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ORIGINAL PAPER

Spatial structure and species composition of soil seed banks in moving sand dune systems of northeast China

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Abstract Soil seed banks can provide a mechanistic for understanding the recruitment dynamics and can inform conservation management of ecosystems. To investigate the contribution of soil seed banks to vegetation restoration in moving sand dune systems, we compared seed structure and species similarity between soil seed banks and standing vegetation among moving sand dunes, ecotones and dune slacks in northeast China. Average seed density in dune slacks was greater than in ecotones or moving sand dunes. Seed density in the soil layer of 0–10 cm was greater than at 10–20 cm both in the moving sand dunes and the ecotones, but seed densities were similar at depths of 10–20 and 20–30 cm in moving sand dunes. Moreover, the spatial autocorrelation of seed density on moving sand dunes was weak but was strong on the ecotones and dune slacks. The species in the soil seed bank of moving sand dune systems were nearly all annuals, and the low similarity was mainly due to the lack of perennial species that were common in standing vegetation. Consequently, vegetation restoration cannot mainly rely on the soil seed banks in the moving sand dunes and more attention should be paid to protection of the dune slacks because they are the main source of seed disperse and seedling recruitment in moving sand dune systems.

Keywords Compositional similarity · Seed density · Seedling recruitment · Species composition · Horqin sandy land

Introduction

Degradations of dryland areas is a major environmental issue of the twenty-first century because it leads to unsustainable loss of ecosystem services and poses serious threats to life. It is affected by rapid change of plant community structure and composition, and/or soil conditions (Ravi et al. 2010; D'Odorico et al. 2012). Thus, many countries have made enormous efforts to restore vegetation by planting and fencing to control land degradation (Zhang et al. 2005).

The process of vegetation restoration on degraded area could be regarded as succession (Zhang et al. 2005). Soil seed banks are a critical component of the dynamics, conservation and sustainable management of the ecosystems since they play critical ecological and evolutionary roles in linking the past, present, and future of a given community (Bai et al. 2004; Bertiller 1998; Thompson and Grime 1979). The high spatial heterogeneity in structure and composition of seed banks is mainly affected by the heterogeneity of standing vegetation in arid and semiarid areas (Dreber and Elser 2011). If there is a disturbance to the degraded plant community, the seed bank may have an important role in maintaining community diversity. Consequently, understanding of soil seed banks and seed

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population dynamics is critical for clarification of the mechanisms of vegetation regeneration (Li et al. 2004).

Knowledge of the soil seed bank on moving sand dune systems is of practical importance in vegetation restoration by mitigating the risk of species extinction due to harsh conditions and supplying propagules for re-establishment after disturbance (Auld et al. 2000; Wang and Liang 1995). Furthermore, the correlation of species composition between seed banks and associated plant communities attracts the attention of restoration projects (De Villiers et al. 2003; Ma et al. 2012). Examining the similarity between the seed bank and standing vegetation during succession can provide new insights into the mechanisms of the resilience of plant communities, and into restoration strategies (Scott and Morgan 2012).

Our study aimed to investigate the spatial structure of the soil seed bank in moving sand dune systems horizontally and vertically, to determine which species are dominant in the soil seed bank, and to examine whether the soil seed bank can contribute to vegetation restoration and seedling recruitment in moving sand dune systems.

Materials and methods

Study site

The study was conducted at Wulanaodu Experimental Station (119°39′–120°02′E, 42°29′–43°06′N, 480 m a.s.l.), Chinese Academy of Sciences, located in Horqin Sandy land, northeast Inner Mongolia, China. The climate is continental semiarid monsoon with average precipitation of 284 mm, mainly falling between June and August. The mean annual air temperature is about 6.3 °C. Maximum and minimum daily temperatures are about 23.0 °C (July) and −14.0 °C (January). The mean annual wind speed is 4.4 m s^{-1}, and the number of gale days (>16 m s^{-1}) is 21–80.

The moving sand dune system consists of three parts: windward slope of an active dune, dune slack, and ecotone between the moving sand dune and the dune slack (Yan et al. 2005, 2009). Moving sand dunes are usually characterized by low moisture content, strong wind erosion, and sand burial, with vegetation coverage less than 5 % and advancement at a rate of 5–7 m per year (Cao et al. 2004; Yan et al. 2005). The ecotone, located at the foot of the windward slope of the dune, is colonized by pioneering species such as *Setaria viridis*, *Phragmites communis*, *Hedysarum fruticosum* (Jiang et al. 2013). The dune slacks, surrounded by crescent dunes, are composed of psammophytes and non-psammophytes and have relatively high soil moisture (Yan et al. 2005; Liu et al. 2007).

Sampling

Samples were taken from moving sand dune systems in early April 2012. A 50 m × 50 m sampling plot was randomly located on the moving sand dunes, ecotones and dune slacks of three moving sand dune systems. The sampling plot was separated into ten transects at intervals of 5 m. Ten substrate cores, spaced at 5 m intervals, were collected along each transect. Each soil sample was collected using a cylindrical container of 7 cm diameter and 10 cm length from three soil layers (0–10, 10–20 and 20–30 cm) in the moving sand dunes, two soil layers (0–10 and 10–20 cm) in ecotones, and one layer (0–10 cm) in dune slacks. A total of 1800 plots were sampled for soil seed bank analysis. The soil samples were sieved through a 0.5 mm-mesh size to remove stones, roots, and rhizomes after air-drying. Seedling emergence method was used to assess the composition of seed banks. In August 2012, when vegetation was well developed, vegetation composition was investigated in 1 × 1 m^2 quadrats corresponding to soil seed bank cores.

Data analysis

Differences between average seed density of three soil layers at moving sand dunes, two layers at ecotones, and three parts of moving sand dune systems were assessed by one-way analysis of variance (ANOVA) and Duncan's test at a significant level of $P < 0.05$ was used to compare means. The analysis was performed using SPSS statistical package for windows 16.0.

The semivariances (Jiang et al. 2013) of the average seed density on the three moving sand dunes, the ecotones and the dune slacks were calculated by GS+ (Gamma Design Software, version 9.0), and semivariograms were generated.

Principal component analysis (PCA, Canoco 4.5) was used to assess the dominant species in the soil seed bank. Species similarity between the soil seed bank and standing vegetation was calculated using Sorensen's qualitative similarity index [$Cs = 2j/(a + b)$, where a and b are the total number of species in the seed bank and the vegetation, respectively. J is the total species number in both the seed bank and the vegetation].

Results

Soil seed bank structure in moving sand dune systems

The average seed densities at the soil layer (0–10 cm) of the moving sand dunes and of the ecotones were

(713 ± 158) seeds m^{-2} and 3554 ± 405 seeds m^{-2}, respectively (Fig. 1). The seed density at the layer of 0–10 cm of the dune slacks was significantly higher than that of the ecotones or moving sand dunes. On the moving sand dunes, seed density at the soil layer was significantly higher than at 10–20 or 20–30 cm. Seed densities also differed significantly between the soil layer and at 10–20 cm in the ecotones.

Average seed density varied along the slope from the top of the moving sand dunes to the bottom of the dune slacks (Fig. 2). Average seed density was lowest on the moving sand dunes and there were nearly no significant variations. However, average seed density on the ecotones increased gradually along the slope. The differences occurred on the dune slack because the average seed density gradually increased to the highest value, and then declined slightly.

Semi-variance analysis of seed density on the moving sand dunes showed that the spatial variability of soil seed bank on the moving sand dunes could be fitted with a linear model (Table 1). Both the nugget variance and sill of the average seed density on the moving sand dunes were 1.9 million. However, the spatial variability of soil seed bank on the ecotones and on the dune slacks fitted well with the exponential models. The nugget variances on the ecotones and dune slacks were 50,000 and 8.7 million, and sills were 13.76 and 66.42 million, respectively. Soil seed banks on both the ecotones and dune slacks showed high heterogeneity.

Species composition of soil seed bank and the relationship with vegetation

There were 4, 12, and 16 species recorded in the soil seed banks of the moving sand dunes, the ecotones, and the dune slacks, respectively, and 18 species of seven families in total (Table 2). The dominant species of the soil seed bank in the moving sand dunes were *Agriophyllum squarrosum*

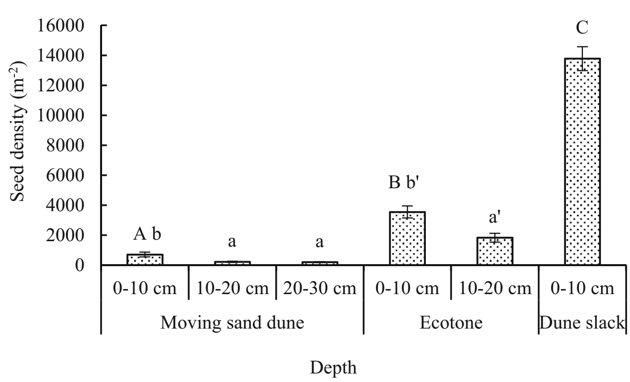

Fig. 1 Variation in average seed density (±SE) by components and substrate layers of moving sand dune systems

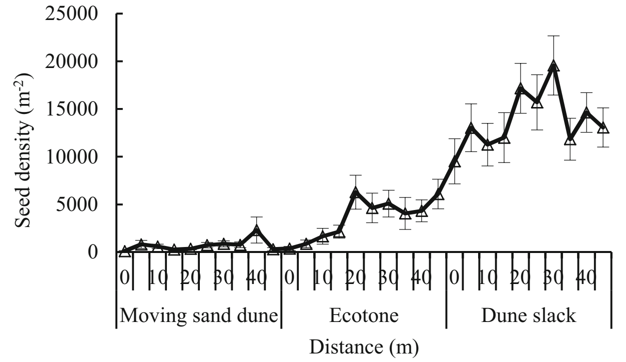

Fig. 2 Average seed density (±SE) along the slope from the top of the moving sand dunes to the bottom of the dune slack

and *Artemisia wudanica* (Fig. 3). Both *Setaria viridis* and *Chenopodium acuminatum* were the dominant species in seed banks of the ecotones and dune slacks.

There were 6, 30, and 57 species recorded in the vegetation on the moving sand dunes, ecotones, and dune slacks, respectively, and 58 species of 17 families in total. Similarities between vegetation and the soil seed bank of the moving sand dunes (Fig. 4), the ecotones, and the dune slacks were 13.30, 15.66, and 29.76 %, respectively. Moreover, the similarity for dune slacks was significantly higher than for ecotones or moving sand dunes.

Discussion

Contribution of abiotic and biotic factors to the structure of the soil seed bank

Soil seed banks can be important sources of seeds for vegetation restoration. The role of soil seed banks in vegetation development during restoration is determined by their seed densities and species richness (Bakker et al. 1996). Dune slacks at Horqin Sandy Lands were characterized by higher seed density than in ecotones or in moving sand dunes at a sampling depth of 0–10 cm. Moving sand dunes had the lowest seed density. Seed density on the moving sand dunes was highest in the upper 10 cm of the soil and generally declined with depth. Seed density in the upper 10 cm of ecotones was higher than at 10–20 cm. Both of the seed densities on the moving sand dunes and ecotones showed a declining trend from the upper soil levels to the deeper soil levels. The similarity of the 0–10 cm seed bank and vegetation on the moving sand dunes was nearly 100 %, and the nugget variance and sill indicated that nearly 100 % heterogeneity of the soil seed bank on the moving sand dunes was attributed to random factors. In contrast, 0.36 % of the heterogeneity on ecotones arose from random factors and 99.64 % was

Table 1 The mode and parameters for semivariogram of soil seed bank under isotropy

Sits	Models	Nugget (C_0)	Sill ($C_0 + C$)	Nugget/sill (%)	Range (A_0)	R^2
Moving sand dunes	Linear	1,924,139	1,924,139	100	26.48	0.146
Ecotones	Exponential	50,000	13,760,000	0.36	4.72	0.943
Dune slacks	Exponential	8,700,000	66,420,000	13.10	2.36	0.699

Table 2 Species list for seed banks of moving sand dunes, ecotones, and dune slacks

Species	Abbreviation	Family	Life form	MSD	ET	DS
Silene jenissensis	Sj	Caryophyllaceae	AH			√
Agriophyllum squarrosum	As	Chenopodiaceae	AH	√	√	√
Chenopodium acuminatum	Ca	Chenopodiaceae	AH		√	√
Corispermum candelabrum	Can	Chenopodiaceae	AH	√	√	√
Artemisia wudanica	Aw	Compositae	SS	√	√	
Card uus nutans	Cu	Compositae	BH			√
Senecio argunensis	Sa	Compositae	PH		√	√
Bolboschoenus compacts	Bc	Cyperaceae	PH		√	√
Cyperus glomeratus	Cg	Cyperaceae	AH			√
Chloris virgata	Cv	Gramineae	AH		√	√
Eragrostis pilosa	Ep	Gramineae	AH		√	√
Setaria viridis	Sv	Gramineae	AH	√	√	√
Glycine soja	Gs	Leguminosae	AH			√
Hedysarum fruticosum	Hf	Leguminosae	SS		√	√
Sophora flavescens	Sf	Leguminosae	PH		√	√
Swainsonia salsula	Ss	Leguminosae	SS			√
Thermopsis lanceolata	Tl	Leguminosae	PH			√
Polygonum divaricatum	Pd	Polygonaceae	PH		√	

AH annual herb, *BH* biennial herb, *PH* perennial herb, *SS* semi-shrub, MSD Moving sand dune, *ET* Ecotone, *DS* Dune slack

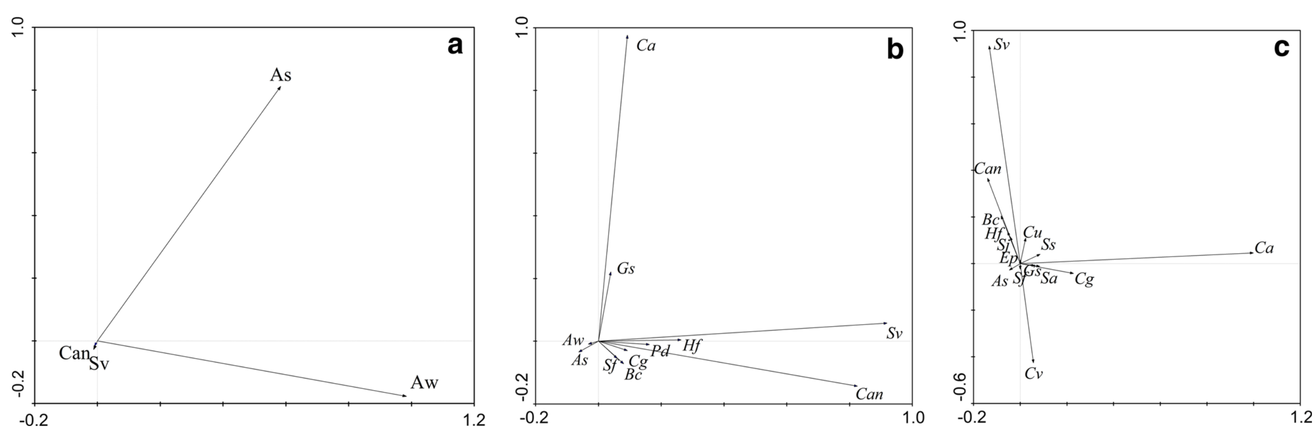

Fig. 3 PCA biplot of species in the soil seed bank of moving sand dunes (**a**), ecotones (**b**), and dune slack (**c**). Species names are abbreviated, see Table 2 for full names

attributed to spatial autocorrelation. 13.10 % of heterogeneity on dune slacks was attributed to random factors and 86.90 % was a result of spatial heterogeneity. In other words, the degree of spatial autocorrelation of the seed density on the moving sand dunes was weak but it was strong on the ecotones and dune slacks.

The size of a soil seed bank is attributed to the balance between seed input and output. The low seed density in the soil seed bank could have resulted from a low seed input due to low seed production by dominant species in the vegetation (Bossuyt and Hermy 2004; Miao et al. 2013). The low seed density on moving sand dunes is due mainly

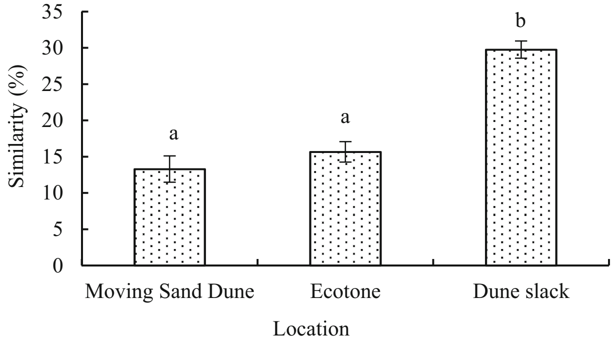

Fig. 4 Similarity (±SE) of species composition in the seed bank and standing vegetation in moving sand dune, ecotone, and dune slack

to the low seed input when vegetation species are rare (Bossuyt and Hermy 2004; Holzel and Otte 2004; Bossuyt et al. 2007). Species clustered in the soil seed bank generally caused by the clustered distribution of seed producing plants in the vegetation (Thompson 1986; Bossuyt and Hermy 2004; Bossuyt et al. 2007). Therefore, more seeds may have been present on the dune slacks than moving sand dunes because of the well-developed vegetation on the former.

Spatial variation in seed banks is mainly determined by abiotic factors including wind condition, topography, soil condition (Chambers and MacMahon 1994; Okubo and Levin 1989; Thompson and Grime 1979; Yan et al. 2005). In particular, wind action and sand movement are the most important abiotic factors controlling seed distribution in the moving sand dune systems (Yan et al. 2005, 2009). Dune slacks had abundant reserves of seeds because of the wind-breaking effect of dense vegetation and optimal landform (Yan et al. 2005, 2009). However, hardly any seeds occurred on the moving sand dunes and at the side of ecotones that were subject to the impacts of wind erosion and sand movement.

Species composition of soil seed banks and implications for restoration

Similarity between the soil seed bank and standing vegetation ranged from 13 to 30 %, lower than what is often reported for grassland systems (De Villiers 2003; Kalamees et al. 2012). Low similarity in the dune ecosystem might be attributable to low seed production by the dominant species of vegetation and generally low seed production on the moving sand dune systems (Ma et al. 2012). The species in the soil seed bank of moving sand dunes were nearly all annual species, and the low similarity between species in the seed bank and those in the vegetation can be partially attributed to the missing perennial species in the soil seed bank, as reported by Major and Pyott (1966) and Morgan (1998), and consistent with the conclusion of Scott and Morgan (2012).

Species present in the seed bank or dispersal are important factors affecting the dissimilarity between the standing vegetation and the soil seed bank (Thompson and Grime 1979; Dolle and Schmidt 2009). Our results showed that the contribution of soil seed banks to vegetation restoration was limited in the moving sand dune systems, and soil seed bank composition was insufficient to explain standing vegetation composition (Yan et al. 2005). Consequently, restoration of moving sand dunes is dependent on seeds dispersal from nearby plant communities. Dispersal is one of the most important factors in vegetation restoration. When seeds required for restoration are neither in the established vegetation nor in the soil seed bank of the target community, they can only be dispersed from local or regional species pools (Bakker et al. 2005). In Horqin Sandy land, soil seeds in the ecotones and moving sand dunes were mainly dispersed from dune slacks.

Conclusion

The Horqin seed banks tended to reflect former vegetation but could not drive the process of vegetation restoration. The species in the soil seed bank of moving sand dunes were nearly all annuals, and the low similarity between the seed bank and the vegetation was due in part to the perennial species that were missing from the soil seed bank but were common in the standing vegetation. Consequently, vegetation restoration cannot rely on the seed bank on the moving sand dunes, and more attention should be paid to protection of dune slacks they are the main source of seed dispersal and seedling recruitment in the moving sand dune fields.

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