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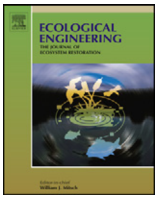

The role of local species pool, soil seed bank and seedling pool in natural vegetation restoration on abandoned slope land

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ABSTRACT

Theory and empirical evidence suggest that natural vegetation restoration depends on both the availability of seed resources and on successful seedling establishment. In the hill-gully Loess Plateau region, it remains unclear whether a rich diversity of species persists in the fragmented landscape in spite of intensive human activities and whether the distribution of the soil seed bank and the establishment of seedlings are threatened by serious soil erosion. We investigated vegetation composition in a series of plots with different slope aspects and degrees in a watershed of 8.26 km^2 in Shaanxi Provence, China to determine the local species pool. The soil seed bank and seedling recruitment on typical eroded slopes over varied erosion zones were simultaneously studied to characterize soil seed bank resources and seedling establishment. In this study, 133 species were identified in the local species pool. The species' frequency within the soil seed bank, seedling and standing vegetation was positively correlated with the frequency of matched species in the local species pool. The soil seed bank density and species richness had no significantly decreasing with the soil erosion intensity increasing on the hill slope. However, the seedling density and species composition showed significant difference among the investigative times and different erosion zones. Furthermore, the species frequency declined with increasing seed mass. Results of this study indicate that the seeds of widely distributed species always have small size, persist in soil under eroded conditions and have stable seedling density over the growing season. Therefore, these species can successfully recolonize in abandoned slope land. However, late-successional species with large seeds that lack dispersal vectors are less able to disperse and recolonize in areas that need to be restored.

1. Introduction

Restoration of fragmented habitats and degraded ecosystems is an increasingly relevant focus of current ecological research (Eriksson, 1996; Krauss et al., 2010). The successful restoration of plant communities often depends on the richness of a local species pool, the availability of seeds (Duncan et al., 2009; Eriksson and Ehrlén, 1992; Zobel et al., 1998), and the spatial interconnection of species-rich (source) and species-deficient (sink) habitats (Bruun and Ejrnaes, 2006; Zobel and Kalamees, 2005). However, habitat fragmentation can lead to shortages of seed sources (Russell and Roy, 2008) and long distances to remnant patches, influencing the rate and trajectory of succession (Poulsen et al., 2007). While, the persistent soil seed banks play an important role in the species reappearance after disturbance (Bakker et al., 1996; Stöcklin and Fischer, 1999). But, missing species must be actively seeded during restoration (Török et al., 2012).

The available species pool and soil seed bank are not always sufficient, however, to ensure the recovery of degraded vegetation, and seedling recruitment is often a central limitation to plant community restoration (Bakker et al., 1996; Seabloom et al., 2003). The period between seed germination and seedling establishment is considered to be one of the most vulnerable transitions in life cycle of plants (Garrido et al., 2005; Harper, 1977). In arid and semiarid climates, drought is one of the major causes of mortality in natural seedling populations (Bochet and García-Fayos, 2004; García-Fayos et al., 1995; Lauenroth et al., 1994). The precipitation regime, micro-topographical characteristics of ground surface, soil crust, litter and vegetation canopy are main factors influencing seed germination, seedling emergence and seedling colonization

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patterns (García-Fayos et al., 2000; Lauenroth et al., 1994; Tsuyuzaki and Haruki, 2008).

Geographical, topographical, historical and environmental circumstances influence local species richness (Maestre, 2004). In the study region, land surfaces in hill-gully region are fragmented by deeply incised and densely distributed gullies, creating many small areas of slopes with different gradients and aspects (Zhang and Liu, 2009). Uniform agricultural activity thus cannot be applied in this type of region, and many sloped lands are quickly abandoned due to nutrient loss resulting from soil erosion. Additionally, steep slopes or small patches that are not used as farmland can conserve many native species and serve as diaspore sources (LeCoeur et al., 2002; Moore and Swihart, 2007). There are abandoned slope farmlands, grasslands, scrublands and artificial woodland areas in a mosaic landscape pattern within the Loess Plateau (Fu et al., 2004). The unique landscape and agricultural history may be favorable to conserve a large species pool and to connect diaspore sources and sink habitats. On the other hand, slope gradients and aspects influence the distribution of solar radiation and soil water availability as well as the soil erosion intensities, and then influence the plant colonization and distribution (Bochet et al., 2009).

Due to the special geographic landscape, soil and climatic conditions, and long history of human activity, the Loess Plateau region is well known for its serious soil erosion (Shi and Shao, 2000). Erosion as an ecological driver influences vegetation composition, structure and spatial pattern (Bochet et al., 2009; García-Fayos et al., 2010). On the slope land with serious soil erosion, overland flow and sediment transport can carry away both the seeds that arrive at the soil surface and those that were previously deeper in the soil (García-Fayos et al., 1995, 2000). And seed size and shape also influence the seed remove during erosion process (Cerdà and García-Fayos, 2002; García-Fayos and Cerdà, 1997; García-Fayos et al., 2010). Additionally, the high erosion rates lead to soil impoverishment and a very short duration of available water, limiting plant colonization in eroded slope lands (Bochet et al., 2009; Cipriotti et al., 2008; García-Fayos et al., 2000). However, the species from the local species pool with high colonizing capacity and resistance to seed removal are able to colonize the slope lands with serious erosion and water stress (Bochet et al., 2009).

Thus, knowledge of local species pool, characteristics and distribution of soil seed bank on eroded slopes, and patterns of seedling emergence and establishment will increase our understanding of the factors limiting establishment from the soil seed bank in this eroded habitat. We investigated the following three questions: how many species persist in the local species pool in this special landscape; whether an available soil seed bank persists in the soil on the eroded slope; and whether the establishment, survival and growth of the seedlings are limited by the harsh habitat on eroded slopes.

2. Materials and methods

2.1. Study site

The Zhifanggou watershed, with an area of 8.26 km^2, is located in the north of Shaanxi province in the Loess Plateau region, China (109°19′30″E, 36°51′30″N) at 1010–1431 m above sea level. The watershed has a semiarid climate with an average annual precipitation of 504 mm based on data from 1970 to 2006. Over 60% of the precipitation falls during the rainy season in July–September, usually during storms. The annual evaporation is over 1460 mm, and the mean temperature is approximately 8.8 °C (−11 °C to 30 °C), and the annual average of frost-free days is 159 days. The landscape within the study region includes hill and gully slopes and the soil erosion on slopes shows clear vertical zonation (Zheng et al., 2005). The soil erosion patterns change from sheet and rill erosion to shallow gully (like ephemeral gully) erosion from top to bottom along the hill slopes, and the dominant gully erosion zone includes water and gravity erosion on the gully slope. Additionally, abandoned lands always distribute on the hill slope and remnant vegetation always distribute on the gully slope.

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 activities which destroy the natural vegetation and farm on slope land. But in the past decades many slopeland were abandoned in order to restore the vegetation and control soil erosion. The main species in different successional stages and landscapes include annual herbs *Artemisia scoparia*, perennial herbs *Artemisia giraldii*, grasses *Stipa bungeana* and *Bothriochloa ischaemun*, sub-shrubs *Artemisia gmelinii*, *Lespedeza davurica*, and shrubs such as *Sophora davidii*, *Rosa xanthina*, *Syringa oblata* and *Ostryopsis davidiana* (Jiao et al., 2007).

2.2. Vegetation survey

To determine the richness of local species pool, sample plots were located in a series of slopes. Several aspect and slope angle classes were defined in order to evenly sample them. The slope angle classes were classified as follows: 1, <15°; 2, 15–25°; 3, 25–35°; 4, 35–45°; 5, >45°. The slope aspect was classified as follows: 1, north (315–45°); 2, east (45–135°); 3, west (225–315°); 4, south (135–225°). In every of each aspect and slope classes we searched for at least three different slopes and installed one sampling plot per slope. The sample plots were laid where there was a homogeneous natural population or community. In each plot, six quadrats (2 m × 2 m) were randomly chosen and all of the vascular species were investigated in each quadrat. The density and coverage of each species was recorded. In total, 69 plots were investigated during August and September in 2010.

2.3. Soil seed bank

To determine the soil seed bank distribution patterns of the eroded slopes, soil samples were collected from different erosion zones. There were four erosion zones on a typical slope with a gradient of increasing erosion intensity (Zheng et al., 2005): a zone dominated by sheet erosion (Zone 1), a zone dominated by rill erosion (Zone 2), a zone dominated by ephemeral gully erosion (Zone 3) located from top to bottom along loessial hill slopes, and a zone on gully slopes dominated by water and gravity erosion (Zone 4). Two typical slopes were selected for soil sample collection. Three sampling plots of 5 m × 5 m each were located in each erosion zone. In each plot, 20 soil cores with a diameter of 4.8 cm were collected from the 0 to 2 cm, 2 to 5 cm and 5 to 10 cm soil layers. The soil samples were collected in April, July and October in 2008 and in 2009.

The soil seed bank was identified using the seedling emergence method. It has been reported that concentrating the soil samples by washing and sieving will improve the germination of most species and reduce emergence time and space requirements (TerHeerdt et al., 1996). Accordingly, air-dried soil samples were sieved using a pore size of 0.15 mm (Wang et al., 2011a) the unsieved/larger fragment soil fraction tested for germination. The concentrated soil samples were distributed in a depth of 0.5 cm over a 2-cm-deep perlite layer in 24 cm × 15 cm × 5 cm plastic trays. Six trays containing only the perlite layer were placed among the sample trays as a control to check for windborne seed. The trays were watered during the trial as necessary. 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.

The soils were stirred every month to expose ungerminated seeds following the cessation of the initial flush of germination. The germination experiment was terminated when there was no seedling emergence for two weeks. The germination continued for approximately four months from March 15th to July 15th in both 2009 and 2010.

2.4. Seedlings and standing vegetation in the field

In each seed bank plot, three 1 m × 1 m quadrats were marked for a seedling survey. The seedling survey was taken every month from June to October in 2010. Following the definition of Fenner and Thompson (2005), the individuals were considered emerged when coleoptiles or cotyledons appeared above the soil surface and established when possessing a fully expanded leaf. All of the established individuals were recorded and identified. During the seedling survey we simply count the number of seedlings observed on each date.

In each soil sample plot, three 1 m × 1 m quadrats were randomly selected for a standing vegetation survey. The standing vegetation in the sample plots was surveyed in August 2010.

2.5. Seed attributes

Mature seeds were collected from natural vegetation community in the experimental watershed. Seed dimensions and mass were measured after the seeds were air-dried. The seed mass was defined from average of 100 seeds per species unless the seeds were large (>100 mg). Average of ten seeds was used to determine the seed mass for these larger seeds. Seed length, width and height were measured to micrometer precision using vernier calipers from 10 seeds per species.

2.6. Statistical analysis

A modified Braun–Blanquet cover-abundance scale was used to describe the vegetation composition (scale 1, Cover small, isolated (<3); 2, Cover <1%, few individuals; 3, Cover 1–5%, numerous individuals; 4, Cover 5–25%; 5, Cover 25–50%; 6, Cover 50–75%, 7, Cover >75%). The slope angle and aspect were used as environmental gradients to analyze the vegetation distribution patterns in this study. The slope angle scale was classified as follows: 1, <15°; 2, 15–25°; 3, 25–35°; 4, 35–45°; 5, >45°. The slope aspect was classified as follows: 1, north (315–45°); 2, east (45–135°); 3, west (225–315°); 4, south (135–225°). A canonical correspondence analysis (CCA) was used to analyze the vegetation distribution in different environments using the Canoco 4.5 program (Plant research international, Wageningen, Netherlands. Authors: C.J.F. ter Braak and P. Smilauer). Species with <10% frequency (species frequency = the number of quadrats occupied by a species/the number of all the surveyed quadrats × 100) were removed from the analysis to reduce the influence of rare species. The factors were chosen using a forward selection procedure and tested with a Monte Carlo permutation test for significance ($P < 0.05$).

The difference of density and species richness of soil seed bank over different erosion zones were analyzed using one-way ANOVA. Seed density was transformed using $\log(x + 1)$ to satisfy the homogeneity of variance assumption. The distribution patterns of the seedling on different erosion zones and at different investigating times were analyzed using one-way ANOVA.

The correlation between species frequency in species pool and seed mass was analyzed using Spearman rank correlation coefficient. The correlation between species frequency of the species pool and soil seed bank, seedling and standing vegetation were analyzed using Pearson correlation coefficient.

The Sorensen index (C) was used to measure the similarity of species between every two subject pools, from the three pools of the soil seed bank, the seedlings and the standing vegetation, using the following equation: $C = 2w/(a + b)$ where w is the number of species found in both pools and a and b are the number of species in one of the two pools. The comparisons among the Sorenson indices were made using one-way ANOVA.

The important value index (Iv) of standing vegetation was used to analyze the difference of vegetation structure among the sample zones and calculated as follows: $\mathrm{Iv} = (\mathrm{Dr} + \mathrm{Pr} + \mathrm{Fr})/3$ where Dr is the relative abundance, Pr is the relative dominance and Fr is the relative frequency.

3. Results

3.1. Local species pool

In total, 133 species belonging to 38 families were recorded in the local species pool (Appendix Table S1). The dominant representatives were species belonging to the Asteraceae (25 species), Gramineae (21 species), Leguminosae (15 species) and Rosaceae (12 species). Among all of these species, there were 25 annuals/biennials, 19 perennial grasses, 62 perennial herbs, 24 subshrub/shrubs and 3 trees. Forty-one species belonging to 14 families were recorded with a frequency greater than 10%. From these species, 8 annuals/biennials, 7 perennial grasses, 20 perennial herbs and 6 subshrub/shrubs were recorded. The distribution characteristics of these species in the different habitats were analyzed using CCA. The species-environment correlations were 0.770 and 0.717 in axes 1 and 2, respectively ($P = 0.002$). And these species were classified into four groups based on their distribution on the different slope and aspect (Fig. 1). There was 16 species in the first group and they mainly distributed on the gentle slopes. The second group included nine species and always distributed on the north-facing slopes. The third group included six species and always distributed in the remnant patches on the steep south-facing slopes. The fourth group included nine species and distributed widely without close relationship with microenvironments.

3.2. Soil seed bank

The seedling emergence experiment identified 62 species belonging to 23 families (Appendix Table S1). Several families, including Asteraceae, Gramineae and Leguminosae, had abundant species representatives. Twenty-one annuals/biennials, seven perennial grasses, 20 perennial herbs, eight subshrub/shrubs and two trees were identified in the emerged seedlings. The vegetation structure and successional stages on gully slopes were different from hill slopes due to fewer disturbances on gully slopes. And the soil seed bank species composition displayed some difference between the hill slope and gully slope (Table 1). On the hill slope, annuals/biennials took about more than 90% in the soil seed bank density; well the proportion of annuals/biennials had an obvious decline on the gully slope. The species richness and seed density of perennial grasses, perennial herbs and subshrub/shrubs had obvious increasing on the gully slope.

The soil seed bank density and species richness changed with the erosion zone in each sample depth (Fig. 2). The soil seed bank density and species richness were not significantly different among the different erosion zones on the hill slopes, but they were significantly different from the soil seed banks in the gully slope. In the 0–2 cm layer, the mean soil seed bank density on the hill slope varied from 5560 ± 617 seeds m^{-2} to

Table 1
The species composition characteristics of soil seed bank, seedling and standing vegetation in different zones (A/B, annuals/biennials; G, perennial grasses; P, perennial herbs; S, shrubs/sub-shrubs; T, trees; the proportion of different species group in the soil seed bank and seedling were calculated based on the density; the proportion of different species group in the vegetation were calculated based on the species importance value).

	Sample zone	Proportion (%)					Species richness				
		A/B	G	P	S	T	A/B	G	P	S	T
Soil seed bank	Z1	88.3	0.9	8.7	2.1	0.01	11	4	11	4	1
	Z2	95.8	0.3	2.5	1.4	–	13	4	10	3	–
	Z3	96.4	0.4	2.1	1.1	–	12	5	10	4	–
	Z4	52.5	22.9	11.4	13.2	0.1	15	10	19	7	1
Seedling	Z1	56.2	11.0	29.3	3.5	0.1	14	8	16	6	2
	Z2	63.1	7.6	19.1	10.1	0.2	13	8	14	4	3
	Z3	69.5	4.7	19.8	6.0	–	13	7	17	4	–
	Z4	20.3	22.1	39.1	18.5	–	14	12	23	10	–
Standing vegetation	Z1	24.6	22.0	35.0	18.2	0.1	11	7	15	2	1
	Z2	26.2	21.9	27.4	24.3	0.1	8	8	15	3	1
	Z3	31.1	22.5	21.8	24.7	–	8	7	18	5	–
	Z4	7.4	20.1	28.9	43.7	–	7	7	19	8	–

6903 ± 725 seeds m^{-2} which were significantly higher than it on the gully slope 2087 ± 21 seeds m^{-2} ($F = 30.97$, $P < 0.001$); in the 2–5 cm layer, the mean soil seed bank density on the hill slope varied from 2134 ± 148 seeds m^{-2} to 2441 ± 254 seeds m^{-2} which were also significantly higher than it on the gully slope 1896 ± 194 seeds m^{-2} ($F = 25.65$, $P < 0.001$); in the 5–10 cm layer, the mean soil seed bank density on the hill slopes varied from 688 ± 131 seeds m^{-2} to 1149 ± 160 seeds m^{-2} which were still significantly higher than it on the gully slope 648 ± 80 seeds m^{-2} ($F = 5.10$, $P = 0.003$). Additionally, more than 50% of the seeds persisted in the 0–2 cm soil layer.

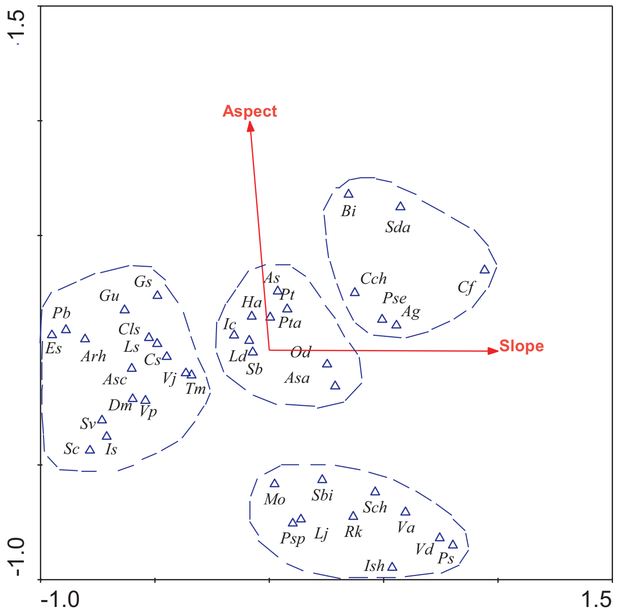

Fig. 1. CCA of vegetation in relation to the environmental gradient (arrows). First axis: $\lambda = 0.20$, percent of the variance explained = 8.2%; second axis: $\lambda = 0.12$, cumulative variance explained = 13.1%. The total inertia is 2.447. Group 1: Arh-A. hedinii, Asc-A. scoparia, Cls-C. squarrosa, Cs-C. setosum, Dm-D. moldavica, Es-E. stephanianum, Gs-G. stenophylla, Gu-G. uralensis, Is-I. sinensis, Ls-L. secalinus, Pb-P. bifurca, Sc-S. collina, Tm-T. mongolicum, Vj-V. joponica Langed), Vp-V. philippica, Sv-S. viridis; Group 2: Ish-I. sonchifolia (Bge.) Hance, Lj-L. juncea, Mo-M. officinalis, Ps-P. scabiosaefolia, Rk-R. kamoji, Sbi-S. bimaculata, Sch-S. chinensis, Va-V. amoena Fisch, Vd-V. dissecta; Group 3: Bi-B. ischaemum, Cch-C. chinensis, Cf-C. fruticosa, Pse-P. sepium, Sda-S. davidii, Ag-A. giraldii; Group 4: As-A. scaberrimus, Asa-A. sacrorum, Ha-H. altaicus, Ic-I. chinense, Ld-L. davurica, Od-O. discolor, Pt-P. tenuifolia, Pta-P. tanacetifolia, Sb-S. bungeana.

However, species richness of the soil seed bank on gully slope was significantly more than it on hill slope. In the 0–2 cm layer, the mean species richness on the hill slope varied from 9.1 ± 0.5 to 10.1 ± 0.6 seeds m^{-2} which were significantly lower than it on the gully slope 13.1 ± 0.6 ($F = 10.61$, $P < 0.001$); In the 2–5 cm layer, the mean species richness on the hill slopes varied from 6.5 ± 0.6 to 7.2 ± 0.4 which were also significantly lower than it on the gully

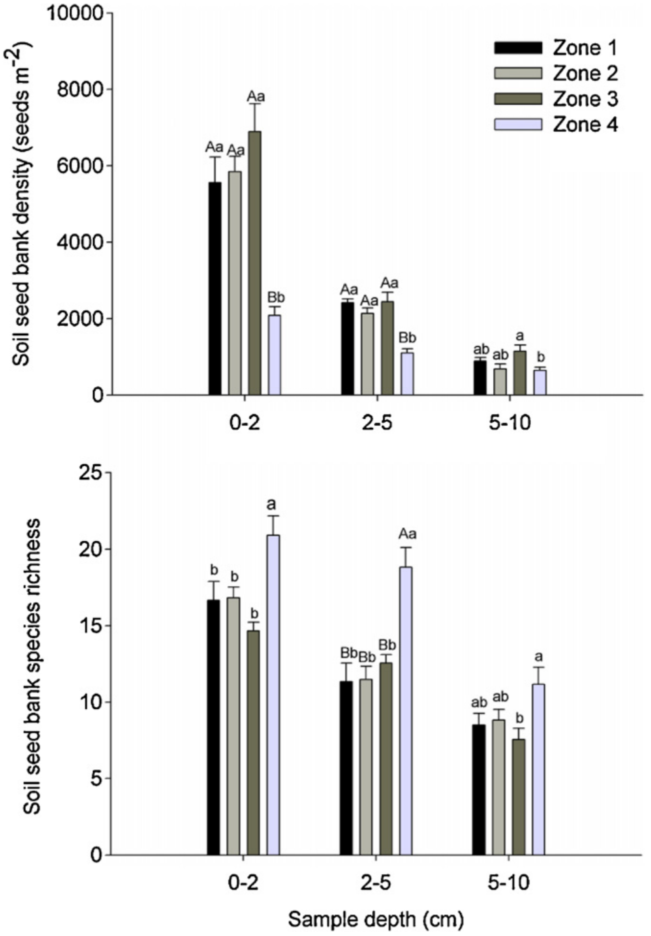

Fig. 2. Soil seed bank density and species richness in different erosion zones. The letter above the error bar indicates the level of difference across the different erosion zones in the same soil layer. The capital letter indicates significant difference at the 0.01 level and lowercase indicates significant difference at the 0.05 level.

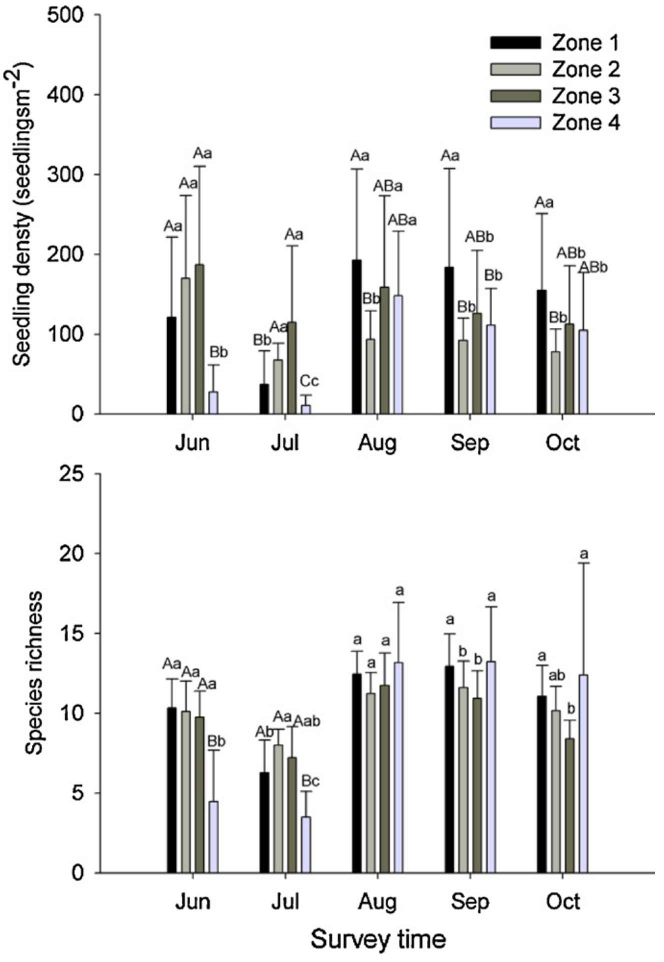

Fig. 3. Seedling density and species richness in different erosion zones at different sampling times. The letter above the error bar indicates the level of difference across the different erosion zones at the same sampling time. The capital letter indicates significant difference at the 0.01 level and lowercase indicates significant difference at the 0.05 level.

slope 10.5 ± 0.5 (F = 14.99, P < 0.001); In the 5–10 cm layer, the mean species richness on the hill slopes varied from 4.3 ± 0.3 to 5.1 ± 0.4 which were significantly lower than it on the gully slope 6.1 ± 0.5 (F = 4.43, P = 0.006).

3.3. Seedlings in the field

Sixty-five species belonging to 25 families were identified in the field seedlings (Appendix Table S1). The families of Asteraceae, Gramineae and Leguminosae were well-represented in the sampled population. Seventeen annuals/biennials, 11 perennial grasses, 24 perennial herbs, 10 subshrub/shrubs and three trees were identified in the field seedlings. On the hill slope, the annuals/biennials species took more than half in density, but on the gully slope, annuals/biennials species only took 20.3% in density. Perennial grasses, perennial herbs and subshrub/shrubs showed obvious increasing both in density and specie richness on the gully slope (Table 1).

In the field, density and species richness of seedlings varied among the erosion zones at each survey time (Fig. 3). In Jun and Jul, the seedling density and species richness on the hill slope were significantly higher than them on the gully slope. And on the hill slope the seedling density varied from 37 ± 10 to 187 ± 31 seedlings m^{-2} with species richness ranging from 6.7 ± 0.6 to 10.3 ± 0.6, but on the gully slope the seedling density varied from 11 ± 3 to 22 ± 5.6 seedlings m^{-2} with species richness ranging from 3.5 ± 0.3 to 4.0 ± 0.5. From Aug to Oct the difference of seedlings density and species richness between the hill slope and gully slope declined. The seedling density varied from 70 ± 6 to 193 ± 28 seedlings m^{-2} and 96 ± 16 to 146 ± 19 seedlings m^{-2} on the hill slope and gully slope respectively. The seedling species richness varied from 8.4 ± 0.4 to 12.9 ± 0.5 and 11.4 ± 1.5 to 13.0 ± 0.8 on the hill slope and gully slope respectively. On the hill slope seedling density among different erosion zones also had obvious difference. In Jun and Jul, sheet erosion zone had the lowest seedling density, but from Aug to Oct rill erosion zone had the lowest seedling density.

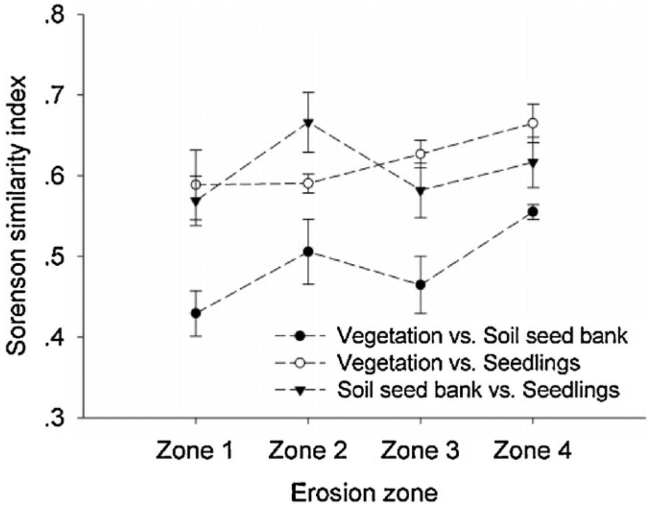

Fig. 4. Sorensen similarity index among standing vegetation, soil seed bank and seedlings at different erosion zones.

3.4. Relationships among the species pool, soil seed bank, seedlings and standing vegetation

Sixty-three species belonging to 23 families were recorded in the standing vegetation in the sampling plots (Appendix Table S1). In this group, there were 12 annuals/biennials, 11 perennial grasses, 27 perennial herbs, 11 subshrub/shrubs and two trees. Thirty-six of these species were equivalent to the widely distributed species in the local species pool. In the standing vegetation, annuals/biennials declined both in the important value and the species richness compared with the soil seed bank and seedling, but species of Perennial grasses, perennial herbs and subshrub/shrubs increased obviously (Table 1).

The Sorensen similarity index among the standing vegetation, soil seed bank and seedlings varied among the erosion zones (Fig. 4). The similarity index between the soil seed bank and vegetation was significantly lower than between the other two pairs (F = 20.48, P < 0.001).

The species frequency in the soil seed bank, seedlings and standing vegetation was influenced by species frequency in the local species pool (Fig. 5). The species with a higher frequency in the local species pool were more likely to be found in the soil seed bank, seedlings and standing vegetation. The Pearson correlation coefficients were 0.71, 0.72 and 0.85 (with P < 0.01) between the species pool and the soil seed bank, seedlings and standing vegetation, respectively. Furthermore, the species frequency in the species pool declined with increasing seed mass (Fig. 6), with a Spearman correlation coefficient of −0.38 with P < 0.01.

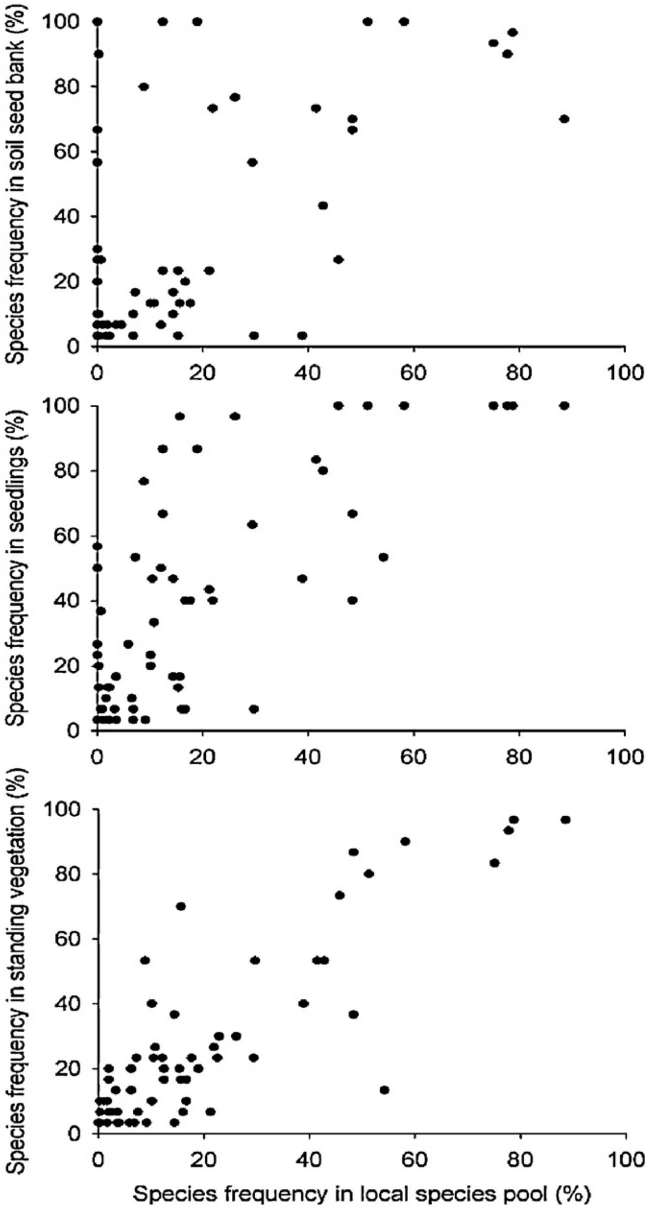

Fig. 5. The corresponding relationships of the species frequency in the local species pool and in the soil seed bank, seedlings and standing vegetation.

4. Discussion

4.1. Local species pool

In the study region, the mosaic landscape pattern can enhance the interconnection of source populations and target sites and is favorable for species conservation and dispersal (Eriksson, 1996). The study site (8.26 km^2) is a subset of the larger-scale Yanhe watershed (7687 km^2) and larger geographic scale northern Shaanxi Province (205,600 km^2). The species in the study site formed 63% and 10% of the species present in the Yanhe watershed and northern Shaanxi Province, respectively. And dominant species in the large region were also frequently identified in this local species pool. These results indicated that there are abundant species present in the study site and these species can compose an available local species pool.

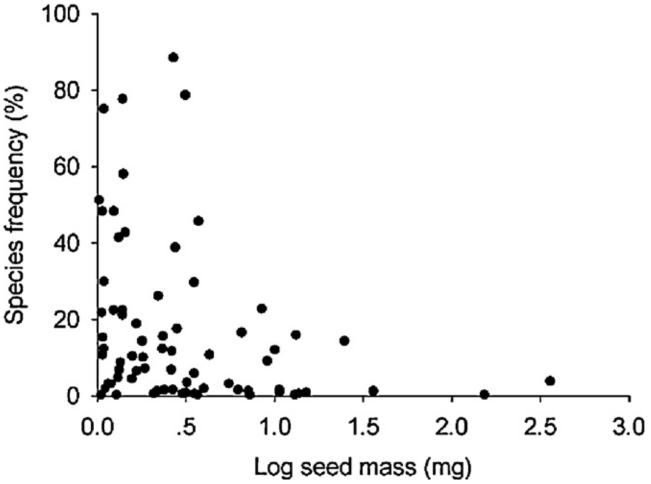

Fig. 6. The relationship between species frequency and seed mass.

In the local species pool, 41 species were recorded with a frequency greater than 10% and were classified into four groups. Species in the first group were always found on gentle slopes where human activity was previously frequent and the unaltered vegetation succession time has been short (Fu et al., 2006). In this group, most of the species have small seeds or specialized anatomical traits and can be easily dispersed by the wind. More than one third of the species in this group are annuals/biennials. Most of the annuals in this group form an extensive, persistent soil seed bank, such as *A. scoparia*, *A. hedinii*, *S. viridis*, *D. moldavica* (Wang et al., 2011a). Species in the second group were always found on north-facing slopes where soil water is more available. Species in the third group were always found in remnant patches on steep south-facing slopes with an extremely dry environment (Bennie et al., 2008; Bochet et al., 2009). All of these species have ability for vegetative propagation and can persist for a long time in harsh environments. Species in the fourth group were distributed widely and therefore did not correlate with the microenvironment. Moreover, these species can continually disperse once established and have a long lifespan. Some of these species can form a dominant population during the succession, such as *A. gmelinii*, *H. altaicus*, *L. davurica* and *S. bungeana* (Jiao et al., 2007).

These results suggest that the species that spread frequently can persist due to their extensive persistent soil seed bank, their ability for vegetative propagation, their capacity for long-distance dispersal or a combination of these traits. So they can persist in the remnants or form metapopulations (Eriksson, 1996), which can provide a seed source for vegetation recolonization in the process of the restoration of abandoned land.

4.2. Soil seed bank

The soil seed bank is an important component of vegetation dynamics effecting both ecosystem resistance and resilience (Thompson, 1987; Stöcklin and Fischer, 1999). In the soil seed bank, 33 species belonged to the widely distributed species in the local species pool. The pioneer species *A. scoparia* was identified in all of the sample plots with a mean soil seed bank density varying from 658 to 13,654 seeds m^{-2}. The dominant species belonging to the late successional stages, such as *A. gmelinii*, *A. giraldii*, *B. ischaemum*, *H. altaicus*, *L. davurica* and *S. bungeana*, were also frequently in the soil seed bank with hundreds of seed per square meter. Additionally, all of these species can persist and spread by vegetative propagation. The companion species such as *C. chinensis*, *I. chinense*, *P. tanacetifolia* and *S. viridis* were also frequent in the seed bank. However, the shrubs such as *C. fruticosa*, *P. sepium* and *S. davidii* were rare in the soil seed bank.

The densities and floristic richness of soil seed bank fluctuated as the succession proceeded. In the present study, the vegetation on gully slope is the remnant species in late successional stages. Compared with the soil seed bank on hill slope, the soil seed bank on gully slope was higher in species richness and lower in seed bank density.

On slope lands where soil erosion is frequent and serious, seed loss during soil erosion may be a limiting factor for the revegetation of eroded slopes (García-Fayos et al., 2000; Jones and Esler, 2004). In the present study, however, the soil seed bank density and species richness were not significantly different among the plots in different erosion zones on the hill slope. The previous studies in this region found that soil seed bank density in eroded open areas was lower than it in micro-topographical areas of high deposition and in microsites that trap eroded soil, but the seed loss in the eroded areas on slopes was not serious (Wang et al., 2011b). Furthermore, several species are widely distributed in the soil seed bank with special traits that help them persist in the eroded habitat; for example, *A. scoparia*, *A. gmelinii*, *A. giraldii* and *D. moldavica* can secrete mucilage when wet and *S. bungeana* can bury itself in a moist environment. These results suggest that on the hill slope, abundant seeds persist in the soil and belong to different successional stages, especially the pioneer species.

4.3. *Seedlings in the field*

The seedling density was heterogeneous in space and time (Appendix Table S2). Seedling emergence and survival depend on both seed and microsite availability (Eriksson and Ehrlén, 1992). In the eroded habitat, micro-topographical characteristics of ground surface influence the distribution of the runoff, nutrient sources and seeds and then become the major causes of seedling emergence and distribution (Isselin-Nondedeu and Bédécarrats, 2007; Maestre et al., 2003; Tsuyuzaki and Haruki, 2008).

Many studies in the arid and semiarid ecosystem have shown that drought is a major cause of mortality in natural seedling populations (García-Fayos et al., 2000; Maestre et al., 2003). Therefore, factors that can influence water redistribution, such as variations in the slope aspect and topographical characteristics of ground surface, become the major factors determining seedling emergence and distribution (Maestre et al., 2003; Tsuyuzaki and Haruki, 2008). In the present study, density and species richness of the seedlings changed along erosion zones. The largest density and greatest species richness were recorded in the sheet erosion zone with gentle slope and low erosion intensity. With the erosion intensity increasing, the lowest density was recorded in the rill erosion zone and the lowest species richness was recorded in the ephemeral gully erosion zone. These results suggest that high-speed surface runoffs occur easily and soil infiltration is difficult on these slopes, and that, particularly on the south-facing slope, solar radiation is strong and intensive evaporation makes the upper soil layer drier, limiting seedling survival and growth (Gutierrez et al., 2004; Leishman and Westoby, 1994). Additionally, the pattern of rain events played a very important role reducing seeds germination and seedlings survival (García-Fayos et al., 2000). In the study region, dry period during early summer is another limit factor reducing the seed germination and seedling survival.

In the present study, species belonging to different successional stages all have seedlings in the field (Appendix Table S2). However, farming on slope lands was a driving force leading to degradation of soil structure and enhance soil erosion (Cerdà, 1998, 2000). Water and nutrients are lost during erosion process, so the soil on abandoned slope lands is dry and poor (Jia et al., 2011; Shi and Shao, 2000). Changes in soil properties after land abandonment are slow in the semiarid environment (Lesschen et al., 2008). The seedling survival and growth are further limited by lack of available soil water and nutrient. Thus, re-vegetation is apparently retarded by the slow rates of seedling emergence and survival.

4.4. *Perspective of vegetation restoration*

Seed limitation tends to occur more commonly in early successional habitats and for early successional species (Turnbull et al., 2000). However, in the present study site, the pioneer species *A. scoparia* can form an abundant, persistent soil seed bank and high seedlings density during the growing season. At the same time, some other widely dispersed species, such as *A. gmelinii*, *A. giraldii*, *B. ischaemum*, *H. altaicus*, *L. davurica* and *S. bungeana* in late successional stages can also form a persistent soil seed bank and high seedlings density during the growing season, and these species can form self-sustaining populations at corresponding successional stages (Jiao et al., 2007).

In the study region, soil erosion is frequent and serious, the seeds of widely dispersed species have the ability to resist the soil erosion and still persist in the soil (Jiao et al., 2011). However, disturbance during the farming activity destroyed vegetation and soil structure which accelerated soil erosion (Shi and Shao, 2000). The poor soil conditions will limit the seed germination and seedling growth. Therefore, the vegetation cannot form enough coverage to reduce soil erosion and improve soil properties. Thus, re-vegetation is slow on the slope due to the limitation of harsh environments on seedlings recruitment.

In the present study, the species with high frequencies in the local species pool are always frequently found in the soil seed bank and seedling pool. The species frequency declined with an increasing seed mass. Generally, the seed mass is related to the seed dispersal ability (Leishman et al., 1995) and the succession process. The seeds of relatively early successional species are easily dispersed by wind due to morphological adaptations (Castroa et al., 2010; Westermann et al., 2011). They can be dispersed from remnant patches or rebuilt populations to new patches. As a result, early successional species can recolonize on the abandoned slope land naturally in several years (Jiao et al., 2007). However, seed size increases with successional shifts in species, and recolonization of the late-successional species with big seeds is limited by seed dispersal (Castroa et al., 2010; Westermann et al., 2011). When there are no available dispersal vectors, even if a high abundance of seeds can be produced, the seeds cannot be spread distantly (Zobel et al., 1998). The present study indicated that the seed dispersal limitation is a limiting factor for the later successional species recolonization. Additionally, the poor soil conditions on the abandoned slope land may be another factor limits the late successional species recolonization.

The results of the present study indicated that more late successional species such as the perennial grasses and herbs and Shrubs/Sub-shrubs were persist on the steep gully slope. These species are the sources of the diaspore and will recolonize on the abandoned slope land. On the abandoned slope land, there were more Annuals/biennials species in the soil seed bank and seedling pool, but in the vegetation their proportion was declining and would replaced by the late successional species. Furthermore, dominant species in the late successional species always have long life span and form tussock by vegetative propagation, such as *H. altaicus*, *A. giraldii*, *A. gmelinii*, *B. ischcemum*, *C. chinensis* and *S. bungeana*. These tussocks are more effective in controlling soil erosion, improving soil conditions and trapping runoff sediment and seeds. And they may play important role in facilitating the late colonizer by reducing the stresses and disturbances, such as drought, strong sunlight and high temperature. However, the late species with large seeds are limited by the seed dispersal, and assisted measures such as seed sowing and seedling planting of these species should be done. And more research should be done to find out the suitable approaches to enhance the seedling survival and growth of the late species.

5. Conclusion

The present study suggested that there is available local species pool persisted in this region and they can provide diaspore for the vegetation recolonize on the abandoned slope land. And seeds of the dominant species on the abandoned slope land can disperse distance and form persist seed bank. And seedlings of these species also had high density during growth season. But poor soil water and nutrient also limit the seedling survival and growth under the erosion conditions. Additionally, the dispersal limit is another key factor limit the late seral species recolonize on the abandoned slope land. Thus further researches should be done to find out the suitable assisted measures to help the late species recolonize in order to stabilize the highly erosive slopes and speed vegetation succession.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2012.12.055. These data include Google maps of the most important areas described in this article.

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