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SOIL SEED BANK AND ITS RELATIONSHIP TO THE ABOVE-GROUND VEGETATION IN GRAZED AND UNGRAZED OXBOW WETLANDS OF THE YANGTZE RIVER, CHINA

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Abstract

Livestock grazing may have a great effect on both standing vegetation and soil seed bank. The present study investigated the characteristics of the soil seed bank and determined its relationship to the above-ground vegetation in grazed and ungrazed sites in the Hei-wa-wu oxbow wetland of the Yangtze River, China. A total of 3700 seedlings across 59 species germinated from the soil seed bank. Annuals and terrestrial species dominated the soil seed banks of both grazed and ungrazed sites. Grazing had no significant effect on the seed density and species richness, but altered the species composition of soil seed bank. Grazing tended to increase the floristic similarity between the soil seed bank and the above-ground vegetation. DCA ordination produced a clear separation of the soil seed bank and above-ground vegetation. Our results suggest that soil seed bank and its relation to standing vegetation in the Hei-wa-wu oxbow wetland are strongly influenced by livestock grazing.

Key words: flooding, human disturbance, vegetation, Yangtze River

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1. Introduction

In temporary wetlands, plant species must have life cycle stages that ensure survival between the alternate wet and dry phases (Brock, 2011; MacGillivray and Grime, 1995; Van Der Valk, 2005). Seed banks are part of the life cycle (Harper, 1977) and provide a mechanism for regeneration of plant communities after natural or human disturbance, such as seasonal flooding, drought, prolonged inundation or grazing (Brock et al., 1994). Survival as vegetative propagules during prolonged disturbance is not feasible for the majority of wetland species. Therefore the soil seed bank may play a vital role in vegetation establishment after disturbance (Liu et al., 2009; Nicol et al., 2007; Thompson, 2000).

The tendency of domestic livestock to congregate around water has meant that wetlands and riparian zones are often more heavily affected by grazing than adjacent terrestrial systems (Jansen and Robertson, 2001; Nicol et al., 2007). Domestic livestock such as cattle, sheep, goats, and horses are found to change the floristic composition of above-ground vegetation in freshwater and riparian systems by selective grazing and trampling (Jansen and Robertson, 2001). Grazing has been shown to affect plant community structure (Blanch and Brock, 1994), survival of species (Mulder and Ruess, 1998), plant

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growth rates (Moon et al., 2013; Zimmerman et al., 1996), resource allocation (Ehrlen, 1995), and the species composition of soil seed banks (Crossle and Brock, 2002; Osem et al., 2006; Tessema et al., 2012).

Grazing by domestic livestock may have various effects on the density and composition of soil seed banks in riparian or freshwater systems. For instance, studies have shown that seed density was reduced (Barnewitz et al., 2012; Erkkila, 1998; Granstrom, 1988; McDonald et al., 1996; Vlad and Toma, 2017), hardly affected (Loydi et al., 2012; Ortega et al., 1997) or even increased (Levine et al., 2012; Russi et al., 1992) by grazing. Variation in patterns of seed bank response to grazing can be attributed to differences among the studied ecosystems in environmental conditions, grazing regimes and type of herbivore, as well as in vegetation composition and species traits (Osem et al., 2006). The interaction of grazing and water regime on soil seed bank has not been widely studied especially in riparian or freshwater systems (Crossle and Brock, 2002; Erkkila, 1998; Nicol et al., 2007). Understanding the effects of grazing on the soil seed bank is of critical importance for conservation and grazing management.

The middle to lower reaches of the Yangtze River is the largest floodplain in China (Li et al., 2002). Many wetlands are distributed across this vast area, and almost all are directly or indirectly connected to the river (Li et al., 2008). The pattern of drawdown and flooding in these wetlands is predictable, due to seasonal rainfall (Liu et al., 2006a). The wetlands are often grazed by cattle or sheep during drawdown, as they are close to residential areas. Our previous studies have shown this area to have a large and persistent seed bank (Liu et al., 2005). However, the effect of grazing by domestic livestock on the soil seed bank and its relation to the above-ground vegetation has not been studied. Water level fluctuations and grazing on the wetlands offer an opportunity to study the effect of disturbances on soil seed banks.

This study investigated the soil seed bank and its relation to the above-ground vegetation of grazed and ungrazed oxbow wetlands of the Yangtze River, China. Our aims were to test the following hypotheses: (1) grazing by domestic livestock during dry phases will reduce seed density, species richness and change the floristic composition of the seed bank; (2) grazing will decrease the similarity between the soil seed bank and above-ground vegetation.

2. Material and methods

2.1. Study sites

This study was carried out in Hei-wa-wu oxbow wetland (29°45′–29°48′ N, 112°41′–112°46′ E) Shishou, China (Fig. 1), the most well-preserved floodplain wetland in the middle Yangtze River (Hao et al., 2004). The oxbow was cut off from the main course of the Yangtze River by purely man-made factors in 1968. It is connected to the Yangtze River during flooding (May to September) and remains intact as a riparian wetland in the dry season. The length of Hei-wa-wu oxbow is about 30 km. The climate in this region is subtropical monsoon with a mean air temperature of 3.4°C in January and 28.5°C in July. Mean annual precipitation is approximately 1153 mm, and 80% of the total rainfall concentrates in the rainy season from May to October (Wu et al., 2006). The soil is a sandy clay loam with organic matter content of 1.75% and pH of 7.3. Clonal perennials (e.g., *Carex cinerascens*, *Hemarthria altissima*, and *Cynodon dactylon*) dominate the vast area and seed germination is mainly restricted by flooding.

The grazed and ungrazed sites were along the oxbow (Fig. 1) and their geomorphology, elevation (32–34 m above sea level), distance from the water (10–30 m) and slope (less than 5%) were similar. The grazed sites lie near populated areas and have been continuously grazed by domestic livestock such as cattle, sheep and horses since the 1970s. Grazing intensity during the time of the study (April 2009) was approximately 16–45 livestock per ha. Ungrazed sites were those where livestock grazing was typically excluded all year.

2.2. Seed bank sampling and germination

Soil seed banks were sampled at the beginning of April 2009, before the spring germination season in the field. Two grazed and ungrazed transects parallel to the flow direction were established along the Hei-wa-wu oxbow wetland, respectively (Fig. 1). Five 1×1 m plots were systematically placed along each transect. Each plot was generally separated by a minimum distance of 300 m from neighbouring plot (Fig. 1). After thoroughly removing the plant material from the soil surface, five soil cores of 10 cm depth were taken with an iron cylinder (diameter 8 cm) in each plot. The cores of each plot were then combined (TerHeerdt et al., 1996). A total of 100 soil cores were sampled. The total surface area represented by the soil cores was 0.503 m^2 (0.025 m^2 per plot).

Methods for seedling emergence followed van der Valk and Davis (1978). Visible tubers, turions, roots, rhizomes and litter were removed carefully after washing the sediment. Each sample was wet-sieved (0.2 mm) and the retained material was spread in a layer (<1 cm deep) over 10 cm of sand in plastic trays (diameter 30 cm). The sand had previously been dried for 24 h at 75ºC to kill any weed propagules. All trays were randomly arranged in an unheated greenhouse at the Wuhan Botanical Garden (30°32′82″ N, 114°25′18″ E) and were watered twice a week with tap water (Reiné et al., 2004). The climate in Wuhan is similar to that in Hei-wa-wu oxbow wetland. Seedlings were counted weekly and were removed as soon as they could be identified.

Seedlings that could not be identified were transplanted to empty trays and allowed to grow until they could be identified. Seedling emergence started in early May, reached a peak in mid-June, and ended in early September of 2009.

Germination was recorded until there had been no further germination for more than 1 month. Non-germinated seeds were considered to be dead or non-viable. Nomenclature followed the Flora of China (Wu and Peter, 2013).

2.3. Vegetation survey

In April 2009, 10 quadrats (50 cm × 50 cm) were established in the grazed and ungrazed sites, respectively. Within each quadrat, density and coverage of each species were recorded. Plant density was measured by directly counting the number of stems at a height of about 20 cm for ungrazed sites and 10 cm for grazed sites (Guan et al., 2013). Vegetation cover was visually determined in each quadrat by a 50 cm × 50 cm frame that was divided into 100 cells (5 cm × 5 cm).

2.4. Data analysis

Seed density was calculated as the density of seedlings per m^2 of a sample. Species were classified into different functional groups according to their life form and longevity (Liu et al. 2009). The percentage of annual and perennial species in each habitat (grazed and ungrazed) was determined. Prior to statistical analyses, data were transformed ($\log(x + 1)$) to improve the normality of the distribution. The differences in seed density and species richness between grazed and ungrazed samples in seed bank were compared by the t-test using SPSS 19.0 (IBM Corporation, Armonk, New York). To compare the species composition between the seed bank and the above-ground vegetation, Sørensen similarity index (S) was used on the total number of species present in the vegetation and seed bank of grazed and ungrazed sites (Eq. 1):

$$S = 2c/(a + b) \quad (1)$$

where: a= number of species in seed bank, b= number of species in vegetation and c= number of species common in both seed bank and vegetation.

We used permutation-based multivariate analysis of variance (PERMANOVA) to assess the effect of grazing on floristic composition of the seed bank using Bray–Curtis dissimilarities (McCune and Grace, 2002). The statistical significance of F values was tested with a randomization procedure with 4,999 runs. We further used indicator species analysis (ISA) to identify species that consistently differed in their seed density between grazed and ungrazed samples (Dufrene and Legendre, 1997). To compare the species composition in the above-ground vegetation and soil seed bank samples (grazed and ungrazed quadrats), a Detrended Correspondence Analysis (DCA) was conducted using species importance values (Hill and Gauch, 1980). Importance values of each species in the seed bank were calculated by averaging relative density and relative frequency, while importance values of above-ground vegetation were calculated by averaging relative density, relative coverage and relative frequency. PERMANOVA, ISA and DCA were performed using PC-ORD 5.0 (McCune and Mefford, 1999).

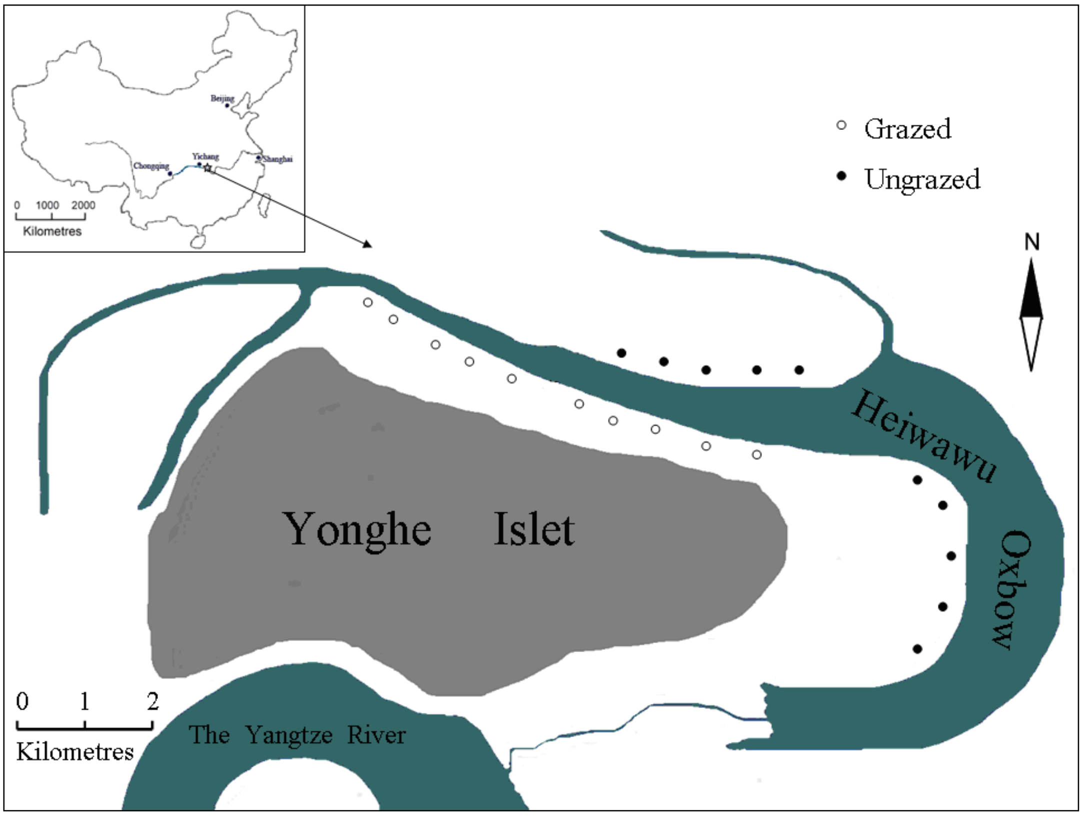

Fig. 1. Map of Hei-wa-wu oxbow wetland showing the grazed and ungrazed plots

3. Results and discussion

3.1. Soil seed bank size and composition

A total of 59 plant species, belonging to 19 families, were recorded in the soil seed bank from grazed and ungrazed plots (Table 1). The observed seed densities in this study (7361 ± 2170 seedlings/m^2) were in the range of those observed in temporary wetlands from the middle to lower reaches of the Yangtze River. For example, 1227–10115 seedlings/m^2 from the lakeshore of Honghu, Longgan and Liangzi Lake have been reported (Li et al., 2008; Liu et al., 2006a; Yuan et al., 2007). However, the species richness found in this study was higher than that found in similar studies in the Yangtze River Basin. For example, 34, 22, and 31 species were recorded in the seed banks of Honghu, Longgan and Liangzi Lakes, respectively (Li et al., 2008; Liu et al., 2006a; Yuan et al., 2007).

The large number of species may be explained by the open nature of the oxbow into which seeds may disperse via wind, water and animals. The oxbow acts as a sink for seeds transported from the upstream of the river during flooding periods. Many wetland plants produce large numbers of seeds, which never have a chance to germinate due to water level fluctuation. The presence of a large and species-rich soil seed bank in the wetland will buffer vegetation change in the short term, although not in the long term (Hulme, 1996).

Annual species accounted for 66% (39 species) of species recorded in the seed banks (Table 1). The most abundant annual species was *Mazus japonicus* which accounted for 22% of total seed density in grazed sites. Consistent with previous studies (Liu et al., 2009; Yuan et al., 2007), annuals dominated the seed banks even though the predominant aboveground plant cover is characterized by perennial species in the oxbow wetland.

The low frequency of seeds of the dominant perennials indicates that many perennials commonly found in the oxbow wetland do not produce a persistent seed bank (Hartman, 1988; Hutchings and Russell, 1989). This was also found in the studies of Ungar and Woodell (1996) in coastal salt wetlands. Research has shown that plant communities are structured predominantly by water regimes and are generally dominated by flood-tolerant species and annuals that can complete their life cycles between the alternate wet and dry phases (Liu et al., 2006b). Annuals show adaptive responses to the seasonal flooding by producing dormant seeds that persist during periods of drought or long-term flooding (Parlak et al., 2011).

Moreover, the Hei-wa-wu oxbow wetland is frequently inundated by floods during spring and summer. Previous work indicated that annuals increased the number of flowers and biomass allocated to seed reproduction with increased duration of inundation (Mony et al., 2010).

3.2. Effect of grazing on size and composition of the seed bank

Although more than double the size, the soil seed bank density of the ungrazed plots (10309 ± 13273 seedlings/m^2) was not significantly greater (P = 0.196) than grazed plots (4413 ± 1829 seedlings/m^2; Table 1). This result may be due to the huge variability in seed bank size among plots. At the local scale, soil seed density can be influenced by many factors, including plant community types and soil physical properties (Csontos, 2007). Similarly, there were not significant differences (P = 0.389) in mean species richness of ungrazed (13.2 ± 6.6) versus grazed (15.4 ± 4.3) plots. The percentages of annuals in the grazed and ungrazed samples were 67% and 60%, respectively. Moreover, over 95% of the species recorded in the grazed samples were terrestrial species, compared with 84% in the ungrazed samples.

The size of the seed bank of several species, e.g. *Carex cinerascens*, *Cyperus michelianus*, *Ranunculus sceleratus* and *Veronica anagallis-aquatica*, was significantly reduced by grazing. These species accounted for 60% of total seed density in the ungrazed samples but only accounted for 9% of total seed density in the grazed samples. The reason for the larger soil seed bank in the ungrazed sites is that livestock intake and trampling may have reduced seed production of this species in grazed sites. Furthermore, taller vegetation collects more sediment and litter including seeds compared to the shorter vegetation in the grazed sites (Erkkila, 1998). In our study, water- and wind-dispersed seeds dominated the seed bank. These seeds can accumulate in local depressions, on the edge of tussocks etc. (Jerling, 1983). Osem et al. (2006) showed that grazing by domestic livestock may have various effects on the density and composition of seed banks. Variation in patterns of seed bank response to grazing can be attributed to differences among the studied ecosystems in environmental conditions, grazing regimes and type of domestic livestock, as well as in vegetation composition and species traits (Osem et al., 2006). Our results suggest that continuous grazing has a moderate effect on soil seed bank density of riverine wetlands.

The 28 species common to the grazed and ungrazed samples (Table 1) accounted for 96 % of total seed density in both grazed and ungrazed plots. However, PERMANOVA indicated that there was a significant difference in seed bank composition between the grazed and ungrazed plots (F = 3.13587; P = 0.0004). Indicator species analysis further indicated that this difference driven by five species (Table 2). Grazing by domestic livestock changed the species composition of the seed banks in the oxbow wetland. Most of the aquatic plants, e.g. *Hydrilla verticillata*, *Myriophyllum verticillatum*, *Nymphoides peltatum*, *Scirpus triqueter* and *Typha orientalis*, were eliminated from the grazed samples, probably because livestock grazing limited the recruitment of seeds into the soil seed bank.

Table 1. Life form, longevity, absolute seed density (mean± SD), relative seed density (%), and species richness in the seed bank of grazed and ungrazed sites

Species	Life form	Longevity	Grazed		Ungrazed	
			Absolute density (n/m^2)	Relative density (%)	Absolute density (n/m^2)	Relative density (%)
Alopecurus aequalis	Ter	A	115 ± 58	2.6	36 ± 19	1.3
Artemisia annua	Ter	A			36 ± 36	0.6
Artemisia selengensis	Ter	P	4 ± 4	0.4		
Arthraxon hispidus	Ter	A			12 ± 8	0.8
Astragalus sinicus	Ter	A			4 ± 4	0.4
Beckmannia syzigachne	Ter	A			36 ± 28	0.9
Bothriospermum tenellum	Ter	A	44 ± 33	1.1		
Capsella bursa-pastoris	Ter	A			72 ± 72	0.7
Cardamine hirsute	Ter	A	44 ± 27	1.8	52 ± 47	1.0
Cardamine lyrata	Ter	A			115 ± 67	1.7
Carex argyi	Ter	P	12 ± 8	0.8	12 ± 8	0.8
Carex dimorpholepis	Ter	P	4 ± 4	0.4	48 ± 48	0.6
Carex unisexualisa	Ter	P	247 ± 76	5.7	123 ± 83	2.1
Carex cinerascens	Ter	P	12 ± 8	0.8	1977 ± 1041	11.5
Centella asiatica	Ter	A	4 ± 4	0.4		
Chenopodium album	Ter	A	4 ± 4	0.4		
Cnidium monnieri	Ter	A	48 ± 19	2.5	203 ± 172	3.6
Conyza canadensis	Ter	A	8 ± 5	0.7	4 ± 4	0.4
Cynodon dactylon	Ter	P	143 ± 86	3.2	28 ± 28	0.5
Cyperus michelianus	Ter	A	16 ± 16	0.5	2427 ± 2423	12.5
Digitaria ciliaris	Ter	A			32 ± 32	0.5
Echinochloa crusgali var. mitis	Ter	A	8 ± 8	0.4	4 ± 4	0.4
Eleusine indica	Ter	A			12 ± 12	0.4
Fimbristylis dichotoma	Ter	A	8 ± 8	0.4		
Gnaphalium affine	Ter	A	159 ± 55	4.1	48 ± 40	1.0
Heleocharis valleculosa f. setosa	Ter	P	215 ± 116	5.4	207 ± 107	3.3
Hemarthria altissima	Ter	P	4 ± 4	0.4		
Hemistepta lyrata	Ter	A	8 ± 5	0.7		
Hydrilla verticillata	S	P			32 ± 32	0.5
Lindernia antipoda	Ter	A			36 ± 22	1.3
Lindernia crustacea	Ter	A	8 ± 8	0.4		
Mazus japonicus	Ter	A	975 ± 298	14.3	1631 ± 1255	10.9
Medicago sativa	Ter	P	48 ± 20	2.2	16 ± 9	1.2
Myriophyllum verticillatum	S	P			4 ± 4	0.4
Nymphoides peltatum	R	P			12 ± 12	0.4
Oenanthe javanica	Ter	P	8 ± 5	0.7		
Paspalum thunbergii	Ter	P			12 ± 12	0.4
Poa annua	Ter	A	318 ± 254	4.6	64 ± 51	1.4
Polygonum hydropiper	T	A	40 ± 21	1.7	12 ± 8	0.8
Polygonum plebeium	Ter	A	99 ± 32	3.1	92 ± 58	2.3
Polypogon fugax	Ter	A	517 ± 110	8.8	330 ± 189	3.9
Potamogeton malaianus	S	P	40 ± 40	0.8	44 ± 44	0.6
Potentilla supine	Ter	A	155 ± 49	4.4	322 ± 296	3.1
Ranunculus chinensis	Ter	A			4 ± 4	0.4
Ranunculus sceleratus	Ter	A	107 ± 46	3.5	943 ± 459	6.8
Rorippa cantoniensis	Ter	A	390 ± 209	6.4	203 ± 59	4.0
Rorippa globosa	Ter	A	24 ± 14	1.2		
Rumex dentatus	Ter	A	8 ± 8	0.4	72 ± 30	3.4
Salvia plebeian	Ter	A	16 ± 9	1.2	4 ± 4	0.4
Scirpus triqueter	T	P			8 ± 8	0.4
Scirpus wallichii	Ter	P	8 ± 8	0.4	16 ± 16	0.5
Stellaria media	Ter	A	4 ± 4	0.4		
Torilis scabra	Ter	A	4 ± 4	0.4		
Triarrhena lutarioriparia	Ter	P			12 ± 8	0.8
Typha orientalis	T	P			20 ± 9	1.6
Veronica anagallis-aquatica	Ter	P	259 ± 194	4.9	796 ± 593	6.5
Veronica peregrina	Ter	A	235 ± 94	5.6	139 ± 53	2.6
Youngia heterophylla	Ter	A	4 ± 4	0.4		
Youngia japonica	Ter	A	40 ± 19	1.7		
Total density			4413 ±1829	100	10309 ±13273	100
Species richness			42		45	

A = annual; P = perennial; R= amphibious-responders; S= submerged species; T= amphibious-tolerators; Ter= terrestrial species.

Table 2. Significant indicator species for the grazed and ungrazed soil seed bank community. To be significant, species had to have an indicator value of ≥25 and a P value ≤0.05

Plant species	*Treatment*	*Indicator value*	*P value*
Carex unisexualisa	Grazed	69.0	0.0066
Gnaphalium affine	Grazed	61.9	0.0082
Polypogon fugax	Grazed	61.4	0.0406
Rumex dentatus	Ungrazed	73.1	0.0016
Carex cinerascens	Ungrazed	48.4	0.0444

C. cinerascens, *R. sceleratus* and *V. anagallisaquatica* were reduced by grazing both in the seed bank and in the vegetation. Selective grazing and trampling in freshwater and riparian systems gives less palatable species a competitive advantage (Lodge, 1991; Nicol et al., 2007). Grazing is known to increase the number of gaps in the vegetation and may be responsible for an increase in the cover of annuals (Ungar and Woodell, 1996). *Polypogon fugax*, *Rorippa cantoniensis*, and *Poa annua* benefited from grazing (Table 1). These species were dominant in grazed samples (28%) but rare in the ungrazed samples (6%). Grazing increases the number of ruderal species, such as these (Jutila, 2003). Through selective grazing, livestock can reduce or eliminate the palatable species from the seed bank but increase the seed density of the unpalatable species in a managed ephemeral wetland (Nicol et al., 2007).

3.3. Effect of grazing on the similarity between the soil seed bank and above-ground vegetation

A total of 44 species were recorded in the above-ground vegetation (Table 3). Sørensen's coefficient of similarity between soil seed bank and above-ground vegetation showed that the grazed samples had a higher similarity value (0.62) than the ungrazed samples (0.47). Many terrestrial annuals in the seed bank of ungrazed samples, such as *Polypogon fugax, Rorippa cantoniensis, Cnidium monnieri, and Cyperus michelianus* were not found in above-ground vegetation. Different responses of species to grazing have been found previously depending on environmental conditions and whether the vegation is dominated by annual or perennial communities (Bakker and Vries, 1992; Chaideftou et al., 2009; Erkkila, 1998; Peco et al., 1998; Ungar and Woodell, 1996).

In general, there are high similarities in annual-dominated vegetation, but low similarities in most perennial-dominated communities (Osem et al., 2006). In the oxbow wetland, grazing can increase the number of gaps in the vegetation and promote germination of species that are inhibited by dense sediment or plant cover (Peco et al., 1998; Ungar and Woodell, 1996).

The first two DCA axes accounted for 28% of the total variance in species composition among soil seed bank and above-ground vegetation. The distribution of above-ground vegetation samples was more dispersed than that of the seed bank samples (Fig. 2). This indicates greater heterogeneity in species composition in the above-ground vegetation than in the seed bank. The first axis of the DCA separated grazed vegetation samples from ungrazed vegetation samples, while the second axis showed a clear separation of the seed bank and above-ground vegetation (Fig. 2). These results reflect the minor contribution of the dominant species to the seed bank (Chang et al., 2001; Xiao et al., 2010). *Phalaris arundinacea*, which was characteristic of the oxbow wetland vegetation, was not found in the seed bank.

Table 3. List of species found in the above-ground vegetation of grazed and ungrazed sites

Species	*Grazed sites*	*Ungrazed sites*
Alopecurus aequalis	√	√
Alopecurus japonicus	√	√
Artemisia annua		√
Artemisia selengensis	√	
Astragalus sinicus	√	
Beckmannia syzigachne		√
Cardamine hirsuta		√
Cardamine lyrata		√
Carex argyi	√	
Carex unisexualis	√	
Carex cinerascens	√	√
Centella asiatica	√	
Centipeda minima		√
Cnidium monnieri	√	
Cynodon dactylon	√	
Cyperus rotundus	√	
Echinochloa crusgali var. mitis	√	
Euphorbia helioscopia	√	
Geranium wilfordii	√	
Gnaphalium affine	√	
Heleocharis valleculosa f. setosa	√	√
Hemarthria altissima	√	
Hemistepta lyrata		√
Kalimeris indica	√	
Lindernia antipoda	√	
Mazus japonicus	√	√
Medicago lupulina	√	
Medicago sativa	√	
Myriophyllum verticillatum		√
Phalaris arundinacea	√	√
Poa annua	√	
Polygonum hydropiper	√	√
Polygonum plebeium	√	
Polypogon fugax	√	
Potentilla supina		√
Ranunculus chinensis	√	
Ranunculus sceleratus	√	√
Rumex dentatus		√
Salvia plebeia	√	
Scirpus wallichii	√	
Trigonotis peduncularis	√	
Veronica anagallisaquatica	√	√
Veronica peregrina	√	√
Youngia heterophylla	√	

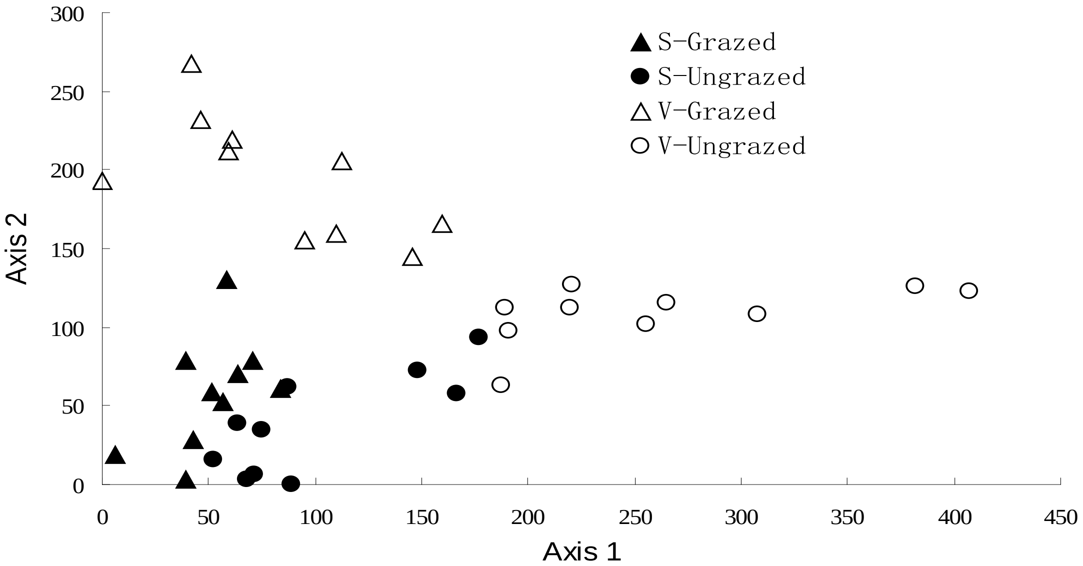

Fig. 2. Detrended Correspondence Analysis (DCA) ordination of seed bank and above-ground vegetation samples (S= seed bank; V= above-ground vegetation)

Carex cinerascens, *Carex argyi*, and *Heleocharis valleculosa* were frequently found in the above-ground vegetation, but they only accounted for 16 % of the total seed density.

The reason may be that these species have a limited seed production because they alternate between sexual reproduction and vegetative forms and their seeds persist in the soil for short periods of time (Boedeltje et al., 2003; Thompson, 2000; Touzard et al., 2002). In contrast, *M. japonicus*, *P. fugax*, and *C. michelianus* accounted for 40% of the total seed density, possibly due to a production of large numbers of small seeds. It is commonly believed that small-seeded species usually form more abundant seed banks than large-seeded species (Honda, 2008; Thompson et al., 2001).

4. Conclusions

In the Hei-wa-wu oxbow wetland of the Yangtze River, grazing by domestic livestock during dry phases does not significantly impact the seed density and species richness of the soil seed bank. However, grazing changes the species composition of both soil seed bank and standing vegetation. Moreover, the similarity between the soil seed bank and the above-ground vegetation in grazed samples was higher than that in ungrazed samples. We suggest that current grazing practices in the Hei-wa-wu oxbow wetland have moderate effects on the soil seed bank. Reduced grazing intensity or rotational grazing can increase the seed density of several annual species (e.g., *Cyperus michelianus* and *Ranunculus sceleratus*) in soils and may thus promote the development of above-ground vegetation in the Hei-wa-wu oxbow wetland.

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