International Soil and Water Conservation Research 10 (2022) 414–421

Contents lists available at ScienceDirect

International Soil and Water Conservation Research

journal homepage: www.elsevier.com/locate/iswcr

Original Research Article

The feasibility of using soil seed bank for natural regeneration of degraded sandy grasslands

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A R T I C L E I N F O

Article history:
Received 15 July 2021
Received in revised form
28 October 2021
Accepted 6 November 2021
Available online 12 November 2021

Keywords:
Degradation
In-situ
Restoration
Seed bank
Semi-arid

A B S T R A C T

Desertification in degraded grasslands is manifested through the development of bare sandy patches, which eventually lead to habitat fragmentation. The ability of these bare sandy patches to regenerate naturally through *in-situ* soil seed banks is not well understood. To fill this knowledge gap, we randomly selected 24 bare sandy patches with areas ranging from 19 to 898 m^2 in a desertified grassland of the Horqin sandy land, Northern China to determine whether soil seed bank can be used for natural regeneration of bare sandy patches. Species composition and density of soil seed bank as well as aboveground vegetation composition, abundance and coverage were investigated. We then determined their relationships with *in-situ* habitat characteristics. Our observations showed that the studied area had low soil seed bank density and species richness, as well as depauperate soil seed bank communities. Consequently, local soil seed bank was not able to provide sufficient seed source for natural regeneration. This was indicated by the relationships between aboveground vegetation, soil seed bank and the *in-situ* habitat characteristics. For bare patches with an area between 300 m^2 and 900 m^2, increase the soil seed bank density and species richness should be the main restoration measures. For bare patches with a small area of less than 50 m^2, restoration of vegetation density should be the main measure. Our data highlighted that different extents of desertification, indicated by different bare patches, are requiring distinct restoration measures.

1. Introduction

Grassland degradation has been one of the urgent ecological and environmental issues that need to be resolved. Some characteristics of degraded grasslands are desertification and sandification, which cause patchy habitat segments or habitat fragmentation (Wu et al., 2019). Due to high level of fragmentation, degraded sandy grasslands usually consist of spatially isolated patches, making it difficult for seeds to disperse (Godefroid et al., 2018; Zhou et al., 2019a, 2019b). Therefore, habitat fragmentation is considered one of the major threats to biodiversity (Brunet et al., 2011; Ducatez & Shine, 2017; Murphy & Romanuk, 2014; Wu et al., 2019).

Natural regeneration is an ecological process to conserve *in-situ* species diversity in disturbed areas (Crouzeilles et al., 2017). Natural regeneration is also known as a low cost approach for regeneration of vegetation biodiversity (Wakshum et al., 2018). In bare patches areas, natural regeneration process helps maintain biodiversity, which often depends on 1) the availability of seeds (soil seed banks), 2) the ability to obtain seeds from the surrounding vegetation, 3) the environment of *in-situ* habitat (Wang et al., 2013). In degraded and fragmented grasslands, soil seed banks are

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https://doi.org/10.1016/j.iswcr.2021.11.001
2095-6339/

particularly important for vegetation restoration (Wang et al., 2013) because the ability to obtain seeds from the surrounding vegetation is greatly reduced with decreasing vegetation cover.

Most seeds in the soil are sourced from seeds produced by *in-situ* vegetation and seed dispersed by vegetation from nearby habitats. Soil seed bank is known for its ability to maintain a gene pool (Wakshum et al., 2018) and represents a stock of regeneration potential (Wang et al., 2015). When species disappears due to various disturbances, the seeds in these soils can germinate under suitable environment and promote recruitment (Bossuyt & Honnay, 2008). Wang et al. (2013) showed that the seeds of widely distributed species always have small size, persist in soil under eroded conditions, and these species can successfully recolonize. Therefore, soil seed banks help maintaining species diversity where disturbance is frequent (Wang et al., 2015).

After disturbances, soil seed bank co-determines the trajectory of secondary succession at the community level and species diversity at the species level (Pakeman & Small, 2005; Bossuyt & Honnay, 2008). Natural regeneration of bare sandy patches on degraded sandy grasslands is thus most possible through the presence of a persistent soil seed bank in the *in-situ* habitat. Therefore, evaluation the characteristic of soil seed bank is very important for designing conservation and restoration programs in degraded semi-arid ecosystem, especially in degraded sandy grasslands.

While natural regeneration processes are increasingly integrated as restoration tools in many ecological restoration efforts (Rehounkova & Prach, 2008; Prach et al., 2013), further studies are needed to explore which communities and circumstances could initiate spontaneous recovery processes (Valkó et al., 2011). In China alone, desertified and sandified grasslands accounted for 27.20% (2,611,593 km^2) and 17.93% (1,721,175 km^2) of the total land area, respectively (Duan et al., 2019; Piao et al., 2005). Yet little information on soil seed bank is available to promote recovery of these grasslands (Liu, Liu, & Wang, 2012). We therefore conducted a series of field observations specifically aiming to evaluate the following questions: (1) What are the aboveground vegetation and soil seed bank community characteristics and the characteristics in different size of bare patches? (2) What are the relationships between vegetation, soil seed bank communities and habitat characteristics? and (3) What are the contributions of soil seed bank in natural regeneration in bare sandy patches on degraded sandy grasslands. Untangling these questions will contribute to a better understanding of what needs to be done to restore degraded sandy grasslands to a favorable conservation value (Godefroid et al., 2018).

2. Materials and methods

2.1. Study area

The study was conducted in Wulanaodu region (42°29′-43°06′N, 119°39′-120°02′E, altitude approx. 480 m), south-western Horqin Sandy Land of Inner Mongolia, China. The study area is located in a semi-arid climate with an average annual temperature of 6.3 °C. The coldest and hottest months are January and July, respectively. The annual average precipitation is 340.5 mm, 70% of which falls between June and September. The frost-free period extends over 130 days (Liu, Liu, & Wang, 2012). The average annual wind velocity varies between 3.2 and 4.5 m s^{-1}. Wind direction is predominantly from the north-west between March and May and from the south-west between June and September (Wang et al., 2015).

The area has been intensively grazed since 1950, thus, overgrazing is the major force of desertification (Wang et al., 2019). Consequently, vegetation cover and individual plant size decreased, after that, some bare ground without vegetation appeared, forming small bare patches (Liu, Liu, & Wang, 2012). These bare patches increase and enlarge rapidly, and merge into large ones (Fig. 1). The average radius of newly created bare patches is less than 5 m in the degraded grassland, and it can expand to more than 10 m due to wind erosion. The bare sandy patches occur mainly on arenaceous soil. These bare patches are surrounded by species-rich areas with vegetation coverage greater than 50% (Liu, Liu, & Wang, 2012). The aboveground species is dominated by *Agriophyllum squarrosum*, *Setaria viridis* and *Artemisia annua*, with the coverage less than 20%. The area that we selected was free from grazing from 2011 and the area belongs to the herders, who have the rights to use it and the right has not changed.

2.2. Experimental design and data collection

In early April 2016, we randomly selected 24 bare patches with areas ranging from 19 to 898 m^2 (Table 1). Each bare patch was an independent unit with similar elevations. All the bare patches were mostly ellipsoidal, with major axis from north-west to south-east and minor axis from south-west to north-east. These axes were selected based on the dominant wind direction between March and May (north-west to south-east axis) and wind direction between June and September (south-west to north-east).

At each bare patch, we set up two vertical transects along the direction of the major axis and minor axis. The transect from north-west to south-east had a length between 6.1 m and 44.3 m, while the other transect from south-west to north-east had a length between 4.1 m and 26.4 m.

2.3. Vegetation and soil seed bank community investigation

Vegetation species composition and abundance were recorded in each bare patch at the end of July and August 2016, during the peak of the growing season. Percentage cover of all species within each bare patch was recorded using visual assessment. Frequency of each species was determined using data from all bare patches (e.g., if one vegetation species was recorded in 4 bare patches out of all the 24 bare patches surveyed, we calculated the frequency as $4 \times \frac{100}{24} = 16.67\%$). Additionally, we estimated the abundance of each species according to their growth form to subsequently determine an index of importance. For bunchgrasses, we counted the number of clusters, whilst for clonal species we counted the number of ramets, for species with discrete individuals, the number of individuals were counted (Liu et al., 2007).

Soil cores were collected in early May 2016, after winter stratification but before the emergence of early spring annuals. Using a

Fig. 1. The photo of individual bare sandy patch.

Table 1
General description of the investigated bare patches. The length of two cross transects, north-west to south-east (NW-SE) and south-west to north-east (SW-NE).Ratio = NW-SE/SW-NE.

Bare patches	Location		NW-SE (m)	SW-NE (m)	Ratio	Area (m^2)	Number of soil cores
	N	E					
1	43.06208	119.63393	44	26	1.69	898	71
2	43.06080	119.63439	31	26	1.19	633	57
3	43.06147	119.63461	28	21	1.33	462	49
4	43.06102	119.63431	24	22	1.09	414	46
5	43.06030	119.63452	22	20	1.10	345	43
6	43.06017	119.63546	21	19	1.11	313	41
7	43.06140	119.63405	26	15	1.73	306	41
8	43.05986	119.63540	14	14	1.00	154	29
9	43.06036	119.63519	14	12	1.17	132	27
10	43.06064	119.63469	16	9	1.78	113	26
11	43.05996	119.63548	14	10	1.40	110	25
12	43.06017	119.63476	12	10	1.20	94	23
13	43.06184	119.63452	13	8	1.63	82	21
14	43.06009	119.63470	11	8	1.38	69	20
15	43.06049	119.63492	9	10	0.90	71	19
16	43.05978	119.63570	10	8	1.25	63	19
17	43.05943	119.63519	8	8	1.00	50	17
18	43.06053	119.63641	8	8	1.00	50	17
19	43.05928	119.63531	9	7	1.29	49	16
20	43.06087	119.63519	8	6	1.33	38	14
21	43.05964	119.63509	6	7	0.86	33	14
22	43.06100	119.63489	6	6	1.00	28	13
23	43.06145	119.63512	6	5	1.20	24	11
24	43.06163	119.63428	6	4	1.50	19	11

7 cm diameter soil corer to a depth of 10 cm, soil samples were collected from the intersection of a vertical transect to north-west, south-east, south-west and north-east along the four directions of the two vertical transects. The distance between soil samples was 1 m apart. A total of 670 soil cores were sampled for soil seed bank analysis. Each soil sample was air - dried and sieved through a 0.5 mm mesh to extract the seeds. Their viability was then tested using tetrazolium chloride (Wang et al., 2015). Only viable seeds were used to assess the composition and density of soil seed banks.

2.4. Statistical analyses

Data analyses were performed using SPSS version 16.0 and CANOCO software.

Importance values (IV) of species in vegetation communities were calculated as the mean of the relative density, relative frequency and relative dominance,

$$IV_{vegetation} = (A + B + C)/3, \tag{1}$$

where A, B and C are the mean of relative density, relative frequency and relative dominance in vegetation communities (Mata et al., 2011; Wang et al., 2015). The last three indices were calculated using the following equations:

Relative density (A) = (number of individuals of a species/total number of individuals) x 100, (2)

Relative frequency (B) = (frequency of a species/sum frequencies of all species) x 100, (3)

Relative dominance (C) = (total cover for a species/total cover for all species) x 100, (4)

Importance values (IV) of species in soil seed bank communities were calculated as the mean of the relative density:

$IV_{soil\ seed\ bank}$ = (number of seeds of a species/total number of seeds) x 100, (5)

Simpson diversity index (D), Shannon-wiener Index (H), and Pielou index (J) of the observed bare patches were calculated as:

$$\text{Simpson diversity index (D)}: D = 1 - \sum P_i^2, \tag{6}$$

$$\text{Shannon} - \text{wiener Index (H)}: H = -\sum (P_i \ln P_i) \tag{7}$$

$$\text{Pielou index (J)}: J = H/\ln S \tag{8}$$

where Pi is the relative importance value of species (Pi = IV/100), and S is the total number of species.

Detrended correspondence analysis (DCA) (Plassmann et al., 2009; Yassir et al., 2010) was used to examine similarities between vegetation communities and soil seed bank communities in the bare patches. Redundancy analysis (RDA) was used to examine the correlations between vegetation, soil seed bank and *in-situ* habitat characteristics in the bare patches. Except log transformation the default settings in CANOCO were used for all the analyses.

3. Results

3.1. Patterns in vegetation and soil seed bank communities

For vegetation communities, 18 species were recorded in all 24 bare patches while eight species were recorded for soil seed bank communities (Table 2). All eight species in soil seed bank communities were found in vegetation communities (Table 3). All the eight species in soil seed banks were annual herbs, but different life forms were found in vegetation communities. Annual herbs were the most abundant, followed by biennial herbs, perennial herbs and shrubs (Table 3). The average vegetation densities were 1.09 individuals m^{-2} and the average soil seed bank densities at 0–10 cm

Table 2
Characteristics of above-ground vegetation and soil seed bank in bare patches. Values are mean ± SE.

	Density (individuals m^{-2})	Total species richness	Simpson diversity index (D)	Shannon-Wiener Index (H)	Pielou index (J)
Vegetation	1.09 ± 0.11	18	0.995	3.684	1.274
Seed bank	387.30 ± 113.98	8	0.747	1.652	0.794
F	11.48				
P	0.001				

Table 3
Mean importance values (IV) for all the species in above-ground vegetation and soil seed bank communities in bare patches. AH = annual herb, BH = biennial herb, PH = perennial herb, S = shrub, P = psammophyte, LMS = limnocryptophyte - meadow species, STS = steppe species.

	Species	Abbreviated code	Family	Life form	Ecological group	Importance values				Appendage Seed	Dispersal agen	Regional significance
						Vegetation		Soil seed bank				
1	*Diarthron linifolium*	*D. lin.*	Thymelaeaceae	AH	STS	✓	6.88	✓	7.23	_	Wind	
2	*Tribulus terrestris*	*T. ter.*	Zygophyllaceae	AH	LMS	✓	27.35	✓	1.42	Spine	Animal	
3	*Corispermum candelabrum*	*C. can.*	Chenopodiaceae	AH	p	✓	24.10	✓	6.90	Wing	Wind	
4	*Agriophyllum squarrosum*	*A. squ.*	Chenopodiaceae	AH	P	✓	59.08	✓	9.20	_	wind	Pioneer
5	*Setaria viridis*	*S. vir.*	Gramineae	AH	LMS	✓	46.80	✓	42.06	_	Wind	
6	*Digitaria sanguinalis*	*D. san.*	Gramineae	AH	LMS	✓	18.24	✓	8.43	_	Wind	
7	*Chenopodium acuminatum*	*C. acu.*	Chenopodiaceae	AH	LMS	✓	1.41	✓	22.34	_	Wind	
8	*Artemisia annua*	*A. ann.*	Compositae	AH	STS	✓	43.35	✓	2.41	Pappus	wind	
9	*Euphorbia humifusa*	*E. hum.*	Euphorbiaceae	AH	LMS	✓	13.48	_				
10	*Cuscuta chinensis*	*C. chi.*	convolvulaceae	AH	STS	✓	5.71	_				
11	*Eragrostis pilosa*	*E. pil.*	Gramineae	AH	LMS	✓	3.17	_				
12	*Carduus crispus*	*C. cri.*	Compositae	BH	STS	✓	1.61	_				
13	*Echinops gmelinii*	*E. gme.*	Compositae	PH	STS	✓	7.26	_				
14	*Oxytropis hailarensis*	*O. hai.*	Leguminosae	PH	STS	✓	1.47	_				
15	*Peucedanum terebinthaceum*	*P. ter.*	Umbelliferae	PH	STS	✓	1.43	_				
16	*Cynanchumthesioides*	*C. the.*	Asclepiadaceae	PH	STS	✓	1.53	_				
17	*Caragana microphylia*	*C. mic.*	Leguminosae	S	P	✓	19.02	_				Rare
18	*Lespedeza bicolor*	*L. bic.*	Leguminosae	S	STS	✓	2.82	_				

were 387.30 seeds m^{-2}. There were significant differences between vegetation and soil seed bank communities (P = 0.001, Table 2). Simpson diversity index (D), Shannon-wiener Index (H) and Pielou index (J) in vegetation communities were higher than in soil seed bank communities (Table 2).

Most of the eight species in soil seed bank communities were wind - dispersed seeds with no appendages. *Setaria viridis* had the highest IV (IV = 42.06) of all eight species in soil seed banks, followed by *Chenopodium acuminatum* (IV = 22.34). Of the total 18 species in vegetation communities, annual herb was the majority and had the highest IV. *Agriophyllum squarrosum*, *Setaria viridis*, *Artemisia annua* were the top three IV. All these three species were all annual herbs and wind-dispersed species (Table 3).

3.2. Correlations between above-ground vegetation, soil seed bank and bare patch area

The average vegetation density showed a power relationship with the bare patch area; it rapidly decreased as bare patch area increased ($R^2 = 0.71$, p = 0.00). The average vegetation density was low, ranged from 0.28 to 1.97 individuals m^{-2} (Fig. 2a). Vegetation species richness and bare patches area showed a linear relationship, with a significant positive correlation between the two ($R^2 = 0.62$, p = 0.00). Vegetation species richness were low, and it varied between 2 and 13 (Fig. 2b). There was no significant relationship between average seed density and bare patch area ($R^2 = 0.02$, p = 0.72). The average seed density ranged from 18.57 to 2268.89 seed s m^{-2} (Fig. 2c). Soil seed bank species richness and bare patch area showed a binomial relationship. There was a weak significant correlation between seed bank species richness and bare patch area ($R^2 = 0.28$, p = 0.03). Seed bank species richness ranged from 1 to 8 (Fig. 2d). Overall, vegetation and soil seed bank communities had the different relationships with the bare patch area.

The DCA of vegetation and soil seed bank communities in the bare patches showed that vegetation communities were relatively clustered along both the first and the second DCA axis, while soil seed bank communities were relatively decentralized. This finding suggested that soil seed bank communities were at a more dire state than the vegetation communities (Fig. 3). There was a small overlap in community composition between vegetation communities and soil seed bank communities along the first DCA axis (Eigenvalue = 0.498), but there was a big overlap along the second DCA axis (Eigenvalue = 0.185), highlighting that the composition of vegetation communities had low similarity to soil seed bank communities in each of the 24 bare patches.

3.3. Correlation of vegetation, soil seed bank communities and in-situ habitat characteristics

The RDA results indicated that the vegetation communities in most large (300 $m^2 \leq$ area <900 m^2) (patch ID: 2, 3, 4, 5) and small (<50 m^2) (patch ID: 19, 20, 21, 22, 23, 24) bare patches had a significant division along the first RDA axis (Eigenvalue = 0.308). Bare patches of most large area had strong positive correlation with soil seed bank species richness, annual herb richness, soil seed bank density, vegetation species richness, coverage, area, but a strong negative correlation with vegetation density, annual herb density, and perennial herb density. In contrast, bare patches of small area had a strong positive correlation with vegetation density, annual herb density, perennial herb density and strongly negative correlation with soil seed bank species richness, annual herb richness, soil seed bank density, vegetation species richness, and coverage area.

For the soil seed bank communities, most large (patch ID: 2, 3, 5, 6) and most small (patch ID: 19, 20, 21, 22, 24) bare patches also had a significant division along the first RDA axis (Eigenvalue = 0.443).

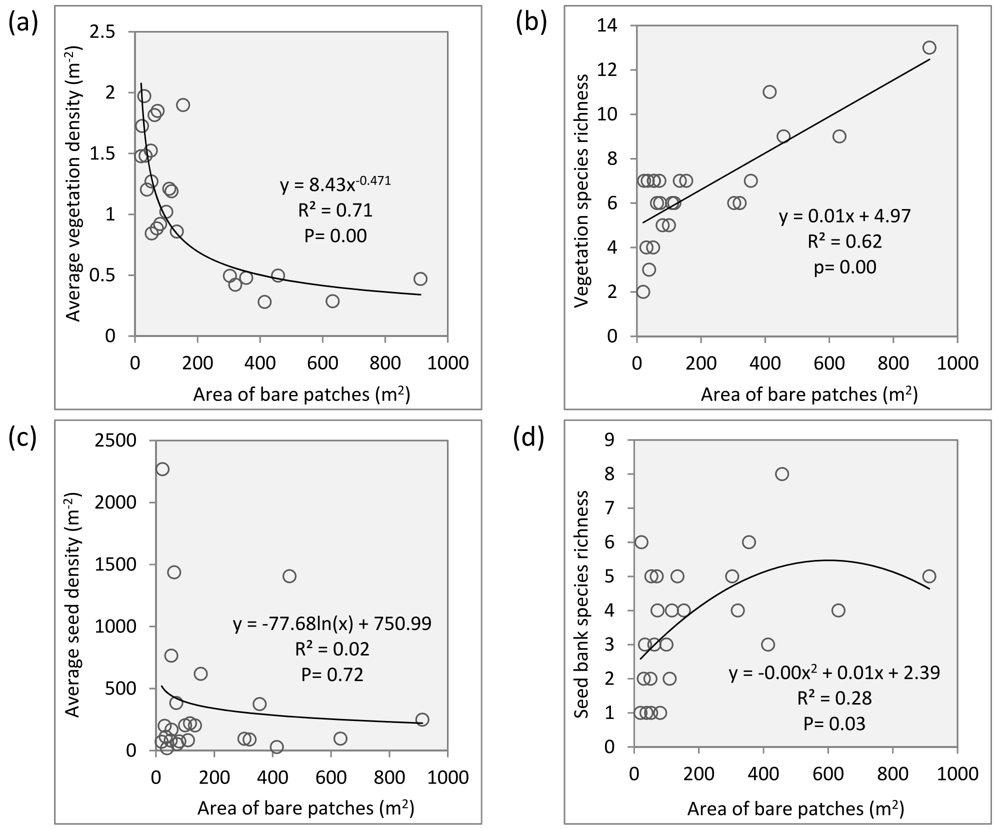

Fig. 2. Above-ground vegetation and soil seed bank characteristics changes with bare patches area.

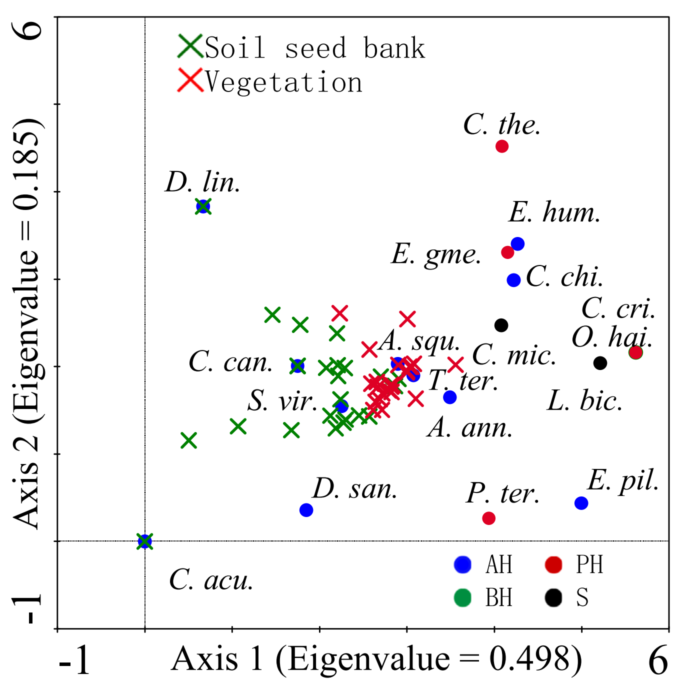

Fig. 3. Detrended Correspondence Analysis (DCA) of species composition between above - ground vegetation and soil seed bank communities in bare patches.

Most large bare patches had a strong positive correlation with coverage, shrub density, soil seed bank density, soil seed bank species richness, but a strong negative correlation with vegetation density, annual herb density, perennial herb density. In contrast, most small bare patches had a strong positive correlation with vegetation density, annual herb density, perennial herb density, but a strong negative correlation with coverage, shrub density, soil seed bank density, soil seed bank species richness. The extremely large bare patch (patch ID: 1; 898 m^2) had the strongest correlation with biennial herb richness, biennial herb density, perennial herb richness, ratio (the ratio of the transect lengths from north-west to south-east to the transect lengths from south-west to north-east) and soil seed bank richness. Overall, the RDA results indicated that the relationship between the bare patches with the vegetation and soil seed bank communities was contradictory for small and large patches. The largest and the smallest patches also had a significant different correlation with *in-situ* habitat characteristics. Most large bare patches (300 m^2 $\leq$ area <900 m^2) had a strong positive correlation with coverage, soil seed bank species richness and soil seed bank density, while most small patches (area <50 m^2) had a strong positive correlation with vegetation density, annual herb density and perennial herb density (Fig. 4).

Both vegetation and soil seed bank species showed a similar correlation with *in-situ* habitat characteristics based on the RDA analysis. Most vegetation and soil seed bank species had a positive correlation with area, coverage, vegetation species richness, shrub richness, ratio, soil seed bank species richness, soil seed bank density, annual herb richness, shrub density, biennial herb richness, biennial herb density and perennial herb richness. Meanwhile, most vegetation and soil seed bank species had a negative correlation with vegetation density, annual herb density and perennial herb density (Fig. 5).

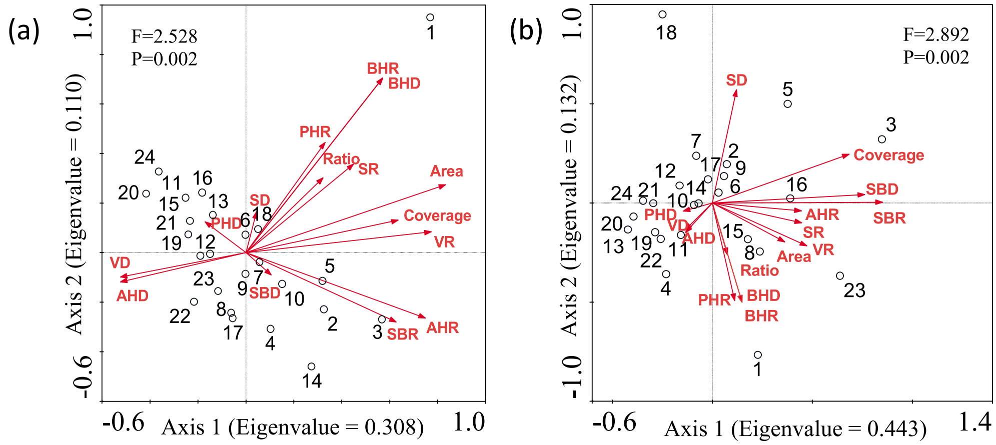

Fig. 4. Redundancy Analysis (RDA) of the correlation between above-ground vegetation (a), soil seed bank (b) communities and *in-situ* habitat characteristics in bare patches. Area = bare patch area, VD = vegetation density, SBD = soil seed bank density, VR = vegetation species richness, SBR = soil seed bank species richness, AHD = annual herb density, AHR = annual herb richness, BHD = biennial herb density, BHR = biennial herb richness, PHD = perennial herb density, PHR = perennial herb richness, SD = shrub density, SR = shrub richness.

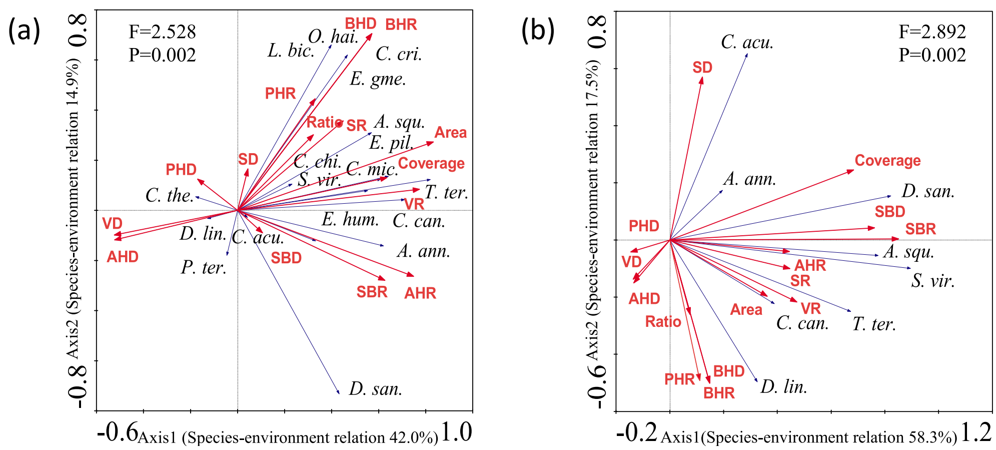

Fig. 5. Redundancy Analysis (RDA) of the correlation between above-ground vegetation (a), soil seed bank (b) species composition and *in-situ* habitat characteristics in bare patches. Area = bare patch area, VD = vegetation density, SBD = soil seed bank density, VR = vegetation species richness, SBR = soil seed bank species richness, AHD = annual herb density, AHR = annual herb richness, BHD = biennial herb density, BHR = biennial herb richness, PHD = perennial herb density, PHR = perennial herb richness, SD = shrub density, SR = shrub richness.

4. Discussion

4.1. The above-ground vegetation and soil seed bank community characteristics

Our data showed that the average soil seed bank density at 0–10 cm was extremely low (only 387.30 seeds m^{-2}), much lower than inter-dune lowland in the same area where the overall average seed density at 0–10 cm was 9570 seeds m^{-2} (Wang et al., 2015). Soil seed bank density in this region was also lower than fen meadows (64,000–94,000 seeds m^{-2}), dry-mesophilous (4400–6300 seeds m^{-2}) (Valkó et al., 2011) and some chalk grasslands in Germany (6000–7000 seeds m^{-2}) (Poschlod & Jackel, 1993). Our research thus suggested that soil seed bank in this region could not be considered the dominant source for the establishment of species following disturbances and unlikely to be a driving force in successional change. Earlier study suggested that soil seed banks can only play a subordinate role in restoration, because the most abundant species in the seed bank were annual herb and species composition of the seed bank reflected earlier stages rather than the corresponding established vegetation (Wang et al., 2015). At the same time, the soil seed bank species richness was extremely low; only eight species were recorded in soil seed bank communities in all 24 bare patches (Table 2). This number was much lower than inter-dune lowland in the same area that had 30 species (Wang et al., 2015).

Several causes might be responsible for the extremely low average density and species richness of soil seed bank in our study area. First, the average vegetation density and vegetation species richness was already low (only 1.09 individuals m^{-2} and 18 species), which limited seed production and soil seed banks. Seed production can be more limited if the dominant perennials only contribute minimally to the formation of soil seed stock (Lemauviel et al., 2005). Our data showed that all the eight species which we recorded in the soil seed bank were annual herbs. Because early successional species are not supported by other life forms, natural regeneration that relies only on soil seed bank in most cases is not feasible (Bossuyt & Honnay, 2008). Second, low vegetation density and cover make it difficult to intercept seeds as these seeds can be easily dispersed by the wind on the bare soil (Hyatt & Casper, 2000). Wind erosion in these areas generates not only soil loss, but also the loss of soil seed banks. Third, even the seeds manage to germinate after rainfall, it is difficult for the seedlings to survive because of unsuitable habitat (Ling et al., 2005). In this particular habitat, recruitments from soil seed banks constraint ecological restoration.

4.2. The relationship between aboveground vegetation and soil seed banks

Bare patch areas indirectly affected soil seed bank density by decreasing vegetation density. However, soil seed bank density is also determined by other factors, such as seed transmission (Wang et al., 2015). Therefore, although there is high correlation between vegetation density and bare patches area, there is no significant relationship between average seed density and bare patch area ($R^2 = 0.02$, $p = 0.72$). The same reason explained why the correlation between soil seed bank species richness and bare patches area was weak ($R^2 = 0.28$, $p = 0.03$). Some studies found a decrease in similarity as succession progressed in grassland systems (Kalamees & Zobel, 1998; Wagner et al., 2003). This is also consistent with Wang et al. (2015) who showed higher similarity occurred during early succession in frequently disturbed habitats. Similar to our findings, irrespective of the vegetation type, only a small number of target species built up detectable in soil seed banks (Valkó et al., 2011).

The relationship between soil seed banks and the aboveground vegetation is crucial for evaluating the role of soil seed banks in regeneration potential (Lu et al., 2010). Our finding showed that soil seed bank in this region only consisted of annual herbs. In disturbed regions, annual species are favored, as also shown in the soil seed banks of grey dune and cleared habitats (Lemauviel et al., 2005). Annual herbs produce large quantities of seeds (Wang et al., 2015), having a high longevity index (Plassmann et al., 2009), a capacity for fast dispersal (Bossuyt & Hermy, 2004), and allocating a higher fraction of their resources to seeds than their perennial counterparts (Thompson et al., 1993). Because soil seed bank communities were depauperate and restoration of former richness could not be based exclusively on the local soil seed banks (Valkó et al., 2011), the missing species must be actively seeded during restoration (Toeroek et al., 2012; Wang et al., 2013).

4.3. The relationship between above-ground vegetation, soil seed bank and in-situ habitat characteristics

Population patterns in sand dunes is a result of long term interactions between living vegetation and soil seed bank as well as their relationships with the habitat characteristics (Zhang et al., 2015). In our study, most large bare patches ($300\ m^2 \leq$ area $<900\ m^2$) had a strong positive correlation with coverage, soil seed bank species richness and soil seed bank density, while most small bare patches (area $<50\ m^2$) had a strong positive correlation with vegetation density, annual herb density and perennial herb density.

These results indicated that different factors can influence the success of restoration in different-sized bare patches. Consequently, different sizes of bare patches require distinct restoration measures. For bare patches with an area between $300\ m^2$ and $900\ m^2$, we need to increase soil seed bank density and species richness. For bare patches with area less than $50\ m^2$, we should increase vegetation density.

5. Conclusions

We showed that the Horqin region had low soil seed bank density and species richness, as well as depauperate soil seed bank communities. These results suggested that soil seed bank might not be feasible to provide sufficient seed source for natural regeneration. Because different extents of degraded areas required distinct restoration measures, maintaining soil seed bank and natural regeneration potentials need to be backed by conducive policies, strategies and action plans. This study provided a foundation for ecological restoration strategies of degraded sandy grasslands, which is a vital element for sustainable development.

Declaration of competing interest

No conflict of interest exits in the submission of this manuscript, and manuscript is approved by all authors for publication. All authors declare no competing financial interests.

Acknowledgments

We thank Yongming Luo and Hongmei Wang for assistance with field work. This study was supported by National Natural Science Foundation of China (41601588), Natural Science Foundation of Liaoning province (2019-MS-340), National Natural Science Foundation of China (31971732, 41501573).

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