

金沙江干热河谷山地植被恢复区土壤 种子库和地上植被研究

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摘要:土壤种子库在植物种群动态中起着重要作用。土壤种子库可缓解种群的灭绝过程, 保存群落中植物种的表现特征, 是植被天然更新的物质基础。通过对金沙江干热河谷山地植被恢复区(包括水平阶、自然坡面、沟底)和未恢复区(包括放牧地)的土壤种子库和地上植被的组成、大小及多样性进行比较研究表明, 植被恢复区土壤种子库和地上植被的密度、丰富度、多样性及均匀度均大于未恢复区。恢复区地上生物量要远大于未恢复区。水平阶和各类型间的土壤种子库密度与地上植被密度差异显著。土壤种子库中草本植物占很大比例。孔颖草和扭黄茅是土壤种子库和地上植被的两大优势种, 两者的个体数量、重要值及生物量最大。土壤种子库和地上植被有较高的相似性, 且随着恢复程度的加深, 相似性有增高的趋势; 土壤种子库密度和地上植被密度之间关系可以用二次和三次曲线拟合。

关键词:土壤种子库; 地上植被; 物种多样性; 干热河谷

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Soil seed bank and aboveground vegetation in Jinshajing Hot-Dry River Valley Hillslope vegetation restoration site

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Abstract: Soil seed bank plays an important role in the composition of different plant communities and especially in their conservation. Although Soil seed bank, aboveground vegetation and their relationship have been the subject of much recent attention, little is known about the size and species composition of soil seed bank and aboveground vegetation in semi-arid hillslope grasslands and understanding of how these components interact to determine the importance of seed banks to regeneration is limited. We assessed the size and species composition of a soil seed bank and aboveground vegetation in an experiment with 36 vegetation quadrats and 108 soil samples in terrace, slope, gully and grazing land that represent a range of habitats within a hillslope grassland in Jinshajing hot-dry river valley of Yunnan. Terrace, slope and gully represent restored site and grazing land typifies unrestored site. We identified 21 taxa in the seed bank with a median of 7 species/m² and a median density of 5498 seeds/m², while in aboveground vegetation, 19 species were observed with a median of 6 species/m² and a median density of 1088 plants/m². Both seed bank density and aboveground vegetation density among grazing land, gully, slope and terrace differed significantly. There was an absolutely high proportion of herbaceous species in the seed bank and aboveground vegetation. Gramineae predominated over both seed bank and vegetation. The most frequent seeds and plants were *Bothriochloa pertusa* (L.)

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A. Camus and *Heteropogon contortus* (L.) Beauv that had the highest individual number, importance value and biomass. In the seed bank, the seeds of *Bothriochloa pertusa* (L.) A. Camus and *Heteropogon contortus* (L.) Beauv accounted for 50.68% and for 33.10% of the total seeds respectively. In aboveground vegetation, the individual number of *Bothriochloa pertusa* (L.) A. Camus accounted for 55.66% of the total and *Heteropogon contortus* (L.) Beauv accounted for 29.86%. The biomass of *Bothriochloa pertusa* (L.) A. Camus and *Heteropogon contortus* (L.) Beauv. accounted for more than 70% of total, reaching 206.71 g/m² and 147.76 g/m² respectively. *Bothriochloa pertusa* (L.) A. Camus and *Heteropogon contortus* (L.) Beauv had the highest importance value of 193.01 and 159.99 respectively.

Density, biomass, species richness, species diversity and evenness were the highest in terrace while those in grazing land were the lowest. Similarities between the seed bank and aboveground vegetation were moderately high and not very different among slope, gully and terrace, except for grazing land, tending to increase when restorative stage progressed. This result contrasts with some other studies where the seed bank contributes very little to the seedling flora and vegetative growth clearly overwhelms sexual reproduction. The hypothesis about significant functional correlation between soil seed bank density and aboveground vegetation density is conformed. Correlation between soil seed bank density and aboveground vegetation density can be described as quadratic and cubic curves. The strong similarity between vegetation and the seed bank is attributed to the great proportion of the species *Bothriochloa pertusa* (L.) A. Camus and *Heteropogon contortus* (L.) Beauv. that are seed-profusive and whose seeds have a significant viability in the ground. The high density, biomass, species richness, species diversity and evenness of the reclaimed site is related to the sufficiency of heat and water supplies for species establishment and growing in the site, which partly reflects our effective efforts on the hillslope grassland restoration. We believe that our vegetation restoration efforts have altered the microhabitat conditions of the site and provided a favorable habitat for species to establish and grow.

Key words: soil seed bank; aboveground vegetation; species diversity; hot-dry river valley

1 Introduction

Soil seed bank refers to the ungerminated but viable seeds that lie in the soil^[1]. Many plant species have the capacity to produce seeds that remain dormant in the soil for several years to several decades. In most habitats, ranging from the arctic to the tropics, deserts to wetlands, natural to cultivated lands investigators have found evidence for seed banks. Seed banks are thought to be ecologically and evolutionarily important in the dynamics of plant populations. Seed banks can function as reservoirs of genes and/or gene complexes. This means that seed persistence, the carry-over of viable seeds in the soil for multiple years, can buffer the effect of local extinction of genotypes in the non-dormant portion of the population, and act to maintain genetic variation, during periods when seedling do not survive to become reproductive adults. Seed banks can also buffer a population from extinction and preserve the representation of a plant species within a community^[2].

Seed banks and their relationships to vegetation have been the subject of much recent attention. The understanding of the potential of a seed bank to alter vegetation composition, its potential for restoring richness in species and maintaining floristic diversity are some of the reasons that have motivated researchers to compare the composition of the aboveground vegetation with seed reserves hidden in the soil. The seed bank is a major functional compartment of a plant community, in that its role as a storage compartment allows population maintenance according to changes in reproduction performances either between years or between sites^[3]. Thompson & Grime defined four types of seed banks among the most common species in temperate regions, characterized by singularities in the persistence of their seeds in soil^[4]. These types range from transient seed banks constituted by seeds that germinate in greater numbers immediately after dispersal, to persistent seed banks with seeds that remain dormant in the soil over a longer period (more than 1 year) until environmental and/or temporal conditions are favorable. Seed banks of trees, shrubs and shade-tolerant herbaceous species in temperate woodlands are generally transient, while shade-intolerant species are the primary constituents of persistent seed banks^[5].

However, most past studies of seed banks and their relationships to aboveground vegetation have been concentrated on arable lands, alluvial wetlands, and successional forest where seed bank composition reflects historical land use. While fewer investigation of seed banks in semi-arid waste hillslope grassland have been made, it is clear that seed banks are important in waste grassland recovery after disturbance. If we aim to regenerate the local vegetation with a certain modification, the ecological function of seed banks in semi-arid hillslope grassland must be fully understood.

In this study, we characterized the soil seed bank and aboveground vegetation in a 10-hectare tract of previously abandoned hillslope grassland that is without precise boundaries but surrounded by agricultural land in Jinshajing hot-dry river valley. We sampled many diverse habitats within the tract of the grassland. With this approach we were able to explore relationships among the existing vegetation and seed bank composition, within a single, continuous, regenerating, hillslope grassland ecosystem. Our general objectives were: (i) to determine the size, composition, species richness and species diversity of the seed bank and aboveground vegetation in a broad range of habitats within this large fragment of grassland, (ii) to describe the relationships between the seed bank and existing vegetation within this grassland, and (iii) to examine whether and to what extent the community structure and productivity had been optimized by our facilitating restoration efforts.

2 Materials and Methods

2.1 Study site

The present study was affiliated with the project of Mechanics and Application of Micro-Catchment Water Harvesting Agriculture and Forestry in Jinshajing River, which was initiated in 2002. It was carried out in the hilly land of Laocheng Village, Yuanmou County ($25^{\circ}43'52''$ North, $101^{\circ}51'03''$ East; altitude: 1100 – 1200 m) in the north-central part of Yunnan Province (located \approx 190 km northwest of Kunming City), which is a typical hot-dry river valley area in southwest China.

This region is alternatively affected by tropical monsoon and foehn from the Indian Ocean. Under the frequent domination of foehn, the region is characterized by the aridity and hotness of weather. Moreover Foehn winds cause a hot dry season of seven months, and scorching dry spells afflict the wet seasons. Ecologically the areas are similar to tropical savannas and called semi-natural savanna or secondary savanna^[6]. The mean annual temperature is 21.7°C ranging from 14.9°C in December to 27.1°C in May, and the mean annual precipitation totals 629 mm (most of which is rainfall). The mean annual evaporation, which is nearly 6 times the precipitation, averages 3729 mm. Rainfall is not distributed evenly throughout the year, and most rain falls during June to October. The 7-month-long dry season, from November to May, averages less than 100 mm or 14% of the mean annual rainfall (Fig. 1).

The dry climate makes successful tree planting a challenging operation. It also makes natural regeneration extremely difficult after forests are harvested or cleared. The survival rate of trees planted using planting technologies that are effective in other areas was very low in this area during the period 1952 – 1988. Only 6% of Yuanmou's land area was covered with forests in 1993. The majority of its designated forestland is covered with poor quality bushes or grass and sometimes there is just bare land. In the short wet season, severe soil erosion and serious land degradation resulting from excessive exploitation and unsustainable practices haunts the area. To address this problem, restoration of cover by planting trees, shrubs and grasses is necessary. Although it is very challengeable for foresters/ecologists to improve the deteriorating ecological environment and achieve economically and ecologically sustainable development of this ailing region, many researches have been successfully undertaken and the vegetation in certain area has been partly restored.

2.2 Sampling design

The experiments were conducted in four contrasted vegetation types. The first is a frequently mowed and grazed agricultural field (called grazing land). This field remaining as a control tool epitomizing unrestored plot is butting against

the experimental field. The experimental field is not enclosed but kept away from human and animal disturbances under the watchout of a peon. The second is an intact hillslope, which was not modified by our agricultural activities. The third is a gully, which was worn originally by running water and through which water usually runs only after heavy rains. Both hillslope and gully are representatives of moderately restored plots. The fourth is terraces along the hillsides, which had been tilled for further growing plants (trees, shrubs and grass), representing highly restored plots. Except for the controlled field, the others are all within the experimental area. Three 40m long, nonparallel transects with different bearings were selected within each vegetation type. Each transect comprised 3

regularly spaced quadrats (1m × 1m, 10m apart) and epitomized the vegetation around^[7]. Altogether, 12 transects and 36 quadrats were set up.

2.3 Seed bank sampling

The seed bank was sampled in January 2004. At that time, seeds released the previous summer had a natural cold stratification, seeds from the 2004 season had not been released, and there had not been an opportunity for the seeds to germinate that spring. There is some disagreement in the literature on the best time to sample seed banks; we recognize that we are sampling both persistent and transient seed banks^[8]. We used the method developed by Lavorel *et al.* consisting of a randomly sampling within each sampling quadrat (three replicates per quadrat, each replicate 30 cm apart)^[9]. Altogether 108 soil samples were collected (9 per transect; 27 per vegetation type). Soil samples were taken in form of a square (10 cm × 10 cm) along a central transect running the length of each quadrat devoted to seed bank sampling. The majority of viable seeds is normally concentrated in the very first centimeters of the ground (i.e. the litter-fermentation -humus layers), with fewer seeds found out to 10 cm^[8]. The depth of sampling was 5 cm, to yield a total volume of 0.5 L and a total soil surface area of 0.03 m² per quadrat. The soil samples were then sorted to eliminate the plant fragments and stones and kept in ventilating bags.

2.4 Seedling emergence technique

The density and composition of the seed bank were determined by observing seedling emergence. We chose the "emergence method" for analysis of the seed bank, because our primary goal was to determine the abundance and distribution of viable seeds that could germinate under field conditions. Gross showed that elutriation, by including nonviable seeds, gave higher estimates of seed density than emergence^[10]. Poiani and Johnson found that the "emergence method" gave an accurate assessment of the number of species and the relative abundance of seeds present compared with the actual identification of seeds^[11]. Although it is generally accepted that the "emergence method" gives biased assessments of the seed bank because greenhouse conditions are never exactly the same as field conditions^[12], it is the most appropriate method for measuring the seed bank composition and exploring relationships between the seed bank and aboveground vegetation.

The seedling emergence study began in spring (March). The soil samples were placed in a warm greenhouse where temperatures are similar to those outdoors in the Yunmou area and they were kept moist. Each sample was divided in half and spread out in two germination flowerpots (φ130cm × 90 cm) to the depth of 2 cm over 4 cm of sand (The sand was previously sterilized and put into the pots to let exogenous seeds in it fully germinate). Each pot from each plot was

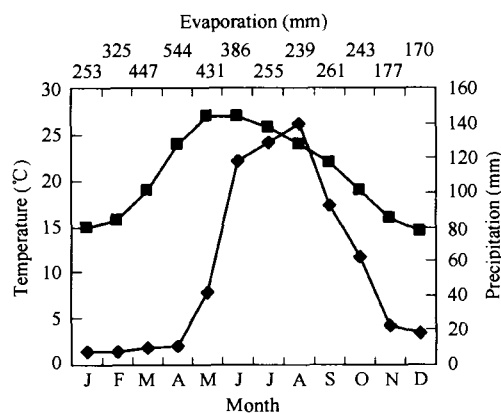


Fig.1 Climate diagram and mean monthly evaporation (top of figure) for study site

assigned a random position in one of two replicates. All pots were watered as often as needed to keep the soil moist. We fertilized the pots with standard plant food every 2 weeks to encourage faster growth and avoid seedling death^[13]. Once the first seedlings appeared observations and identifications were facilitated using seedling floras. Emerging seedlings were identified, recorded and removed weekly or transplanted to grow to maturity for later identification. In order to favor the maximum of germination, seedlings were pulled out after identification to maintain a low density in the germination pots and to allow the germination of other seeds. At the end of the first two months of the experiments, the soil samples were carefully turned over in order to facilitate the emergence of new seedlings^[14]. After six months, the sampling was terminated as no more emergence occurred for several consecutive weeks. To quantify germination of ambient seeds blown into the experimental pots inside the greenhouse, several control pots containing a 2cm layer of sterile weed-free potting soil over 4 cm of sand were placed randomly in each replicate block. We found no significant differences in the number or density of species between replicate blocks, so the results were combined for all analyses.

2.5 Vegetation characterization

To record every species of vascular and herbaceous plant present within the whole study plots, we made surveys in mid-autumns of 2003 when the development of plants was optimal. Floristic information including taxa, percent coverage, individual number and biomass was obtained by surveys carried out in each quadrat. We used the nomenclature of Flora Sinicae (Delectis Flora Sinicae Agendae, 1959 — 1999). After visually estimating taxa, percent coverage and counting the individuals, we cut down all the individuals within the quadrats for further determining the biomass of each taxon. Finally plant samples of each taxon within each quadrat were dried completely in an oven and then weighed.

2.6 Data analyses

We analyzed two different aspects of seed bank: composition and properties. Composition is simply the number of seedlings of each kind at each quadrat. To characterize the seed bank of each vegetation type as a whole, we calculated the mean species richness (S), mean seed density (seeds/m² soil surface), the proportion of taxa, and the mean species diversity from all the quadrats of the same vegetation type. We used the Shannon-Wiener index, the Simpson index and Hurlbert's probability of intraspecific encounter to indicate species diversity, and the Pielou index to indicate species evenness^[15-18]. We also calculated these same characteristic properties for aboveground vegetation of each type after determining relative abundance (RA), relative coverage (RC), relative frequency (RF) and importance value (IV) of each species.

$$\text{Simpson diversity index: } D = 1 - \sum P_i^2;$$

$$\text{Shannon-Wiener diversity index: } H' = - \sum P_i \ln P_i;$$

$$\text{Probability of intraspecific encounter: } PIE = \sum [(N_i/N)(N - N_i)/(N - 1)];$$

$$\text{Pielou evenness index: } J = D/(1 - 1/S).$$

where S = the species richness, N_i = the individual number of the i th species, N = the individual number of all species, and P_i = the proportion of the i th species.

Soil seed bank density, aboveground vegetation density and soil property among different types of vegetation were both compared by means of a one-way analysis of variance (ANOVA) followed by Tukey's multiple comparison test at $p = 0.05$. All analyses of variance were conducted with MINITAB Release 14.13. (Minitab Inc., 1972 — 2004). Before performing ANOVA all data was calculated as a mean \pm standard deviation and rounded to the nearest whole number.

The similarity between species composition in the seed bank and in the aboveground vegetation was assessed using Jaccard's similarity coefficient based on species presence and absence^[19]. This coefficient was calculated between all types of vegetation and seed bank.

$$C_i = a/(a + b + c)$$

where a = the number of species common in sample A and sample B , b = the number of species present in A but absent in B , c = the number of species present in B , absent in A . The result, as measured by the Jaccard's coefficient, ranged between 0, for no species shared in common, and 1, for complete concurrence.

We assessed the relationships between the density of the seed bank and the aboveground vegetation, which is possible by using a regression analysis. The data of density was logarithmically transformed before the statistical analysis to meet the assumption of normality and homogeneous variances and reduce positive skew^[20, 21].

3 Results

3.1 Overall richness and density of the soil seed bank and aboveground vegetation

A total of 1980 seedlings (265 in grazing land, 392 in gully, 447 in slope, 876 in terrace) and 21 species (16 species in grazing land, 13 species in gully, 15 species in slope; 17 species in terrace) were observed during the trial (Table 1). The total seed number varied significantly among the samples. The density was significantly higher ($p < 0.001$) in terrace (9738 seeds/m²) than in grazing land (2941 seeds/m²), gully (4369 seeds/m²) and slope (4942 seeds/m²). The number of seed bank taxa per quadrat ranged from 4–15 with a median of 7 species, while seed density in individual quadrats ranged from 2464 to 11605 seeds/m² with a median of 5498 seeds/m² overall. A total of 19 species was identified in the aboveground vegetation (8 species in grazing land, 14 species in gully, 16 species in slope; 18 species in terrace) ranging from 3 to 11 per quadrat with a median of 6, while vegetation density in individual quadrats ranged from 606 plants/m² (in grazing land) to 1904 plants/m² (in terrace) with a median of 1088 plants/m² (Table 2).

3.2 Composition of the soil seed bank and aboveground vegetation

The soil seed bank was dominated by only a few species; 91.56% of the seedlings came from 3 shade-intolerant graminoid species occurring in more than 95% of the quadrats: *Bothriochloa pertusa* (L.) A. Camus (50.68%), *Heteropogon contortus* (L.) Beauv. (33.10%) and *Eulaliopsis binata* (Retz.) C. E. Hubb. (7.78%). Seeds of *Bothriochloa pertusa* (L.) A. Camus were the most numerous overall (Table 1). 4 species (*Acacia confusa* Merr., *Eupatorium adenophorum* L., *Datura stramonium* L., *Eucalyptus camaldulensis* Dehn-hardt.) were only sampled in grazing land and 2 species (*Alysicarpus molle* (Willd.) Benth., *Phyllanthus urinaria* L.) were observed in gully, slope and terrace except in grazing land. Most species we found in the aboveground vegetation had almost emerged. Notably absent from the seed bank were shade-tolerant herbs and some semi-shrubs (*Taraxacum mongolicum* Hand.-Mazz., *Stellera chamaejasme* L., *Desmodium podocarpum* ssp. *oxyphyllum* DC.), which are found in a moderately high number in the aboveground vegetation in the hot-dry valley. There was an high proportion (98.53%) of herbaceous species in the seed bank and with the exception of *Albizia mollis* (Wall.) Boiv., we found relatively few tree seeds.

Like the soil seed bank the aboveground vegetation was overrepresented (95.92%) by the 3 graminoid species: *Bothriochloa pertusa* (L.) A. Camus (55.66%), *Heteropogon contortus* (L.) Beauv. (29.86%) and *Eulaliopsis binata* (Retz.) C. E. Hubb. (10.40%). Besides these 3 dominant species, *Cynodon dactylon* (L.) Pers., *Alysicarpus molle* (Willd.) Benth., *Albizia mollis* (Wall.) Boiv. and *Dodonaea viscosa* (L.) Jacq. occurred in all types of vegetation. Of 21 taxa identified in the seed bank, 5 (*Acacia confusa* Merr., *Eupatorium adenophorum* L., *Datura stramonium* L., *Eucalyptus camaldulensis* Dehn-hardt., *Oxalis corniculata* L.) were not found in the vegetation samples of any of the 36 quadrats (Table 2). These 5 alien species are likely to have been blown or carried in from the adjacent modified landscape or from locally disturbed intersection between the abandoned field and the agricultural land. As mentioned above, except for *Oxalis corniculata* L. the other 4 were only observed in grazing land that was most likely exposed to unexpected human and animal intrusions. There was a little higher proportion (99.05%) of herbaceous species in the aboveground vegetation than in the seed bank, which can be attributed to some herbaceous species found in the vegetation that were not

present in the seed bank.

Table 1 Characteristics of soil seed bank (Mean \pm SD, seeds/m²)

Family	Species	Lf	Grazing land	Gully	Slope	Terrace	F	P
	Total number of species		16	13	15	17		
	Total density of seeds		2941.4 \pm 503.6a	4369.1 \pm 929.9b	4942.0 \pm 990.4b	9737.8 \pm 2062.6c	100.696	0.000
Gramineae	<i>Bothriochloa pertusa</i>	P	1535.1 \pm 195.0a	2256.7 \pm 433.9b	2759.3 \pm 558.4b	4594.1 \pm 1172.1c	32.099	0.000
Gramineae	<i>Heteropogon contortus</i>	P	986.2 \pm 151.5a	1269.4 \pm 208.6b	1534.9 \pm 202.5a	3487.8 \pm 387.5b	179.828	0.000
Gramineae	<i>Eulaliopsis binata</i>	P	198.6 \pm 78.7a	431.6 \pm 128.9b	314.2 \pm 93.4b	766.8 \pm 156.3c	38.676	0.000
Gramineae	<i>Cynodon dactylon</i>	P	90.8 \pm 25.6a	197.6 \pm 63.1b	153.1 \pm 41.3b	320.1 \pm 74.3c	28.542	0.000
Gramineae	<i>Eremopogon delavayi</i>	P	—	—	38.2 \pm 16.8a	62.4 \pm 39.1a	2.159	NS
Leguminosae	<i>Vicia sativa</i>	B	33.7 \pm 14.7a	52.9 \pm 25.5a	42.6 \pm 22.4a	58.4 \pm 31.9a	2.424	NS
Leguminosae	<i>Flemingia macrophylla</i>	W	37.8 \pm 11.8a	58.4 \pm 20.2a	39.3 \pm 18.9a	102.2 \pm 57.9a	3.500	NS
Leguminosae	<i>Atylosia mollis</i>	P	—	39.4 \pm 16.5a	20.2 \pm 14.2a	142.8 \pm 64.5a	4.343	NS
Leguminosae	<i>Albizias mollis</i>	W	19.5 \pm 6.8a	10.1 \pm 5.8a	18.1 \pm 12.3a	15.4 \pm 6.9a	0.434	NS
Leguminosae	<i>Acacia confusa</i>	W	3.2 \pm 1.7	—	—	—	—	—
Compositae	<i>Eclipta prostrata</i>	A	—	11.2 \pm 7.3a	—	17.3 \pm 6.9a	3.873	NS
Compositae	<i>Xanthium sibiricum</i>	A	—	—	4.7 \pm 2.8a	5.1 \pm 3.7a	0.327	NS
Compositae	<i>Eupatorium adenophorum</i>	P	1.8 \pm 0.7	—	—	—	—	—
Solanaceae	<i>Solanum xanthocarpum</i>	A	0.9 \pm 0.8a	—	3.8 \pm 1.7a	2.9 \pm 1.5a	2.636	NS
Solanaceae	<i>Datura stramonium</i>	A	0.2 \pm 0.1	—	—	—	—	—
Oxalidaceae	<i>Oxalis corniculata</i>	A	29.5 \pm 13.8ab	19.1 \pm 8.4a	—	123.3 \pm 42.5b	4.798	0.043
Thymelaeaceae	<i>Wikstroemia dolichantha</i>	W	0.4 \pm 0.2a	0.3 \pm 0.2a	0.8 \pm 0.4a	0.7 \pm 0.3a	2.667	NS
Sapindaceae	<i>Dodonaea viscosa</i>	W	3.0 \pm 1.9a	4.2 \pm 2.5a	5.2 \pm 2.8a	4.2 \pm 2.2a	1.821	NS
Euphorbiaceae	<i>Phyllanthus urinaria</i>	A	—	18.2 \pm 9.0a	7.3 \pm 2.3a	34.1 \pm 14.9b	6.901	0.028
Malvaceae	<i>Sida szechuensis</i>	P	0.4 \pm 0.2a	—	0.3 \pm 0.2a	0.2 \pm 0.1a	1.334	NS
Myrtaceae	<i>Eucalyptus camaldulensis</i>	W	0.3 \pm 0.1	—	—	—	—	—

Note: Values are mean \pm standard deviation; Values with different letters mean significant difference ($p < 0.05$); Lf = Life form, NS = Not significant at $p > 0.05$; A: Annual herb B: Biennial herb P: Perennial herb W: Woody species (shrub or tree)

Table 2 Characteristics of aboveground vegetation (Mean \pm SD, plants/m²)

Family	Species	Lf	Grazing land	Gully	Slope	Terrace	F	P
	Total number of species		14	16	18			
	Total density of plants		678.4 \pm 104.5a	981.6 \pm 119.1b	1251.5 \pm 183.1c	1682.0 \pm 292.3d	48.399	0.000
Gramineae	<i>Bothriochloa pertusa</i>	P	369.5 \pm 45.2d	489.1 \pm 44.6b	685.3 \pm 70.1c	879.1 \pm 148.3d	58.309	0.000
Gramineae	<i>Heteropogon contortus</i>	P	214.1 \pm 36.4a	310.5 \pm 32.6b	343.5 \pm 55.1b	431.7 \pm 55.2c	34.363	0.000
Gramineae	<i>Eulaliopsis binata</i>	P	61.8 \pm 12.6a	89.9 \pm 23.8ab	102.8 \pm 30.3c	198.1 \pm 43.9d	35.257	0.000
Gramineae	<i>Cynodon dactylon</i>	P	28.0 \pm 8.8a	55.3 \pm 8.3ab	53.7 \pm 8.3ab	77.8 \pm 21.9b	9.027	0.003
Gramineae	<i>Eremopogon delavayi</i>	P	—	11.5 \pm 2.1a	24.7 \pm 7.0ab	31.5 \pm 6.4b	7.138	0.026
Leguminosae	<i>Vicia sativa</i>	B	—	4.7 \pm 2.5a	14.7 \pm 2.5ab	18.3 \pm 3.4b	19.038	0.000
Leguminosae	<i>Flemingia macrophylla</i>	W	—	6.5 \pm 1.3a	6.0 \pm 1.2a	10.5 \pm 2.9b	7.115	0.012
Leguminosae	<i>Atylosia mollis</i>	P	2.7 \pm 0.6a	9.3 \pm 1.2ab	11.3 \pm 3.8b	23.5 \pm 4.6c	26.626	0.000
Leguminosae	<i>Desmodium podocarpum</i>	W	—	—	1.7 \pm 0.6a	2.5 \pm 0.6a	3.571	NS
Leguminosae	<i>Albizias mollis</i>	W	1.3 \pm 0.5a	1.5 \pm 0.6a	1.8 \pm 0.8a	1.7 \pm 0.9a	0.485	NS
Compositae	<i>Eclipta prostrata</i>	A	—	0.2 \pm 0.4a	—	0.8 \pm 1.1a	1.091	NS
Compositae	<i>Taraxacum mongolicum</i>	P	—	—	0.4 \pm 0.4	—	—	—
Compositae	<i>Xanthium sibiricum</i>	A	—	0.2 \pm 0.2a	0.4 \pm 0.3a	0.3 \pm 0.2a	1.016	NS
Thymelaeaceae	<i>Wikstroemia dolichantha</i>	W	—	0.3 \pm 0.2a	1.5 \pm 0.6a	1.1 \pm 0.5a	1.688	NS
Thymelaeaceae	<i>Stellera chamaejasme</i>	P	—	—	—	0.1 \pm 0.1	—	—
Sapindaceae	<i>Dodonaea viscosa</i>	W	0.9 \pm 0.3a	1.7 \pm 0.6a	2.6 \pm 1.5a	2.1 \pm 0.8a	1.566	NS
Euphorbiaceae	<i>Phyllanthus urinaria</i>	A	—	0.9 \pm 0.7a	0.8 \pm 0.5a	2.3 \pm 1.2b	16.636	0.004
Solanaceae	<i>Solanum xanthocarpum</i>	A	—	—	0.3 \pm 0.1a	0.4 \pm 0.2a	1.838	NS
Malvaceae	<i>Sida szechuensis</i>	P	0.1 \pm 0.1a	—	—	0.2 \pm 0.1a	2.286	NS

3.3 Properties of the soil seed bank and aboveground vegetation

Both the soil seed bank and aboveground vegetation included mostly herbaceous taxa, and Gramineae followed by Leguminosae and Compositae predominated over both seed bank and vegetation. The analysis of variance showed that the differences of density among grazing land, gully, slope, and terrace were significant in the seed bank (Table 1) and aboveground vegetation (Table 2). Density was much higher in terrace than in grazing land in both seed bank samples and in the vegetation quadrats, and Tukey's multiple comparison test showed that the difference of overall density of soil seed bank and aboveground vegetation between terrace and other types was significant.

For the aboveground vegetation as a whole, *Bothriochloa pertusa* (L.) A. Camus had the highest importance value of 193.01. *Heteropogon contortus* (L.) Beauv. was less copious than *Bothriochloa pertusa* (L.) A. Camus with the importance value of 159.99. *Stellera chamaejasme* L., which sporadically occurred in sunny terraces or slope, was at the bottom of the list with the lowest importance value of 2.86. *Desmodium podocarpum* ssp. *oxyphyllum* DC., *Eclipta prostrata* L., *Solanum xanthocarpum* Schrad. et Wendl., *Xanthium sibiricum* Patr., *Taraxacum mongolicum* Hand.-Mazz. and *Sida szechuensis* Matsuda were less important with values under 20 (Table 3).

There were significant differences of biomass among different vegetation types. The biomass of the plants growing in the terrace was the highest, which reflects the remarkable productivity in highly restored sites. This might be related to the favorable heat and water conditions within the terrace where our assistance to facilitate the plants' growth was applied. The biomass in grazing land was the lowest because of the irregularly heavy grazing and mowing. The biomass in slope and gully was intermediate for the insufficiency of heat and water. The biomass of different plants varied greatly even in the same habitat. With more than 70% of the total biomass *Bothriochloa pertusa* (L.) A. Camus and *Heteropogon contortus* (L.) Beauv. dominated the whole vegetation, while other species contributed relatively little biomass to vegetation. The biomass of these two species reached 206.71 g/m² and 147.76 g/m² respectively (Table 4).

Species richness in terrace was the greatest both in the soil seed bank and in aboveground vegetation. Richness also tended to be greater in aboveground vegetation than in the soil seed bank, although not significantly. Similarly, higher richness in plant in the seed bank was linked to a higher one in vegetation. Terrace followed by gully had the highest diversity (H' & PIE) both in the seed bank and in vegetation, while grazing field had the lowest. In seed bank, evenness or relative distribution of individuals among species was greater in terrace and gully. However, in aboveground vegetation the individuals in gully and grazing land had a higher evenness (Table 5).

Table 3 Importance value of all species in aboveground vegetation

Species	RA	RC	RF	IV
<i>Bothriochloa pertusa</i>	52.75	40.26	100	193.01
<i>Heteropogon contortus</i>	28.3	31.69	100	159.99
<i>Eulaliopsis binata</i>	9.85	7.81	88.89	106.55
<i>Cynodon dactylon</i>	4.68	4.62	41.67	50.97
<i>Alylosia mollis</i>	1.02	5.59	41.67	48.28
<i>Albizia mollis</i>	0.14	0.44	47.22	47.80
<i>Dodonaea viscosa</i>	0.16	0.28	38.89	39.33
<i>Flemingia macrophylla</i>	0.5	1.73	36.11	38.34
<i>Vicia sativa</i>	0.82	2.52	27.78	31.12
<i>Eremopogon delavayi</i>	1.46	2.13	25.00	28.59
<i>Phyllanthus urinaria</i>	0.09	0.14	25.00	25.23
<i>Wikstroemia dolichantha</i>	0.06	0.82	22.22	23.10
<i>Desmodium podocarpum</i>	0.09	0.45	19.44	19.98
<i>Eclipta prostrata</i>	0.02	0.24	16.67	16.93
<i>Solanum xanthocarpum</i>	0.02	0.44	13.89	14.53
<i>Xanthium sibiricum</i>	0.02	0.39	11.11	11.52
<i>Taraxacum mongolicum</i>	0.01	0.12	11.11	11.24

Note: RA = Relative abundance, RC = Relative coverage, RF = Relative frequency, IV = Importance value

Table 4 Biomass in aboveground vegetation (g/m²)

Species	Grazing land	Gully	Slope	Terrace	Average
<i>Bothriochloa pertusa</i>	113.06	143.04	266.52	304.22	206.71
<i>Heteropogon contortus</i>	85.53	97.47	165.67	242.39	147.76
<i>Eulaliopsis binata</i>	15.35	20.28	32.55	40.19	27.09
<i>Cynodon dactylon</i>	9.71	14.73	23.02	56.32	25.95
<i>Eremopogon delavayi</i>	—	11.44	18.52	26.21	18.72
<i>Vicia sativa</i>	—	8.14	16.57	27.52	17.41
<i>Alylosia mollis</i>	4.21	8.59	14.28	36.68	15.94
<i>Flemingia macrophylla</i>	—	10.32	7.96	20.87	13.05
<i>Albizia mollis</i>	3.86	6.05	6.92	8.31	6.29
<i>Dodonaea viscosa</i>	1.52	4.53	6.63	7.81	5.12
Other	1.32	5.18	5.46	6.13	4.52
Total	234.56	329.77	564.1	776.65	488.56

Table 5 Species richness, diversity and evenness in soil seed bank and aboveground vegetation (Soil seed bank/Aboveground vegetation)

Type	Species richness (<i>S</i>)	Simpson index (<i>D</i>)	Shannon index (<i>H'</i>)	Hurlbert's <i>PIE</i>	Pielou index (<i>J</i>)
Grazing land	16/8	0.728/0.703	1.156/1.089	0.609/0.595	0.776/0.804
Gully	13/14	0.733/0.752	1.306/1.280	0.637/0.640	0.794/0.810
Slope	15/16	0.688/0.700	1.162/1.274	0.587/0.616	0.737/0.747
Terrace	17/18	0.777/0.727	1.315/1.345	0.641/0.645	0.826/0.770

3.4 Similarity and relationship between the soil seed bank and aboveground vegetation

Similarity between soil seed bank and aboveground vegetation at individual quadrats was high: values of Jaccard's coefficient of community ranged from 0.412 to 0.842 (with a mean of 0.719) and tended to increase when the restorative stage progressed (Table 6: sv). Fluctuating similarities among different types were observed both in vegetation quadrats and in seed bank samples: Similarity among different types of aboveground vegetation varied between 0.412 and 0.790 (Table 6: v) and similarity among different type of seed bank ranged from 0.526 to 0.790 (Table 6: s); The degree of similarity in seed bank was moderately higher than that in vegetation quadrats, which reflects less fluctuation in seed bank in successional process. In general, the similarities were about 0.649 among different types of vegetation in seed bank and aboveground vegetation, revealing a relatively strong similarity in most of the cases.

Regression analysis showed there was moderately strong positive correlation between soil seed bank density and aboveground vegetation density. Quadratic and cubic curves are suitable for describing the relationship between soil seed bank and aboveground vegetation in density (Fig. 2). Our result agreed with that one of the research conducted by O' Connor & Pickett, Zhao *et al.* and Zhao *et al.* during which significant correlation was found, but differed from the Thompson & Grime study during which they found weak correlation between soil seed bank and aboveground vegetation^[4, 21-23].

4 Discussion

4.1 Seed bank and aboveground vegetation similarity

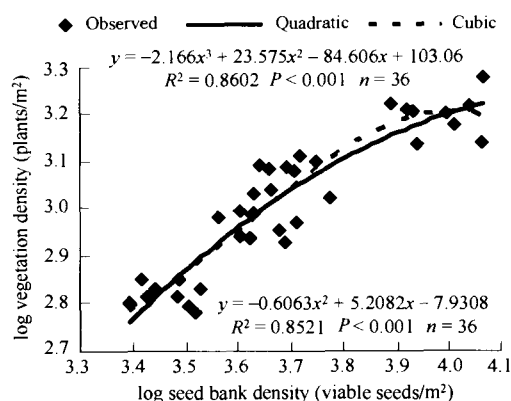
Similarity between soil seed bank and aboveground vegetation has long been a contention for many researchers. Most studies of grasslands predominated by perennial grasses have found few similarities between the seed bank and the vegetation. These discrepancies have been explained by the minor contribution of the dominant perennial meadow species to the formation of seed banks. These species generally have a low seed production because they alternate sexual reproduction with vegetative forms and their seeds have a short-term persistence in the soil^[3]. Moreover, where important seed banks can be found in such perennial grasslands, the soil seed banks often contain large numbers of seeds of annual ruderal species (species 'R' sensu) that reduce the similarity between the vegetation and the seed bank^[24].

In recent years, exceptions to the weak similarities between seed bank and vegetation have been found, with close similarities as in freshwater tidal marshes, in annual

Table 6 Jaccard's similarity coefficient among different types of soil seed bank and aboveground vegetation

Type	Grazing land	Gully	Slope	Terrace
Grazing land	0.412 _{sv}	0.467 _v	0.412 _v	0.444 _v
Gully	0.526 _s	0.800 _{sv}	0.765 _v	0.778 _v
Slope	0.550 _s	0.647 _s	0.823 _{sv}	0.790 _v
Terrace	0.571 _s	0.765 _s	0.790 _s	0.842 _{sv}

v) Similarity among different types of vegetation; s) Similarity among different types of seed bank; sv) Similarity between seed bank and aboveground vegetation of the same type

**Fig. 2** Hypothetical relation between soil seed bank density and aboveground vegetation density

Mediterranean pastures or in a desert short grass community in New Mexico^[25-28]. The common denominator of these disturbed areas is the predominance of annual species that excessively produce seeds during growing season^[29]. Even in tropical forest dominated by wooden species, strong similarities are found^[30]. Although the seed bank has been studied in many types of habitats, its functioning remains rather poorly known^[3].

Unlike most studies of temperate perennial grasslands, we do find a correspondence between the species composition of the seed bank and the aboveground vegetation in this subtropic hillslope grassland. This accordance is much higher in restored sites and tends to increase when the restorative stage progresses. The strong similarity between vegetation and seed bank is attributed to the great proportion of perennial species (mainly *Bothriochloa pertusa* (L.) A. Camus and *Heteropogon contortus* (L.) Beauv.) that are present in the vegetation and whose seeds have a significant viability in the ground in relation to the strategies of opportunistic species. Although these species are perennial yet they almost promote sexual reproduction compared to the vegetative way and have a considerably high seed production as well as vegetative growth, as could greatly contribute to increasing this similarity. At the same time we also find factors that tend to cause the dissimilarity between vegetation and seed bank: factors particularly contributable to the dissimilarity between vegetation and seed bank could be caused by species, which are only present in the vegetation but absent in the seed bank (described as the disporum type, i.e., species that show no evidence of forming a seed bank, sensu Thompson)^[5]. In addition, some wooden species identified as having a persistent seed bank do not always emerge in the seed bank. The results show these species were identified only once or twice in the seed bank. It is thus inherently difficult to detect these rare species in the seed bank. Although these factors incline to decrease the similarity between soil seed bank and aboveground vegetation to a certain extent, the predominance of seed-profusive perennial largely offsets such inclination.

4.2 Comparison between restored and unrestored sites in seed bank and aboveground vegetation

The structure and composition of the seed bank and aboveground vegetation in grazing land (unrestored plots) is oversimplistic with low density, biomass, species richness, species diversity and evenness. This is inseparably related to the hot and dry climate providing harsh growing conditions for plants and critical constraints (such as lack of water supply) to vegetation establishment and can be partly attributed to the relative lack of abundance in seed bank. Lack of seed bank in these unrestored plots may be a result of the combined effect of erosion, foraging animals and wind. However, compared to grazing land, the reclaimed site (including slope, gully and terrace) represents relatively high density, biomass, species richness, species diversity and evenness in the seed bank and aboveground vegetation. This is inextricably related to the sufficiency of heat and water supplies for species establishment and growing in the restored site, which partly reflects our effective efforts on the hillslope grassland restoration.

We believe that our micro-catchment's water harvesting system initiated in 1998 has provided a favorable habitat for species to establish and grow by reducing erosion, providing sufficient water supply and improving edaphic conditions. Moreover it alters microhabitat conditions of the site and litter accumulation promotes germination and seedling survival that leads to the establishment of alien species. Evidence for this is the number and diversity of grass and shrubs species that have volunteered onto the reclaimed site since the original foundation of the system.

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