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Regenerative Role of Soil Seed Banks of Different Successional Stages in A Saline-alkaline Grassland in Northeast China

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Abstract: Soil seed banks can act as a potential seed source for natural revegetation and restoration. However, in a saline-alkaline grassland, it remains unclear how the stages of vegetation succession affect the characteristics of soil seed banks and the potential of soil seed banks of different successional stages for vegetation restoration. In this study, seasonal changes of the soil seed bank, and seed production and dispersal dynamics along degradation successional gradients were investigated in a saline-alkaline grassland in Northeast China, where the dominant grass during the 1960s, *Leymus chinensis* was replaced with the secondary successional order of *Puccinellia chinampoensis*, *Chloris virgata*, and *Suaeda salsa*, together with bare patches. It was found that the soil seed bank composition varied according to the changing vegetation and had the highest species richness (7–16) in the climax successional stage, but had a low Sørensen similarity (0.22–0.37) with the aboveground vegetation. There was a high seed density of the soil seed bank (21 062–62 166/m^2 in August and December) and also high Sørensen similarity index values (0.47–0.60) in the secondary successional stages of *P. chinampoensis*, *C. virgata*, and *S. salsa*. In bare patches, there were many seeds in the soil seed bank and some seedlings also appeared in the aboveground vegetation, indicating the existence of a persistent soil seed bank. Seed density and species richness differed substantially among the different successional stages, which was related to the reproductive characteristics of the standing plants in vegetation communities. Due to the lack of propagules of perennial species, especially the climax species of *L. chinensis*, in the soil, the successful restoration of the degraded saline-alkaline grassland was not possible. The study proved that in a degraded saline-alkaline grassland dominated by biennial or annual species, the soil seed bank was important for the revegetation of the current dominant plants, but not for the restoration of the original target species. Therefore, it is necessary to induce seeds or other propagules of the target perennial species.

Keywords: soil seed bank; seed dispersal; ecological restoration; phenology; succession; seed rain

1 Introduction

As a consequence of the intensification of human activi-

ties and global climate change, large areas of grassland have been degraded throughout the world, especially since the middle of the 20th century (Matus et al., 2005;

Zhan et al., 2007; Wang G D, 2013). Soil salinity affects 7% of the earth's land surface and contributes to the problem of land degradation (Panta et al., 2014). Restoration of these degraded ecosystems is a significant challenge for ecologists (Krauss et al., 2010).

The soil seed bank is the stock of mature viable seeds existing on the soil surface or within the soil (Walck et al., 2005; Martins and Engel, 2007). It can serve as a potential seed source for natural revegetation and restoration (Bakker et al., 1996; Shaukat and Siddiqui, 2004; Hopfensperger, 2007) and is one of the key factors affecting the resilience of ecosystems (Falahati-Anbaran et al., 2011; Ooi et al., 2012; Ge et al., 2013). The soil seed bank is also important in the long-term survival of individual species, as well as plant communities. An understanding of the dynamics and functioning of soil seed banks is critical to determine the role of communities and improve the integrated management of ecosystems (Luzuriaga et al., 2005).

The stage of vegetation succession is an important factor affecting the characteristics of the soil seed bank (Bekker et al., 2000; Figueroa et al., 2004; González-rivas et al., 2009; Erfanzadeh et al., 2010), and the relationships between soil seed banks and the successional series has been studied in many ecosystems, such as forests (Bossuyt and Hermy, 2001; Esmailzadeh et al., 2011; Asadi et al., 2012), wetlands (Ge et al., 2013), inland dune grasslands (Matus et al., 2005; Li et al., 2012), alluvial grasslands (Schmiede et al., 2009), and arable fields (Bai et al., 2010; Wang N, 2013). Species number and seed bank size display different trends along the successional stage, e.g., an increase with the successional stages in dune slacks with increasing seed production (Bekker et al., 2000; Bossuyt and Hermy, 2001), but a decline in fallow land (Falinska, 1999) and salt marshes (Erfanzadeh et al., 2010).

Soil seed banks have a strong regenerative potential in many ecosystems (Baskin and Baskin, 2014). The similarity between the soil seed bank and above-ground vegetation could influence the potential recovery if the standing vegetation was destroyed. However, for the restoration of degraded ecosystems, the main aim is usually to restore the climax species. Bossuyt and Hermy (2001) concluded that if the forest in temperate European forests is destroyed it cannot regenerate from the soil seed bank due to the absence of tree species seeds. The potential vegetation restoration from the soil

seed bank is limited in abandoned cropland (Bai et al., 2010). However, in calcareous grassland (Fagan et al., 2010) or marsh soil (Erfanzadeh et al., 2010; Bai et al., 2014), the soil seed banks contain seeds of many of the early successional species.

The dynamics of a soil seed bank include recruitment into the dormant seed bank population through seed dispersal, loss from the dormant seed bank through seed predation or death, and the formation of a seedling bank through germination and emergence (Walck et al., 2005; Luo and Wang, 2006; Zhang and Chu, 2013). Seed dispersal links the end of the reproductive cycle of adult plants with the establishment of their offspring, and has profound effects on vegetation structure (Du et al., 2007). Only a few studies have analyzed the relationship between the seed bank and the seed rain in the formation of plant communities (Kalamees and Zobel, 2002; Luzuriaga et al., 2005; Aguado et al., 2012). Confirming and quantifying such effects, however, has proven to be a challenge.

Successional changes may cause large differences between the soil seed bank and the aboveground floristic composition (Thompson et al., 1993). There are two main pathways for a seed bank assembly process, with the assembly either mainly composed of early successional species during the whole successional range, or varying according to the changing vegetation (Bossuyt and Hermy, 2001). However, the characteristics of the soil seed bank in saline-alkaline grasslands still remain unclear.

The Songnen Plain in Northeast China was selected as a research area and a chronosequence approach was used to simulate the different successional stages in a saline-alkaline grassland. The Songnen Plain is part of the Euro-Asia steppe, which is dominated by the perennial grass *Leymus chinensis* (Poaceae) and is one of the most important grazing and mowing pastures in China. The chronosequence method is an important and often necessary tool for studying the temporal dynamics of plant communities and soil development across multiple time-scales. The Songnen Plain used to be dominated by *L. chinensis*, which accounted for over 80% of the vegetation cover (Liu, 2001). However, due to human interference, the grassland has become saline-alkaline and most of the original *L. chinensis* grassland has been degraded to some extent, i.e., light, medium, and serious degradation (Liu, 2001; Yang et al., 2010). Under light

degradation conditions, the aboveground vegetation is dominated by *Puccinellia chinampoensis*, a biennial grass (Poaceae), accompanied by *Cleistogenes squarrosa*, *Poa sphondylode*, and *Carex korshinskyi*. Under medium degradation conditions, the original vegetation cover has been replaced by the annual grass *Chloris virgata*, accompanied by *Tripolium vulgare* and *Salasola collina*. In seriously degraded grassland, the aboveground vegetation has been replaced by annual species of *Suaeda salsa* (Chenopodiaceae) (Deng et al., 2006). As degradation has progressed further, large patches of bare land where no plants can grow have appeared. Therefore, with increasing saline-sodic degradation (from light to serious conditions), secondary succession communities have appeared in the sere that consist of *L. chinensis*, *P. chinampoensis*, *C. virgata*, and *S. salsa*, together with large areas of bare land along the degradation gradient (Deng et al., 2006).

The aims of this study were to determine: 1) if successional changes have resulted in significant differences in the composition of the soil seed bank, aboveground floristic composition, and their similarity; 2) the seasonal dynamics of the soil seed bank, which is determined by the processes of seed production, input, movement, and output; and 3) the potential roles of soil seed banks from different successional stages to restore the climax community.

2   Materials and Methods

2.1   Study area and data sources

The study area was situated in the Da'an Sodic Land Experiment Station (45°35′58″N–45°36′28″N, 123°50′27″E–123°51′31″E) in the western part of the Songnen Plain, Northeast China (Fig. 1). The area experiences a combination of temperate, semi-humid, and semi-arid monsoon climates. The annual average temperature is 4.7℃ (ranging from –17.6℃ in January to 23.6℃ in July), and the annual average precipitation is 410 mm, 70%–80% of which occurs during July to September. The average evaporation in this region is 1790 mm, i.e., four times greater than the precipitation. Seasonal drought is frequent in spring and autumn, with a frequency of 90% in spring. These conditions have resulted in salts accumulating throughout the soil profile. In 2010, we selected communities whose representative species were *L. chinensis*, *P. chinampoensis*, *C. virgata*, and *S. salsa* respectively, and bare land was selected to represent the most seriously degraded successional stage.

2.2   Vegetation survey

We conducted a vegetation survey in five communities on 15 July 2011 during the peak of the growing season. Three sites were randomly selected for each of the five successional communities. Three 1-m^2 quadrats were
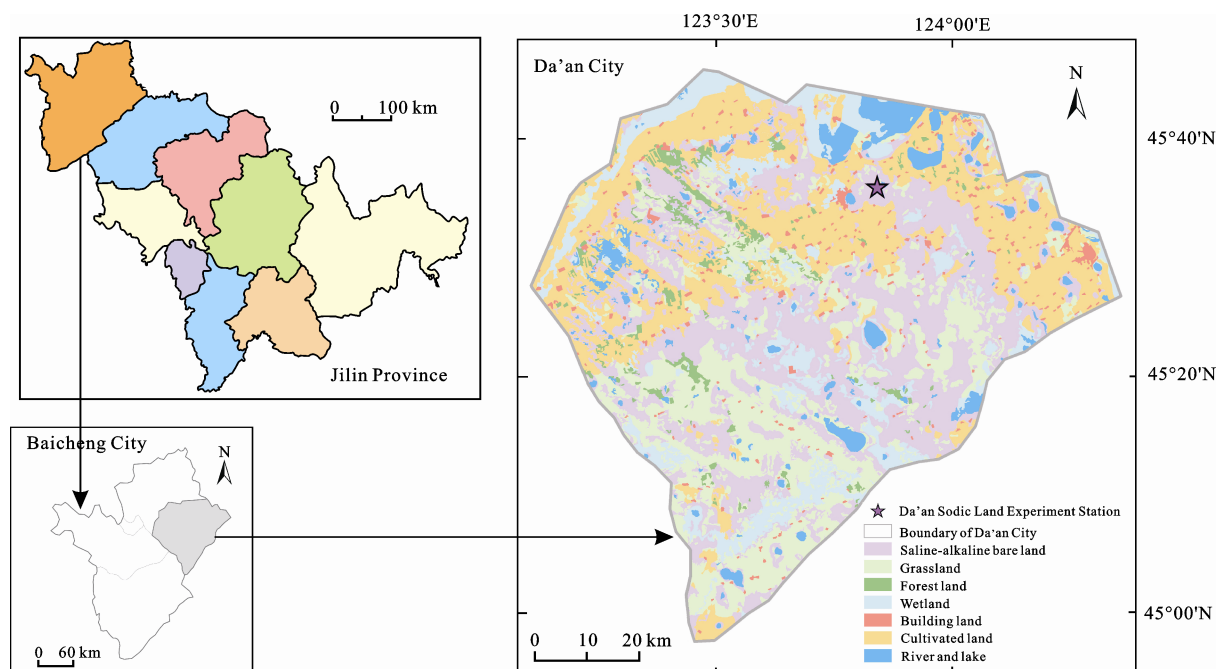

Fig. 1   Location of study area in Northeast China

randomly placed in each site and species presence and abundance (number of individuals) in each quadrat were recorded. The number of *P. chinampoensis* individuals was counted by clumps instead of individual plants.

2.3   Soil sampling

The seed bank was sampled on 24 April (spring), 23 August (summer), and 20 December (winter) in 2011. For each of the five successional communities, three randomly selected sites (20 m × 20 m) were established with at least 500 m between two sites. Three 1-m^2 quadrats were randomly selected at each sampling site. At each sampling site, 12 soil cores were extracted from 0–5 cm depth using a 5-cm diameter soil corer. These 12 soil cores were then composited to a single sample and three samples were collected from each community site. The samples were transported to the laboratory in plastic bags and were then air-dried. Large soil aggregates were broken up to homogenize the soil samples, and vegetative plant material was removed by passing the soil through a 5.4-mm-mesh sieve.

2.4   Analysis of soil properties

During the vegetation survey, another three soil cores of 5 cm (diameter) × 10 cm (depth) in each of the 15 communities were collected separately. All soil samples were air-dried and then passed through a 2-mm sieve. Soil available nitrogen (AN) and available phosphorus (AP) were determined after extraction with potassium chloride, and sodium bicarbonate, respectively. Soil organic carbon (SOC) was determined using a total organic carbon analyzer. Soil pH and EC (soil/water = 1 : 5, w/v) were measured by a digital PHS-3C pH meter (Xishuo Electronic Technology Co., Ltd., China) and a DDS-307 conductivity meter (Xishuo Electronic Technology Co., Ltd., China) respectively. Soluble salt estimates were based on 1 : 5 soil-water extracts. The cations Na$^+$, K$^+$, Ca^{2+}, and Mg^{2+} were determined using inductively couple-plasma spectroscopy (GBC, Scientific Equipment Pty Ltd., Australia), while Cl$^-$, NO$_3^-$, HCO$_3^-$, and CO$_3^{2-}$ were determined by standard methods. Alkalinity and residual sodium carbonate (RSC) were calculated as follows: alkalinity = (HCO$_3^-$ + CO$_3^{2-}$), RSC = (HCO$_3^-$ + CO$_3^{2-}$) – (Ca^{2+} + Mg^{2+}). The sodium adsorption ratio (SAR) was calculated as

$$\text{SAR} = \text{Na}^+ / \sqrt{\frac{1}{2}(\text{Ca}^{2+} + \text{Mg}^{2+})}$$. The exchangeable

sodium percentage (ESP) was determined as the ratio of exchangeable sodium and the cation exchange capacity.

2.5   Seedling germination assay

Soil seed densities and composition were examined using the seedling emergence method. Soil samples were transferred as a 1-cm thick layer to 20 cm × 15 cm × 8 cm plastic trays that were previously filled with washed vermiculite to a depth of 6 cm and placed in a non-heated greenhouse. Soil samples were watered daily to ensure the soil remained moist, but not water-logged. Seedlings were monitored, identified, and removed every two weeks. Any seedlings that were unidentifiable were replanted into pots and grown until they could be identified. When germination ceased, the soil samples were crumbled and mixed to promote the germination of any remaining seeds. This was conducted every four to six weeks for five months, after which the experiment was terminated because no new seedlings emerged. The experiment lasted for five months.

2.6   Dynamics of seed rain

Seed rain records were collected from July to October 2011 using nine seed traps in the 15 communities, with three traps each placed at a distance of 1 m apart. The seed traps consisted of glass petri dishes (diameter 12 cm) buried in the soil, with the top side at the level of the soil surface. Seeds were collected monthly from the traps, and identified using a binocular microscope.

2.7   Seed production and dispersal

The aerial seeds of the four dominant species of *L. chinensis*, *C. virgata, P. chinampoensis,* and *S. salsa* were sampled monthly from the *L. chinensis*, *P. chinampoensis*, *C. virgata*, and *S. salsa* communities from June to October. We randomly selected 30 culms for each species at each time point. We counted the fruiting culms with seeded spikes and the number of seeds per spike to give an estimation of seed production in the population, calculated as the mean number of seeds/m^2.

2.8   Statistical analysis

Sørensen similarity = $2C/(A + B)$, where A is the number of species aboveground, B is the number of species in the soil seed bank, and C is the number of species both above- and below-ground (Legendre and Legendre, 1998). Seed bank density and species richness, as well

as the composition of aboveground vegetation and soil characteristics indices, were compared among the five successional communities by means of an analysis of variance (ANOVA) and Tukey's-test. The data were analyzed with the SPSS 19.0 for Windows software (SPSS Inc., Chicago, USA).

3 Results

3.1 Vegetation composition in successional communities

A total of eight species belonging to four families were recorded across all five communities and four species occurred in the climax community, i.e., *L. chinensis* community (Table 1). However, the middle successional communities i.e., *P. chinampoensis* and *C. virgata*, only contained *P. chinampoensis* and *C. virgata* as the standing vegetation, respectively. In the early successional stage of the *S. salsa* community, three species were present, and two species occurred even in the saline-alkaline bare patches where no plants were observed in the extremely dry year of 2010. In the climax successional community, on the average, the perennial *L. chinensis* accounted for 84.2% of total plants in 1-m^2 quadrats, while it was not present in the other successional communities. With an increase in the degradation succession sere, the vegetation cover had a tendency to significantly decrease.

3.2 Soil properties

The ANOVA results for the soil properties among the five successional stages are shown in Table 2. The Na$^+$,

CO$_3^{2-}$, HCO$_3^-$, and SO$_4^{2-}$ contents, and pH, EC, and SAR all had significant differences among the five stages ($P < 0.001$), while the Cl$^-$, SOM, ESP, and alkalinity displayed less significant differences ($P < 0.05$). The Na$^+$, Cl$^-$, CO$_3^{2-}$, SO$_4^{2-}$, and HCO$_3^-$ contents, and EC, pH, and SAR displayed a clear tendency to increase with an increase in the degree of salinity-alkalinity among the successional stages (Fig. 2).

3.3 Seasonal dynamics of soil seed bank

There were large seasonal variations in both the seed density and species richness in the soil seed bank of the different successional communities (Fig. 3, Table 3). Seed densities were not significantly affected by the successional communities ($df = 4$, $F = 2.412$, $P = 0.079$) and the interaction of community and sampling month ($df = 8$, $F = 2.251$, $P = 0.0514$), but were significantly affected by the sampling months ($df = 2$, $F = 10.420$, $P < 0.0001$). Both the community types ($df = 4$, $F = 7.739$, $P < 0.0001$) and sampling months ($df = 2$, $F = 10.678$, $P < 0.0001$) significantly affected the species richness, but their interaction did not ($df = 8$, $F = 1.914$, $P = 0.094$).

Seeds of the climax species of *L. chinensis* appeared only in the *L. chinensis* community and accounted for 4.5%–13.6% of the total seeds in the soil seed bank. For the following successional communities of *P. chinampoensis*, *C. virgata*, and *S. salsa*, seeds of the dominant species contributed 83.7%–92.7% of the total seeds. In the bare patches, the seed density of the soil seed bank ranged from 3228 seeds/m^2 in April, to 31 932 seeds/m^2 in December, and most of the seeds (97.8% in December and 100% in April) were *C. virgata* and *S. salsa* (Table 3).

Table 1 Aboveground vegetation composition and densities in successional communities

Species	Plant densities in different successional communities (individuals/m^2)				
	Leymus chinensis	*Puccinellia chinampoensis*	*Chloris virgata*	*Suaeda salsa*	Saline-alkaline bare patch
Leymus chinensis	734.7±93.8	0±0	0±0	0±0	0±0
Puccinellia chinampoensis	0±0	89.3±15.4	0±0	0±0	0±0
Chloris virgata	0±0	0±0	1521.3±287.9	142.7±100.7	93.3±29.3
Suaeda salsa	0±0	0±0	0±0	766.7±310.9	150.0±92.3
Sonchus brachyotus	109.3±109.3	0±0	0±0	0±0	0±0
Scirpus triqueter	41.3±41.3	0±0	0±0	0±0	0±0
Artemisia capillaris	3.0±3.0	0±0	0±0	0±0	0±0
Polygonum sibiricum	0±0	0±0	0±0	0.3±0.3	0±0
Vegetation coverage (%)	85.0±2.9	72.0±3.1	33.3±4.4	11.0±2.1	7.0±0.6

Note: Data in the table are mean ± S.E.

Table 2 Analysis of variance (ANOVA) results for soil properties among five successional communities

| Soil properties	Mean square	F value	P
Na^+	10421031	49.028	0.0001[***]
K^+	310.0	0.2217	0.6503
Ca^{2+}	1634.79	2.1963	0.1766
Mg^{2+}	40.96	0.0635	0.8074
CO_3^{2-}	1184871	92.673	1.127e-05[***]
HCO_3^-	2915730	50.653	0.0001003[***]
Cl^-	1953831	21.099	0.001771[**]
SO_4^{2-}	64826	172.49	1.075e-06[***]
pH	7.5645	47.148	0.0001288[***]
EC	8312762	51.495	9.465e-05[***]
SOM	4.3805	6.4573	0.03465[*]
ESP	1200.94	5.7528	0.04328[*]
SAR	91988	40.855	0.000211[***]
AN	3281.9	4.2423	0.0734
AP	0.4682	0.0865	0.7761
Alkalinity	423708	17.444	0.003094[**]

Notes: EC: electronic conductivity; ESP: exchangeable sodium percentage; SAR: sodium adsorption ratio; SOM: soil organic material; AN: available nitrogen; AP: available phosphorus

### 3.4 Seasonal dynamics of seed rain

From July to September, the species richness and the seed number in the seed rain were different among the successional stages and seasons. The climax community of *L. chinensis* had the highest species richness, but lowest seed number. Other successions had a significantly higher seed number, although their species richness was comparatively lower than that of the climax community of *L. chinensis*. For most communities, the highest species richness in the seed rain was recorded in August. For the *P. chinampoensis* community, the highest seed numbers were recorded in July (Table 4). Even in the successional stage of bare patches, three species were present with large seed numbers during all seasons.

3.5 Aerial seed dynamics of dominant species

Seeds of *L. chinensis* and *P. chinampoensis* matured in
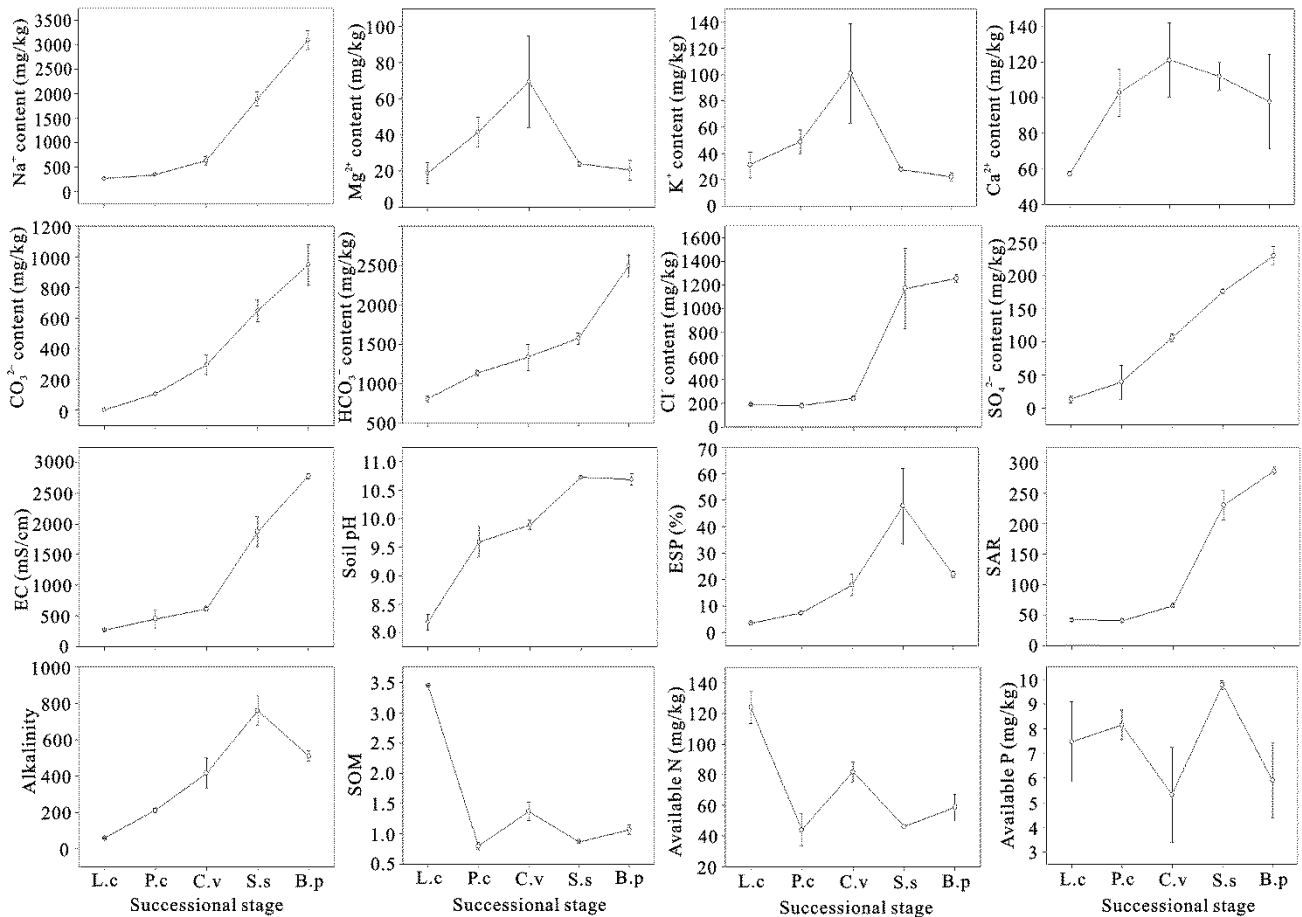
Fig. 2 Na^+, Mg^{2+}, K^+, Ca^{2+}, CO_3^{2-}, HCO_3^-, Cl^-, and SO_4^{2-} contents, and electronic conductivity (EC), pH, exchangeable sodium percentage (ESP), sodium adsorption ratio (SAR), alkalinity, soil organic material (SOM), available nitrogen (AN), and available phosphorus (AP) of soils from successional communities of *Leymus chinensis* (L. c), *Puccinellia chinampoensis* (P. c), *Chloris virgate* (C. v), *Suaeda salsa* (S. s), and bare patch (B. p) which represent the sere from climax community to seriously degraded stages
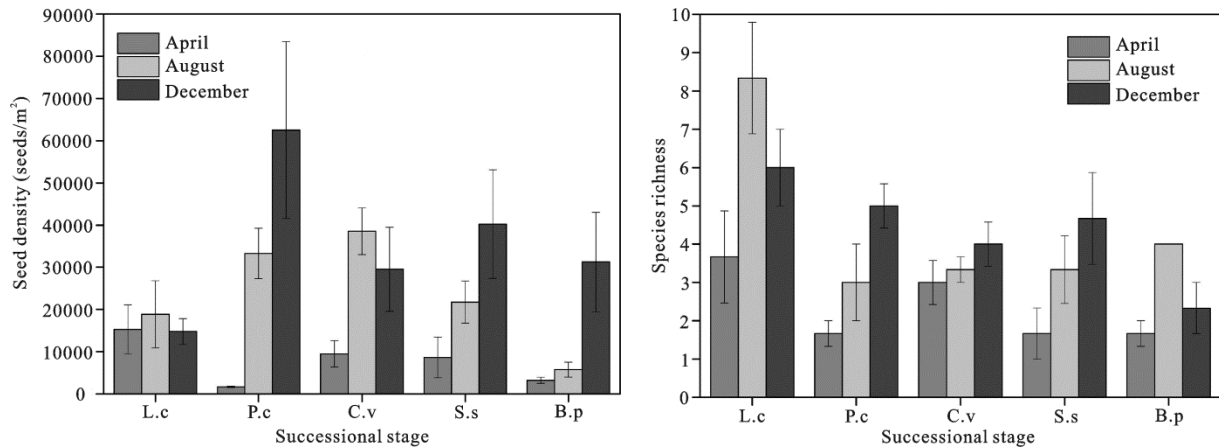
Fig. 3 Seed density (mean number per m² ± S.E.) and species richness in different successional communities following land degradation at Songnen Plain from April to December. Communities of *Leymus chinensis* (L. c), *Puccinellia chinampoensis* (P. c), *Chloris virgate* (C. v), *Suaeda salsa* (S. s), and bare patch (B. p) represent sere from climax community to seriously degraded stage

Table 3 Soil seed bank composition and densities in April, August, and December among five successional communities

| Species | Seed densities in different successional communities (seeds/m²) | | | | | | | | | | | | | | |
| | *Leymus chinensis* | | | *Puccinellia chinampoensis* | | | *Chloris virgata* | | | *Suaeda Salsa* | | | Saline-alkaline bare ground | | |
	April	August	December	April	August	December	April	August	December	April	August	December	April	August	December
Leymus chinensis	1699	849	679	0	0	0	0	0	0	0	0	0	0	0	0
Puccinellia chinampoensis	0	340	2548	340	28025	53673	1189	0	0	7983	0	0	2718	170	0
Chloris virgata	679	7473	1019	340	0	4246	4416	32272	26327	510	0	340	510	849	12399
Suaeda Salsa	0	340	0	1019	0	170	3737	4586	849	0	19533	36008	0	1868	18853
Sonchus brachyotus	1359	1359	1868	0	510	170	0	0	0	0	170	0	0	0	0
Ixeris chinensis	2887	0	0	0	0	0	170	0	0	0	0	0	0	0	0
Viola dissecta	7304	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla chinensis	340	0	0	0	0	0	0	0	0	170	0	0	0	0	0
Amblytropis pauciflora	679	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artemisia capillaris	0	849	170	0	170	170	0	0	170	0	0	0	0	0	0
Artemisia adamsii	0	1529	6794	0	1019	170	0	0	0	0	0	0	0	0	0
Epilobium hirsutum	0	2887	340	0	1868	1189	0	1019	340	0	170	170	0	1699	0
Saxifraga stolonifera	0	0	679	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus trigueter	0	340	170	0	0	340	0	679	340	0	0	510	0	1019	0
Chenopodium acuminatum	0	170	0	0	0	0	0	0	0	0	0	0	0	0	0
Setaria viridis	0	340	0	0	0	170	0	0	0	0	849	2718	0	0	340
Saussurea runcinata	0	340	0	0	0	0	0	0	0	0	340	0	0	0	0
Stellaria media	0	0	0	0	0	0	0	0	0	0	0	0	0	170	0
Phragmites australis	0	1189	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium setosum	0	510	170	0	0	0	0	0	0	0	0	170	0	0	0
Ixeris sonchiflolia	0	170	170	0	0	1868	0	0	340	0	0	170	0	0	340
Artemisia commutata	0	170	0	0	0	0	0	0	0	0	0	0	0	0	0
Scripus planiculmis	0	0	170	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum sibiricum	0	0	0	0	0	0	0	0	170	0	0	0	0	0	0
Filifolium sibiricum	0	0	0	0	0	0	0	0	170	0	0	0	0	0	0
Total seed number (seeds/m²)	14947	18855	14777	1699	31592	62166	9512	38556	28706	8663	21062	40086	3228	5775	31932

Note: Data in the table are the mean seed number of species found in the soil seed banks of the three sites in each of the five communities

Table 4 Seed rain dynamics in five successional communities

Community	Species	Seed density (seeds/m²)		
		26 July 2011	28 August 2011	23 September 2011
Leymus chinensis	*L. chinensis*	10±10	10±10	
	C. virgata		590±575	
	S. salsa		49±10	20±20
	Sonchus brachyotus	29±29		
	Viola dissecta			246±246
Puccinellia chinampoensis	*P. chinampoensis*	9391±3109	1072±126	69±69
	S. salsa	39±26		10±10
Chloris virgata	*C. virgata*		26285±1981	6421±2324
Suaeda salsa	*S. salsa*	2478±1247	1210±1165	443±146
	C. virgata		1750±886	11859±4394
	Taraxacum mongolicum		30±17	69±10
Bare land	*S. salsa*	7749±6259	1908±1524	3835±3426
	C. virgata		7188±2830	2242±363
	Saussurea runcinata		39±39	

Note: Data are mean ± S.E. which represent seed number of the three sites in each of the five communities

late June, *C. virgata* seeds matured in August and, *S. salsa* seeds matured in September (Table 5). The number of seeds and the rate of seed setting differed substantially among species. The climax species of *L. chinensis* had the lowest seed setting rate of < 5% and seeds could remain on the plants for a long time. A high rate of seed setting (> 90%) was found in *C. virgata* and *S. salsa*. From the vegetation survey, *P. chinampoensis* and *C. virgata* were found to have the highest number of seeds per spikelet at 525 and 493 seeds per spikelet, respectively, which produced 345 600 (spikelet density of 660 per m²) and 750 017 (spikelet density of 1521 per m²) seeds per m², respectively.

3.6 Similarity between soil seed bank and aboveground vegetation

The Sørensen similarity index between the soil seed bank and the aboveground vegetation was significantly different among the successional communities (*df* = 4, *F* = 6.567, *P* < 0.001). The lowest Sørensen similarity index (0.22–0.37) was found in the climax successional community of *L. chinensis*, while the highest was found in the newest successional stages of bare patches (Fig. 4). In the successional stages of *P. chinampoensis*, *C. virgata*, and *S. salsa*, there were higher similarity index values ranging from 0.47 to 0.60, but they were not significantly different (*P* > 0.05).

4 Discussion

Our results proved that successional changes have re-

sulted in significant differences in the composition of the soil seed bank and aboveground vegetation, with the seed bank and vegetation consisting of similar species in the saline-alkaline grassland. In arid and semi-arid ecosystems, the high spatial and temporal variability of the soil seed bank is a consequence of numerous ecological factors, including the phenology of flowering, seed set, and seed maturation (Busso and Bonvissuto, 2009), seed production (Bonvissuto and Busso, 2007; Jacquemyn et al., 2011), rate of seed predation (DeFalco et al., 2009; Hanin et al., 2013), season (Miao and Zou, 2009; Ge et al., 2013), and environmental factors, such as soil properties (Ge et al., 2013) and precipitation (Aguado et al., 2012).

4.1 Similarity between vegetation and soil seed banks in successional communities

In the saline-alkaline grassland investigated in this study, the climax community had the highest species number, but lowest seed density. However, there was no clear trend between the successional stages and the soil seed bank and aboveground vegetation composition. Along a degradation successional series, both the number of species and seed density in the soil seed bank often decreases, e.g., from fertilized grassland to semi-natural grassland (Bekker et al., 2000), and from a grazed site to a site with 80 years of juniper encroachment (Bakker et al., 1996). However, Milberg and Hansson (1994) found that vegetation changes had only slight effects on seed bank species composition in grazed and non-grazed limestone grasslands. Therefore,

Table 5   Number of seeds and seed setting rates of dominant species from June to September

Community	Seeds	June 25	July 26	August 29	September 23
Leymus chinensis	Number (seeds/plant)	83.9±5.4	77.9±3.9	80.2±4.5	53.9±5.6
	Setting rate (%)	4.2±1.1	4.2±1.2	1.8±0.5	1.5±0.7
Puccinellia chinampoensis	Number (seeds/plant)	524.7±51.9	112.5±11.8	14.9±4.2	0
	Setting rate (%)	100.0±0.0	77.8±3.9	21.4±8.7	0
Chloris virgata	Number (seeds/plant)	/	/	492.5±51.0	29.5±7.9
	Setting rate (%)			98.4±0.7	70.1±9.4
Suaeda salsa	Number (seeds/plant)	/	/	/	229.6±7.9
	Setting rate (%)	/	/	/	97.4±3.9

Notes: Data in the table are mean ± S.E. '/' represents no data for immature seeds. The setting rate is the ratio of fully developed seeds to the whole number of seeds in the same spikelet
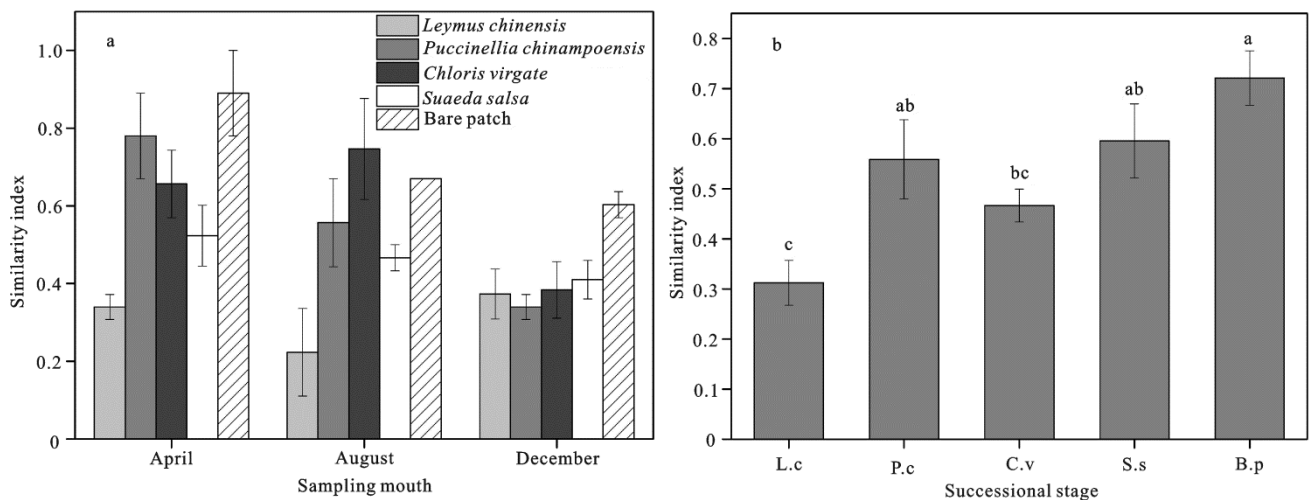
Fig. 4   Sørensen similarity index values between soil seed banks collected in April, August, and December (a) and aboveground vegetation sampled in July (b). The communities of *Leymus chinensis* (L. c), *Puccinellia chinampoensis* (P. c), *Chloris virgate* (C. v), *Suaeda salsa* (S. s), and bare patches (B. p) represent the sere from the climax community to seriously degraded stages. Data in the figures are mean ± S.E. The different lowercase letters represent in (b) significant differences at 0.05 level

the relationship between the composition of the seed bank and vegetation succession has not been fully determined (Hong et al., 2012). It is likely that the aboveground vegetation composition is shaped by many factors and their interactions, rather than by a single variable.

The similarity between the species composition of the soil seed bank and that of the associated plant community is of considerable interest in restoration projects. In this study, the lowest similarity value was found in the climax community (0.22–0.37), while the other successional stages all had higher similarity values of 0.47–0.60, with bare patches having the highest value. Plant life-form in terms of longevity (i.e., annual and perennial) and reproductive strategies are important

factors affecting soil seed banks. The germinable seed bank and aboveground vegetation tend to be more similar in annual than in perennial communities (Bakker et al., 1996; Osem et al., 2006; Pekas and Schupp, 2013). This was also apparent from our analysis of the communities dominated by annual species (i.e., the *C. virgata*, *P. chinampoensis*, and *S. salsa* communities), in which the seeds of the dominant species accounted for 83.7%–92.7% of the total seed bank. Ma et al. (2010b) found that *Plantago asiatica*, *Poa pratensis*, and *Artemisia desertorum* accounted for 76.7%–86.8% of the seed bank in an alpine meadow on the Tibetan Plateau, China. Soil seed banks that were similarly dominated by a few species have been reported in other studies (Shaukat and Siddiqui, 2004; Li et al., 2012).

4.2   Effects of successional stage on soil seed bank

In the degradation successional stages of the saline-alkaline grassland, the seasonal dynamics of the soil seed bank were affected by the processes of seed production, inputs, seed rain, and the dispersal characteristics of the dominant plants in each successional community. Most studies of grasslands dominated by perennial grasses have found that the density of viable seeds of perennial plants is low, compared to the seed density of annuals (DeFalco et al., 2009). This is because perennial grasses adopt a clonal reproduction strategy, whereas annual species rely predominantly on sexual reproduction (Luo and Wang, 2006; Ma et al., 2010b; Li et al., 2012). In our study, seeds in the soil seed bank of *L. chinensis* appeared only in the climax community of *L. chinensis*. *L. chinensis* depends primarily on vegetative reproduction (Jiang et al., 2010) and has a very low seed production and seed setting rate (Table 4). Unlike most temperate perennial species, *P. chinampoensis* reproduces via sexual and vegetative means, and similar characteristics were also found in *Bothriochloa pertusa* and *Heteropogon contortus* (Luo and Wang, 2006). In the late degradation successional stages, the dominant annual species of *C. virgata* and *S. salsa* had a large seed production (Table 4). It is common for annuals to produce large germinable seed banks and use the seed bank as an alternative germination strategy (Pekas and Schupp, 2013).

Propagule dispersal plays a decisive role in maintaining community diversity (Bakker et al., 1996) and the pattern of seeds in the soil is primarily a function of the dispersal process (Shaukat and Siddiqui, 2004). It has been shown that the poor dispersal of seeds significantly limits the seed bank in soil seed banks (Blomqvist et al., 2006; Rosenthal, 2006; Du et al., 2007). In our study, within the climax community, in addition to its low seed production, most of the newly matured *L. chinensis* seeds did not disperse within one year according to our field observations. In addition, no seeds of *L. chinensis* were found in any other successional communities, indicating its poor dispersal ability (Table 2 and Table 3). However, seeds of *P. chinampoensis* dispersed within two months (from June to August), and seeds of *C. virgata* dispersed largely within one month after late August. The seed rain and aerial seed bank dynamics indicated that this occurred in all of the successional communities (Tables 3 and 4). The common denominator in disturbed areas, e.g., freshwater tidal marshes, annual Mediterranean pastures, or the Horqin sand dune system in China, is the predominance of annual species that produce an excess of seeds during the growing season; thus, adding to the soil seed bank (Liu et al., 2007).

4.3   Regenerative role of soil seed banks of different successional stage

The successful restoration of the degraded saline-alkaline grassland is not impossible, despite the lack of climax species seeds and the poor soil properties, e.g., high pH, EC, Na$^+$, and SAR, and limited soil fertilization. The results of this study also proved that if the climax community in the saline-alkaline grassland is destroyed, i.e., the disappearance of climax species, it could not be regenerated from the soil seed bank because of the absence of *L. chinensis* seeds in the following successional stages. This study only used the germination method to evaluate the soil seed bank composition, which might have substantially undervalued the high soil salinity and alkalinity in the degraded successional stages (Table 2 and Fig. 1). Some species could not tolerate the salinity and alkalinity of the soil, especially in the germination and seedling growth stages. Germination is a serious problem in a saline-alkaline environment, due to the stresses resulting from a high EC, and the large concentrations of Na$^+$ and CO$_3^{2-}$, together with some other salinity and alkalinity values (Ma et al., 2010a, 2015; Li et al., 2012; Bai et al., 2014).

For successful restoration and species conservation projects, seed banks or above-ground sources of seeds are necessary (Leck and Schütz, 2005; Ghorbani et al., 2007; Ma et al., 2010b). Some studies have identified the manmade obstacles to the accumulation of seeds in the Songnen Plain (Li and Zheng, 1993). These may need a long time to overcome, with many decades required to restore the original vegetation (Koch et al., 2011). In the early stages of secondary succession, seed availability and environmental stress are considered to be the determining factors for restoration success (Rosenthal, 2006). In the present study, among the five degraded succession series, our results showed that except for the *L. chinensis* community, the soil seed banks would potentially be useful for the restoration of vegetation, especially in the bare saline-alkaline patches. However, the soil seed banks would have no effect on the restoration of target species in the climax *L. chinen-*

sis community. For the saline-alkaline bare patches, 2–5 species with a density of 3228–31 932 seeds/m^2 (mainly *C. virgata* and *S. salsa*) were observed, confirming the existence of a resident, persistent seed bank at these bare sites and that the seed bank was not reliant on annual inputs into the soil from the above ground vegetation. This allows the re-establishment and maintenance of populations after years with poor or no seed setting, e.g., *C. virgata* and *S. Salsa* in our study. One way for an annual species to survive in such an adverse environment is to have a persistent seed bank. Therefore, the presence of a persistent seed bank of the pioneer species is a mechanism for the pioneering annual plant species to adapt to the saline-alkaline environment of the Songnen Plain.

5 Conclusions

In the saline-alkaline grassland investigated in this study, successional changes have resulted in seasonally significant differences in the composition of the soil seed bank, aboveground floristic composition, and their similarity. However, there was no clear trend between the successional stages and the soil seed bank and aboveground vegetation composition. The climax community of *L. chinensis* had the highest species number, but lowest seed density. The lowest similarity value of vegetation and soil seed bank was found in the climax community, while the other successional stages all had higher similarity values and the bare patches had the highest value. In the degradation successional stages of the saline-alkaline grassland, the seasonal dynamics of the soil seed bank were affected by the processes of seed production, inputs, seed rain, and the dispersal characteristics of the dominant plants in each successional community. Among the five degraded succession series except for the *L. chinensis* community, the soil seed banks would potentially be useful for the restoration of vegetation, especially in the bare saline-alkaline patches. The soil seed banks would have no effect on the restoration of target species in the climax *L. chinensis* community. Therefore, it is necessary to induce seeds or other propagules of the target perennial species for further restoration of the *L. chinensis* grassland.

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