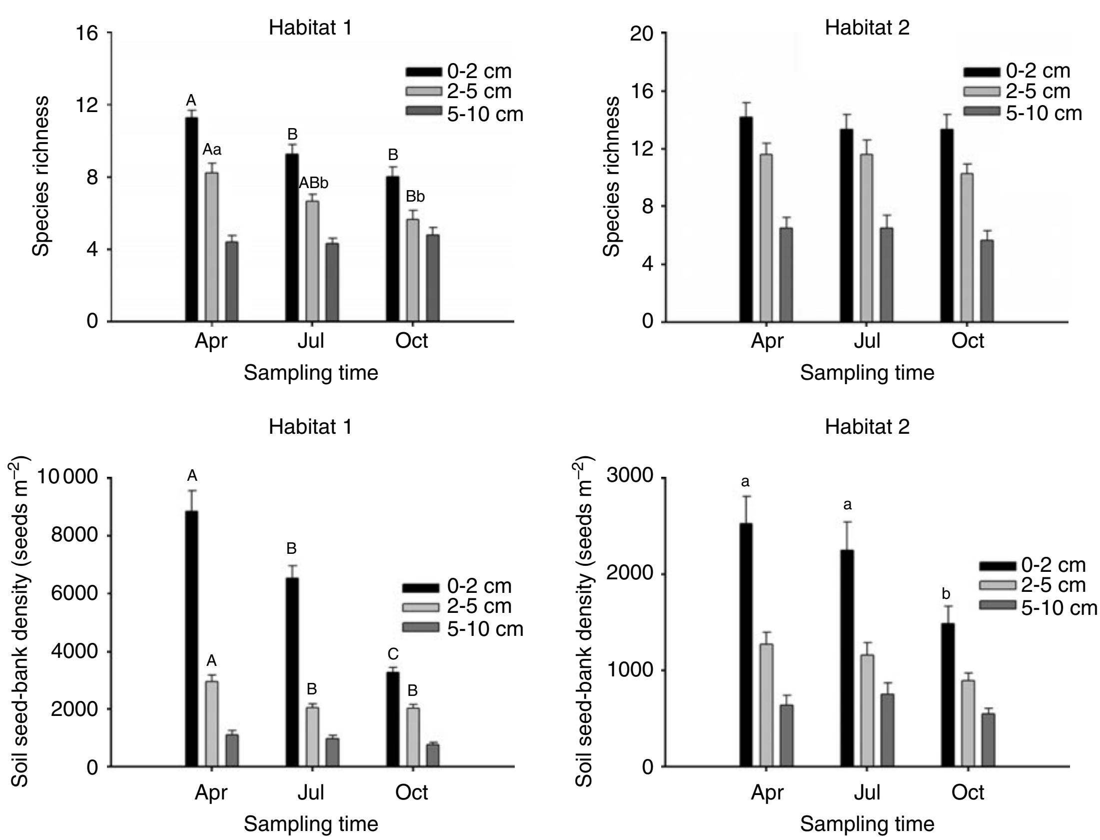

Figure 1. The dynamics of seed-bank species richness and density across different sampling times in the soil profile in different habitats (the letter above the error bar indicates the level of difference across different sampling times at the same soil layer, capital letters indicate a significant difference at the 0.001 level and lowercase letters indicate a significant difference at the 0.05 level).

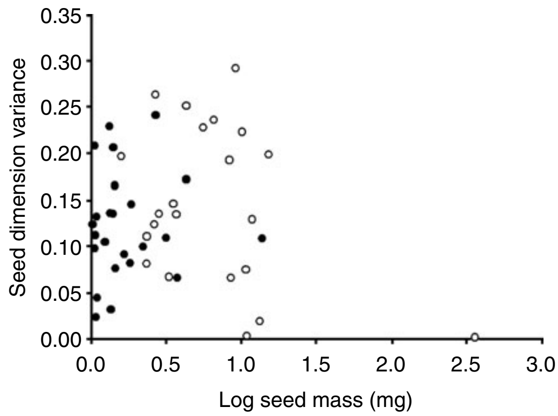

Figure 2. The relationship of seed persistence and seed mass (transformed to log $(x + 1)$) and shape (solid circles indicate the persistent seeds and the open circles indicate the transient seeds).

Discussion

The species composition and density of the soil seed-bank varied between seasons. However, in both habitats the dominant species occurred at every sampling time at a frequency $> 30\%$ and a relatively high density. These results indicated that the seed bank maintained a steady species composition with a fluctuation in density. Similar conclusions have emerged from a study of a gypsum system in central Spain with a semi-arid mesomediterranean climate and vegetation composed of shrubs and tussocks (Caballero *et al.*, 2005). In the present study, on the abandoned slope, the pioneer species *A. scoparia* persisted in the entire soil profile at all sampling times. The mean seed density ranged from 5187 to 11,264 seeds m^{-2}. The other species did not have as high a density, but they were also present at high frequencies in time and space. These species included *L. davurica*, *H. altaicus*, *A. gmelinii*, *Buddleja alternifolia*, *A. hedinii*, *I. chinense*, *E. pilosa*, *S. viridis*, *D. moldavica*, *P. tanacetifolia*, *Androsace septentrionalis* and *Euphorbia humifusa.* In habitat 2 with remnant native vegetation, the observed changes in the species composition and density of the seed bank included some contrasts with habitat 1. The density of *A. scoparia* decreased significantly. Likewise, other annuals also decreased in density and frequency. However, in contrast, perennials such as *P. sphondylodes*, *S. bungeana*, *C. chinensis*, *A. giraldii*, *I. sonchifolia* and *B. ischaemun* increased in density and frequency, both in time and in space. An investigation involving 174 sites by Jiao *et al.* (2008) found that in the hilly-gullied Loess Plateau region, the dominant species in the successional process were *L. davurica*, *H. altaicus*, *S. bungeana*, *A. scoparia*, *A. gmelinii* and *B. ischaemun*, and these species were dominant both in frequency and in coverage. These results suggested that the dominant species at different successional stages can form a persistent soil seed-bank.

The seed-bank density of individual species fluctuated owing to seed dispersal by different species at different times of the year. Thompson and Grime (1979) investigated seed-bank dynamics and classified seed banks into four types. In the area examined by the present study, the greatest numbers of species germinated during the rainy season (July to September) in the field. The seeds of the dominant species always persisted in the soil over the three sampling times within the year. This pattern matched the description of type III of the Thompson and Grime (1979) classification: species mainly germinating in the autumn but maintaining a small persistent seed-bank. Furthermore, the pioneer species *A. scoparia* had a large seed-bank during the year in the abandoned slope land and persisted in the remnant habitat without producing standing vegetation. This species resembled type IV of the classification: annual and perennial herbs with large persistent seed-banks.

Seed mass and shape have been reported to be the main factors influencing the persistence of seeds in the soil (Thompson *et al.*, 1993; Bekker *et al.*, 1998; Cerabolini *et al.*, 2003; Peco *et al.*, 2003; Yu *et al.*, 2007). During the past decades, several studies conducted in different parts of the world have addressed this question and have contributed to the debate regarding this problem. The results of these studies fall into several general categories. Some studies have suggested that the persistence of seeds has a significant relationship with seed mass and seed shape, and that small and compact seeds are frequently persistent in the soil (Bekker *et al.*, 1998; Funes *et al.*, 1999; Cerabolini *et al.*, 2003; Zhao *et al.*, 2011). Another view holds that only seed mass is significant for the persistence of seeds, and that species with persistent seeds have smaller seeds than species with transient seeds (Moles *et al.*, 2000; Thompson *et al.*, 2001; Peco *et al.*, 2003). It has also been claimed that larger seeds persist in the soil (Leishman and Westoby, 1998; Yu *et al.*, 2007). Additionally, in arid parts of the world like Australia, most persistent seeds are of the hard-seeded type, and there is no relationship between seed size and persistence (Leishman and Westoby, 1998). Generally, seed mortality decreases with increasing seed-coat thickness (Gardarin *et al.*, 2010). In the present study, the persistent seeds were always smaller than the transient seeds. However, some species with elongated or flattened seeds also persisted in the soil. This result resembles previous findings for the New Zealand flora (Moles *et al.*, 2000) and for dry Mediterranean grass and scrublands in Spain (Peco *et al.*, 2003). These persistent seeds with elongated or flattened shapes are especially capable of being buried in the soil. For instance, the seeds of *S. bungeana* can bury themselves in the presence of moisture or water.

Seed persistence is also influenced by the adult longevity and the habitat. Thompson *et al.* (1998) have studied the flora of north-western Europe and have found that shorter life histories are correlated with increased seed persistence. Especially in disturbed habitats, the vegetation is dominated by monocarpic species and produces abundant persistent seeds of small size. In the present study, annuals and biennials also had more persistent seeds than the perennials, and the species having the capability to propagate vegetatively always had more transient seeds.

In the region of this study, soil erosion is frequent and intensive in the sloping terrain. Because of the low canopy, intense radiation at the soil surface results in extreme fluctuations in soil temperature and a rapid drying of surface soils (Chen, 2003). The very short span of time during which water is available in the soil becomes the main factor limiting plant colonization in badland areas (García-Fayos *et al.*, 2000; Cipriotti *et al.*, 2008). Moreover, seed germination and emergence and seedling establishment are susceptible to environmental conditions (Harper, 1977; Fenner, 2000). The persistent seed-banks can offset the mortality associated with these stages of the life history (Ortega *et al.*, 1997; Stöcklin and Fischer, 1999; Thompson, 2000; Funes *et al.*, 2001). In the study region, the pioneer species *A. scoparia* can produce a very large persistent seed-bank and can thus provide germinable seeds when the environment is suitable for germination. During succession, the main perennial species can also form persistent seed-banks. These species, including *L. davurica*, *H. altaicus*, *S. bungeana*. *A. gmelinii*, *C. chinensis*, *A. giraldii* and *B. ischaemun*, can replace the pioneer species and gradually come to dominate the community (Du *et al.*, 2007; Jiao *et al.*, 2007, 2008). Furthermore, the number of germinable seeds in the soil shows a seasonal pattern, with a maximum in spring and a minimum in autumn. The seeds accumulate in the soil after the autumn production peak and germinate during the rainy season. This dynamic pattern depends on the occurrence of favourable weather for germination and on the time that seeds can remain viable in the soil (Ortega *et al.*, 1997). These results suggest that the persistent soil seed-bank can play a role in the vegetation recolonization of eroded habitats.

Acknowledgements

We thank the Key NSFC projects (41030532), the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-EW-406), and the innovation project of Northwest A & F University (CX200906) for funding this research. We acknowledge the assistance of the Ansai Ecological Experimental Station for Soil and Water Conservation (CAS). We acknowledge the assistance of the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau. Appreciation is due to Dr Ken Thompson for his valuable suggestions and comments.

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