LAND DEGRADATION & DEVELOPMENT
Land Degrad. Develop. **27**: 305–315 (2016)
Published online 13 September 2015 in Wiley Online Library (wileyonlinelibrary.com) **DOI**: 10.1002/ldr.2428

THE VERTICAL DISTRIBUTION OF SOIL SEED BANK AND ITS RESTORATION IMPLICATION IN AN ACTIVE SAND DUNE OF NORTHEASTERN INNER MONGOLIA, CHINA

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Received: 30 April 2015; Revised: 17 August 2015; Accepted: 17 August 2015

ABSTRACT

Although the functions and characteristics of soil seed banks in topsoil layers have been described for various ecosystems, the spatiotemporal pattern of the seed bank in deep soil and its ecological implications for vegetation restoration of active sand dune have not been fully explored. In 2007 and 2008, seed densities with regard to dune position, soil depth and season were investigated on an active and a stabilized sand dune of northeastern Inner Mongolia, China. Seeds in the 0–10 cm topsoil layer accounted for 60% of total soil seed bank on the stabilized sand dune, while more than 40% of seeds were stored in the 50–100 cm layers on the active sand dune. Seed density declined significantly with soil depth on the stabilized sand dune, but it was relatively constant across the 0–100 cm soil profile on the active sand dune. Seed density fluctuated with soil depth on the active sand dune suggesting that seeds were either relocated upward or downward over time. Seeds of annual non-psammophytic species accounted for the majority of soil seed bank on the stabilized sand dune, while pioneer psammophytes contributed more to the soil seed bank of the active sand dune. Our data suggest that seeds in the deep soil layers of active sand dunes account for a large proportion of the whole soil seed bank. Because of the effect of wind erosion, seeds in deep soil could be gradually exposed to shallow soil layers and potentially contribute to population recruitment and vegetation restoration on active sand dunes.

KEY WORDS: population regeneration; sand burial; semi-arid region; vegetation restoration; vertical distribution

INTRODUCTION

Land degradation is mainly related to the soil degradation caused by human beings, which is taking place because of human activities such as inappropriate agriculture practices and overgrazing (Cerdà *et al.*, 2009; García-Orenes *et al.*, 2012; Parras-Alcántara *et al.*, 2013). Those human interferences change the soil properties and the role of soil in biogeochemical and hydrological cycles, and as a result, soil services could be lost (Keesstra *et al.*, 2012; Berendse *et al.*, 2015).

Soil seed banks are a key biological part of soil systems as upon the seeds, the vegetation will be potentially recovered, and seeds will influence the plant distribution and as a consequence the soil properties and soil erosion (García-Fayos *et al.*, 2010; Kröpfl *et al.*, 2013). Soil seed banks play an important role in population regeneration and vegetation restoration, especially in ecosystems experiencing frequent disturbances (Milberg, 1995; Davies & Waite, 1998; Li *et al.*, 2004; Willems & Bik, 2009; Li *et al.*, 2012; Li *et al.*, 2014). It is important therefore to describe the spatiotemporal pattern of soil seed banks to understand their roles in population recruitment and vegetation restoration. Although the spatiotemporal pattern of soil seed banks have been described for various ecosystems (Russi *et al.*, 1992; Dalling *et al.*, 1997; Guardia *et al.*, 2000), the mechanisms of formation and ecological functions of soil seed banks in active sand dune ecosystems have not been fully explored.

In most soils, seeds accumulate in topsoil layers, and seed density declines rapidly with soil depth (Fenner & Thompson, 2005). Therefore, investigations on soil seed banks by sampling the topsoil layer, usually the top 10 cm, have been extensively performed (Witkowski & Garner, 2000; Valbuena & Trabaud, 2001; Li *et al.*, 2009; Li *et al.*, 2014). The spatiotemporal pattern of soil seed banks in the topsoil layer of sand dune ecosystems, including active sand dunes, stabilized sand dunes and their inter-dune lowlands, have also been partly discussed (Bai *et al.*, 2004; Yan *et al.*, 2009). However, it has been confirmed that wind activities that different sand dunes are exposed to could influence the spatiotemporal pattern of soil seed banks (Yan *et al.*, 2005). Wind erosion tends to be dominant on the windward slope, and sand deposits tend to be dominant over the crest as well as the leeward slope (Liu *et al.*, 2007). Therefore, concerns have been raised on the application of shallow sampling techniques for the study of active sand dunes because seeds can either be blown away by wind or buried deeply during dune migration (Liu *et al.*, 2007). Deep soil samplings should be taken into consideration in

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order to understand the effects of eolian activities on the seed availability and the vegetation restoration of sand dune ecosystems.

Unpredictable sand burial and wind erosion could reduce the opportunity of seedling emergence, seedling survival and vegetation restoration on active dunes (Crawford, 1989; Zhang & Maun, 1990; Maun *et al.*, 1996; Liu *et al.*, 2011). During the rainy season, seeds buried close to the soil surface are prone to germinate and contribute to seedling recruitment. Deeply buried seeds, however, are not available because of the microhabitat limitation on seed germination and seedling emergence (Zhan & Maun, 1994; Bai *et al.*, 2004; Tobe *et al.*, 2005; Liu *et al.*, 2011). During the windy season, seeds can be either buried and accumulate deep in the dune (Thompson & Fenner, 2000; Matus *et al.*, 2005; Liu *et al.*, 2007), carried away by the wind or dug out from deep soil to topsoil layers and potentially become available as a seed supply for population recruitment as soon as the effective rainfall occurs.

The seasonal dynamics of soil seed banks must also be considered to understand the ecological significance of deep soil seed banks in active sand dune ecosystems. Soil seed banks vary in species composition and abundance across seasons and years (Kemp, 1989; Lavorel *et al.*, 1993; Yan *et al.*, 2009). Unlike most ecosystems where soil seed bank dynamics are determined by plant reproductive phenology, seed dispersal, seed predation and other factors (Price & Joyner, 1997; Cubina & Aide, 2001; Liu *et al.*, 2012), seed bank dynamics in active sand dunes are mainly determined by sand burial and wind erosion (Liu *et al.*, 2007; Yan *et al.*, 2009). Spatiotemporal patterns of soil seed banks are closely related to sand dune positions, with the different types and intensities of eolian activities the dune is exposed to determining whether seeds will be buried or blown away. Furthermore, erosion intensities vary along the windward slope, and there is a sand deposit gradient along the leeward slope. However, without considering the seasonal dynamics of soil seed bank, the potential ecological implications of deep soil seed banks for vegetation restoration in active sand dunes have not been revealed.

The Horqin Sandy Land in Inner Mongolia of northern China was populated by temperate grasslands, which has been degraded following series of severe desertification processes in the past decades (Zhu & Chen, 1994). Active sand dunes are now well developed in this region, which have been considered as one of the main sand sources of sand storms in northern China (Zhu & Chen, 1994; Liu *et al.*, 1996). Sand storms affect the total area of about $6{\cdot}24 \times 10^6\,km^2$, which accounts for 65% of China (Zhang, 2008). Therefore, vegetation restoration on active sand dunes is essential to control the desertification and sand storms (Zhu & Chen, 1994; Sun *et al.*, 2001).

From the perspective of biodiversity conservation, active sand dunes could provide the habitat for some pioneer species and endemic species, such as *Agriophyllum squarrosum* and *Artemisia wudanica*. With their deep soil seed banks, these pioneer species could become established on active sand dunes and are helpful for sand stabilization and other species colonization (Yan *et al.*, 2005; Li *et al.*, 2007). However, after active sand dunes stabilized, some annual species, such as *Chenopodium glaucum* L., *C. acuminatum* Willd, *Corispermum candelabrum* Iljin and *Bassia dasyphylla* O. Kuntze, which will encroach naturally, and those pioneer species will be replaced (Li *et al.*, 2007). Therefore, understanding the spatiotemporal pattern of soil seed banks in active sand dunes is helpful for revealing the adaptive strategy of plants and implementing effective measures for desertification control and biodiversity conservation.

Because little is known about the formation mechanisms of the spatiotemporal pattern and ecological significance of soil seed banks in active sand dunes, this study aimed to explore the soil seed bank dynamics with regards to soil depth, dune position and season, with the purpose of testing the hypothesis that (i) there will be a relatively constant seed density across sand profiles in active sand dunes; and (ii) the cycling effect of sand burial and wind erosion results in the sustainable seed supply for population regeneration and vegetation restoration in active sand dunes.

MATERIAL AND METHODS

Study Site

This study was conducted at the Wulanaodu Desertification Experimental Station in the Horqin Sandy Land in northeastern Inner Mongolia, China (119°39′–120°02′E, 42°29′–43°06′N, 480 m asl). To compare the spatiotemporal patterns of soil seed banks in stabilized and active sand dunes and reveal the ecological significance of deep soil seed banks in active sand dunes, a stabilized sand dune was selected in this study for comparison with the studied active sand dune. The investigated stabilized sand dune, which was an active sand dune 20 years ago, was artificially stabilized with both sand barriers and plantation in 1984 (Yan *et al.*, 2005). The selected active sand dune was 25 m high and advancing at a rate of 5–7 $m\,y^{-1}$, and the vegetation coverage is less than 10% (Yan *et al.*, 2005). Its vegetation was composed of only pioneering plant species such as *A. squarrosum* Moq. and *A. wudanica* Liou & W. The stabilized sand dune was populated with many annual species, such as *C. glaucum* L., *C. acuminatum* Willd., *C. candelabrum* Iljin, *B. dasyphylla* O. Kuntze, *Chloris virgata* Swartz, *Setaria viridis* Beauv. and *Digitaria ciliaris* Koel., which had encroached naturally. The vegetation coverage was greater than 50%, and no striking sand accumulation or erosion was observed.

Based on the meteorological data collected from 1957 to 2002, the annual average temperature at the study site was 6·3 °C, with January being the coldest month with an average temperature of −14·0 °C and July being the warmest month, averaging 23·0 °C. Annual mean precipitation was 340 mm, 70% of which occurred during June-August. Annual mean wind velocity at the study site was 4·4 $m\,s^{-1}$, mainly coming from the north, and the number of gale days per year

($>16\,m\,s^{-1}$) ranged from 21 to 80. The windy season generally occurs between early April and late May.

Species Composition of Soil Seed Banks

Seeds were collected across the stabilized and active sand dunes during the growing season (April to September) of 2007 for the species identification in soil seed bank. Soil seed bank samples were collected with a cylindrical borer of 7 cm in diameter and 100 cm in height. Soil columns were set every 10 cm down up to a depth of 100 cm for the active sand dune and up to 30 cm in the stabilized sand dune because very few viable seeds could be found beyond this depth in previous studies carried out on stabilized sand dunes (data not shown in the present study). Soil columns were sampled carefully layer by layer (10 cm segment). *Chenopodium aristatum* was identified as the species with the smallest seed present in our study sites. Its seed's dimensions are greater than 0·5 mm, so a 0·5 mm sieve was used to extract seeds from each soil sample according to the method of Yan *et al.* (2005). Seeds were sorted by species, and the viability of a subsample of seeds for each species (if the seed number for one species in a sample is less than 20, all seeds were tested; for other species, i.e. those seeds more than 20 in one sample, at least 20 seeds were tested) was determined using the 'tetrazolium dyeing method' (Günster, 1994). The proportion of viable seeds in subsamples and the total seed number were used to assess the viable seed density. In this study, only viable seeds were considered. Even though the 'tetrazolium dyeing method' is much labour intensive and could lead to an overestimation of viable seed density compared with the seed germination method, it still was considered as the most accurate method for this study because it can be used to test the viability of both dormant and non-dormant seeds (Copeland & McDonald, 1999) and seeds in sand dunes show different levels of dormancy (Yan *et al.*, 2007; Liu *et al.*, 2011).

Seasonal Dynamics of Soil Seed Banks

Soil seed bank samples were collected from the stabilized and active sand dunes in early April (at the beginning of the windy season), mid-May (in the middle of the windy season), mid-July (in the middle of the rainy season) and in late October (at the end of seed fall) both in 2007 and 2008. Eight parallel transects (10 m apart) were defined along the direction of sand dune migration (Figure 1). The length of transects were defined according to the size of the investigated sand dunes. For transects on the stabilized sand dune, transects were from the lower windward part to the dune crest, while for the active sand dune, transects were from the lower windward part to the lower leeward slope. According to the size of the investigated dunes, 18 cores were collected at 15 m intervals along each transect of the active sand dune. Fifteen from the windward slope, six on the lower part, five on the middle part and four on the upper part and three from the leeward slope (lower, middle and upper parts) (Figure 1). On the stabilized sand dune, 11 cores per transect were collected at 5 m intervals from the windward slope: four on the lower part, four on the middle part and three on the upper part. For each sampling time, transects were randomly established on the two investigated sand dunes, and the direction and the length were the same. For each sampling, we collected 264 soil samples (3 soil depths × 11 sample points × 8 transects) for the stabilized sand dune and 1,140 soil samples (10 soil depths × 18 sample points × 8 transects) for the active sand dune.

Data Analysis

Separated one-way ANOVA in SPSS 18·0 for Windows was applied to analyse the effect of dune type, dune position and soil depth on the seed density, species richness and relative species abundance in soil seed banks. The relative abundance of species was calculated as follows:

$$\text{Relative abundance}(\%) = \text{abundane of species } i \Big/ \text{total abundance of all species} \times 100\%$$

(Ma, 1994)

Prior to analyses, values were tested for normality (Kolmogorov–Smirnov test) and homoscedasticity (Fmax test). Seed density data were square-root transformed to make them conform to normal distribution law and homoscedasticity. If the ANOVA revealed significant effects, a Tukey's honestly significant difference post hoc test ($p < 0{\cdot}05$) was performed to compare the difference in seed density between different dune positions and soil depths. For the same soil layer and dune position, the differences in seed density between different sampling dates were also compared to reveal the seasonal dynamics in soil seed bank.

RESULTS

Change in Seed Bank Density With Regard to Soil Depth

The total seed density was up to approximately 200-fold higher in stabilized compared with active sand dune. The average seed bank density on the stabilized sand dune was 12,839 ± 872 seeds m^{-2} (mean ± SE(standard error), the same hereinafter) in the 0–30 cm soil layer, whereas on the active sand dune, 91 ± 16 seeds m^{-2} stored in the 0–30 cm soil layers and the total seed density in the 0–100 cm soil layer was 221 ± 26 seeds m^{-2}. About 60% of seeds were located

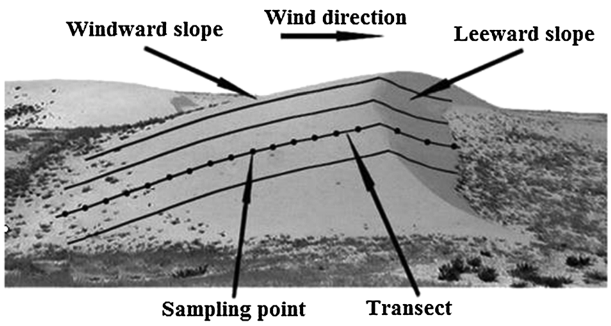

Figure 1. Transects and sampling positions on the investigated active sand dune.

in the top 10 cm of the stabilized sand dune, while only 16% were stored in the same layer on the active sand dune, and more than 40% of seeds were stored in the 50–100 cm soil layers on the active sand dune. Besides, the seed density was relatively constant across the sand profile of the active sand dune (Figure 2).

Change in Seed Bank Density With Regard to Dune Position

On the stabilized sand dune, seed bank density on the upper windward slope was lower ($p < 0{\cdot}05$) than any other parts of the windward slope. On the active sand dune, however, the seed bank density on the upper windward slope was significantly higher than those in other positions ($p < 0{\cdot}05$) except for that of the low windward slope (Figure 3).

Seed Bank Density Changes Over Time

On the stabilized sand dune, seed bank density in the top 0–10 cm layer remained greater than those in any other layer throughout the study. Seed density in the top 0–10 cm layer of the lower windward slope decreased constantly from October 2007 to July 2008 (Figure 4A). The peak seed density (15,152 ± 5,105 seeds m^{-2}) occurred in October 2007 when seed production is completed.

Both the middle and upper windward slopes of the stabilized sand dune had an increase in seed density from October 2007 to May 2008 in the top 10 cm layer, followed by a sharp decrease in July 2008 (Figure 4B and C). The peak seed density of both the middle (11,514 ± 1,571 seeds m^{-2}) and the upper windward slopes (9,777 ± 1,314 seeds m^{-2}) occurred at the end of the windy season (May).

Seed density in the top 0–30 cm layer of the lower windward slope and in the 60–100 cm layer of the upper leeward slope of the active sand dune increased on average by sixfold compared with seed density recorded in those layers at all other time points (Figure 5A and D). Even though seed density in other layers of the windward slope did not change significantly over time, there was a trend in increasing seed density in the top 0–30 cm layer of the middle windward slope and an increase in seed density in the 30–60 cm layer of the upper windward slope in May

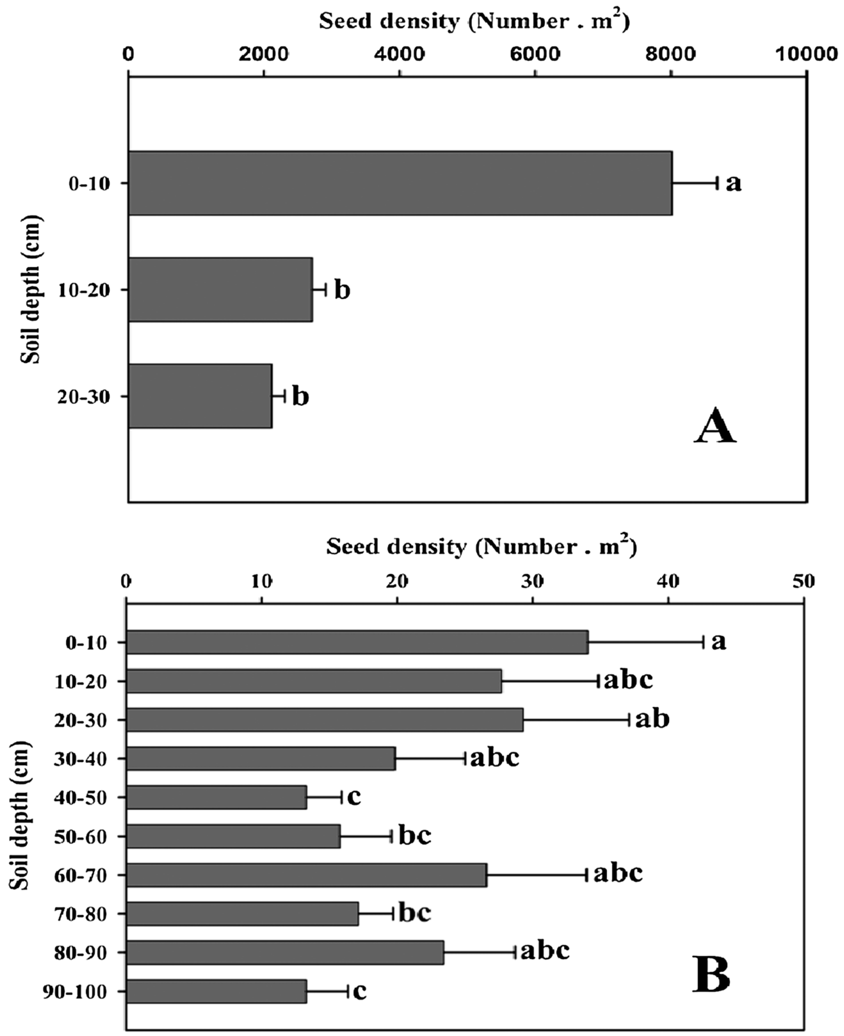

Figure 2. Two-year average seed densities across soil layers of the stabilized (A) and active (B) sand dunes. Values are means ± SE. Different letters indicate that the differences between soil depths are significant at $p < 0{\cdot}05$ level.

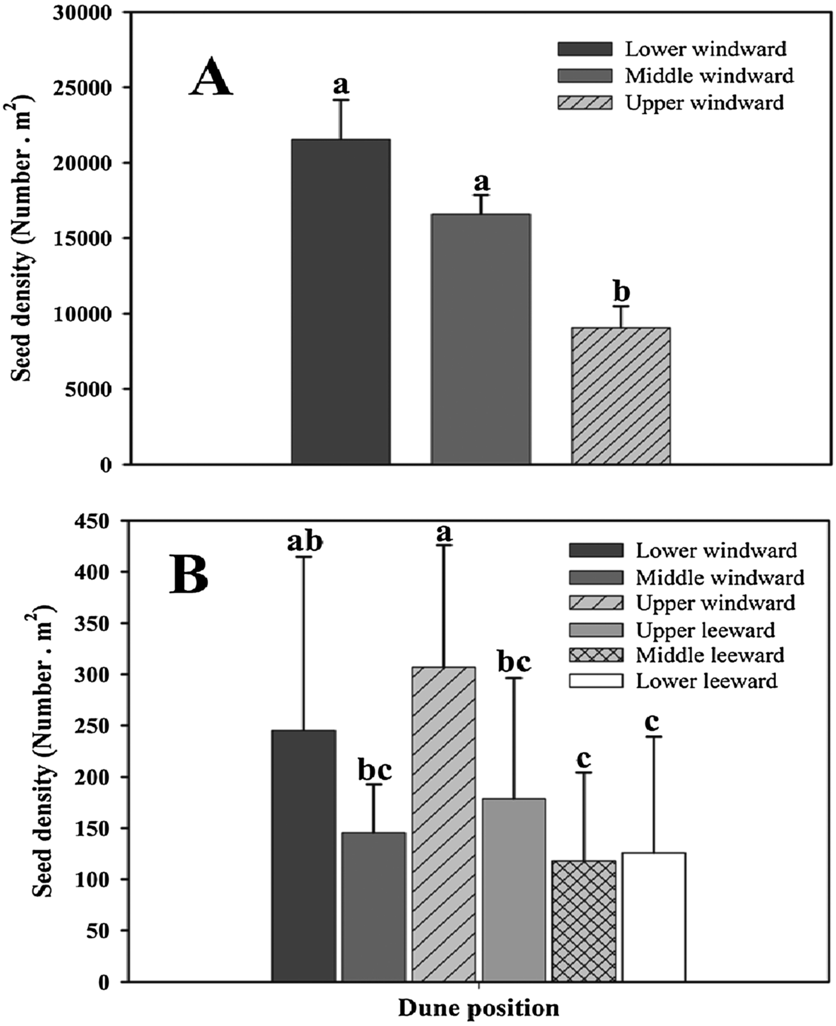

Figure 3. Two-year average seed densities at each sampling position of the stabilized (A) and active (B) sand dunes. Values are means ± SE. Different letters indicate that the differences between dune positions are significant at $p < 0{\cdot}05$ level.

(Figure 5B and C). There was also an increase in seed density in the top 0–30 cm layer in May for the middle leeward slope and in July for the lower leeward slope of the active sand dune (Figure 5E and F).

Species Composition of the Soil Seed Banks

There were 25 species belonging to nine families in the soil seed bank of the stabilized sand dune, while there are 18 species belonging to nine families in that of the active sand dune (Table I). The total species richness of the stabilized sand dune was significantly higher than that of the active sand dune ($p < 0{\cdot}05$; Table II). On the stabilized sand dune, the species richness on the upper windward slope was significantly lower than those of the lower and middle windward slope ($p < 0{\cdot}05$), and the species richness of the soil seed bank in the 0–10 cm layer was significantly higher than those of the 10–20 and 20–30 cm soil layers ($p < 0{\cdot}05$). On the active sand dune, the species richness on the windward slope was significantly higher than that of the leeward slope ($p < 0{\cdot}05$). However, there were no significant differences between different positions on both the windward and leeward slopes, respectively. Surprisingly, the species richness in the 30–60 cm layer was significantly lower than those of the 0–30 and 60–100 cm layers ($p < 0{\cdot}05$) (Table II).

The five most abundant species in the soil seed bank of the stabilized sand dune were annual non-psammophytic species: *S. viridis*, *C. acuminatum*, *C. glaucum*, *C. candelabrum* and *D. ciliaris*, with their total abundance accounting for 94–95% of the soil seed bank (94% with regard to soil depth and 95% with regard to dune position). Soil depth and dune position had no significant effects on the relative abundance of these species except for the fact that the relative abundance of *S. viridis* on the upper windward slope was significantly higher than that of the lower windward slope, while the relative abundance of *C. acuminatum* on the lower windward slope was significantly higher than those of other dune positions ($p < 0{\cdot}05$) (Table III). On the active sand dune, the two most abundant species in the soil seed bank were pioneer psammophytes: *A. squarrosum* and *A. wudanica*, with their total abundance accounting for 45–59% of the total abundance of the soil seed bank (45% with regard to soil depth and 59% with regard to dune position) (Table IV).

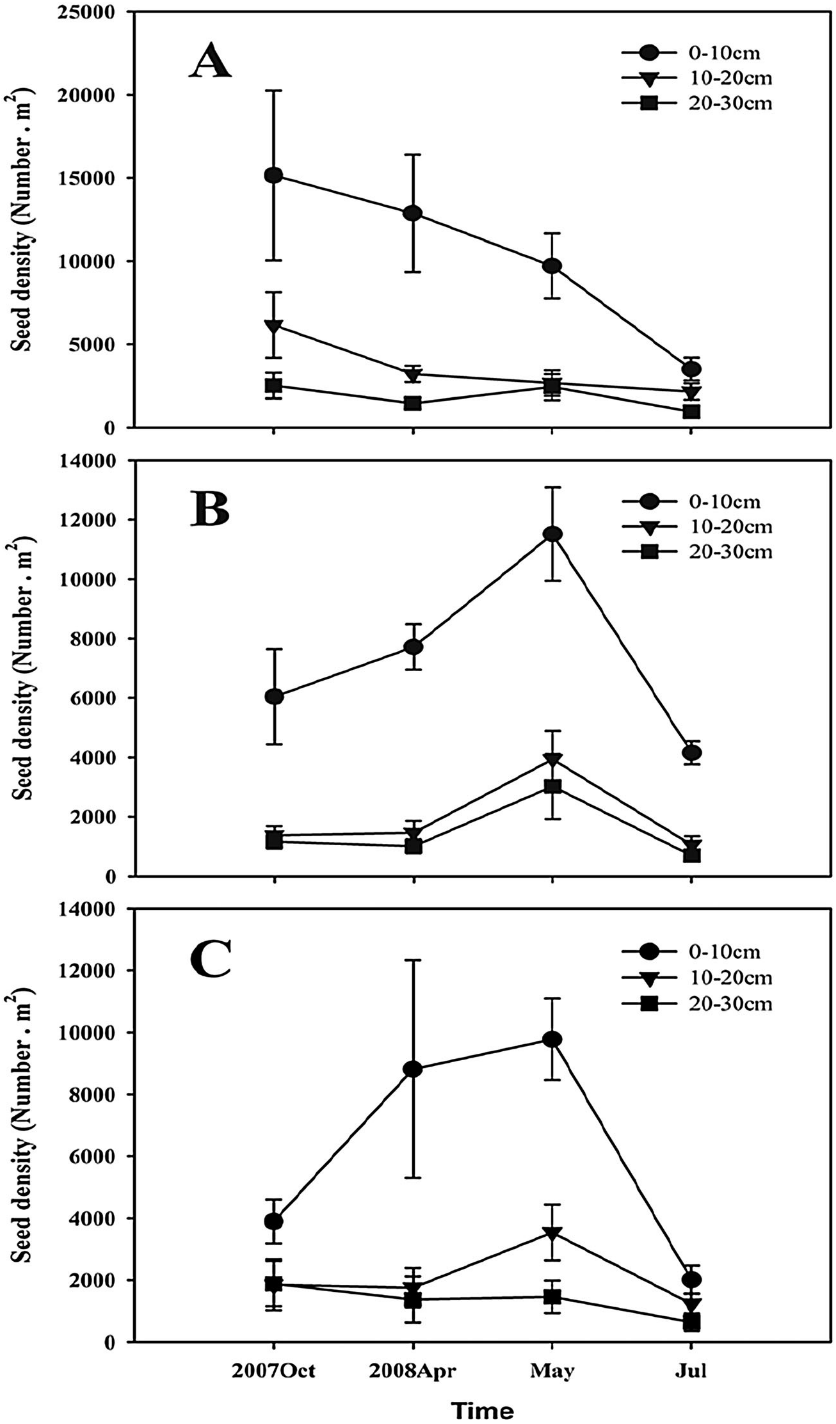

Figure 4. Seasonal changes in seed bank density with regard to depth and position of the stabilized sand dune. (A) The lower windward slope; (B) the middle windward slope; (C) the upper windward slope. Winter: October to April; windy season: April to May; rainy season: May to July. Values are means ± SE.

DISCUSSION

Wind activities are the main factors driving many ecological processes in dune ecosystems and have the potential to mould the spatiotemporal pattern of soil seed banks by alternately causing seeds being buried and exposing them to soil surface when dunes are eroded (Zhu & Chen, 1994; Ma & Liu, 2008). With regard to dune positions, seed density at the upper windward slope was lower than those on other positions of the stabilized sand dune (Figure 3A). This is most likely due to the fact that compared with other positions, the relatively sparse vegetation on the upper windward slope produces less seeds and could not retain seeds *in situ*. Besides, the relatively weak eolian activities on the stabilized sand dune means less seeds can be transported to the upper windward slope. For the active sand dune, our results are consistent with the findings of Wang *et al.* (2005) that seed density on

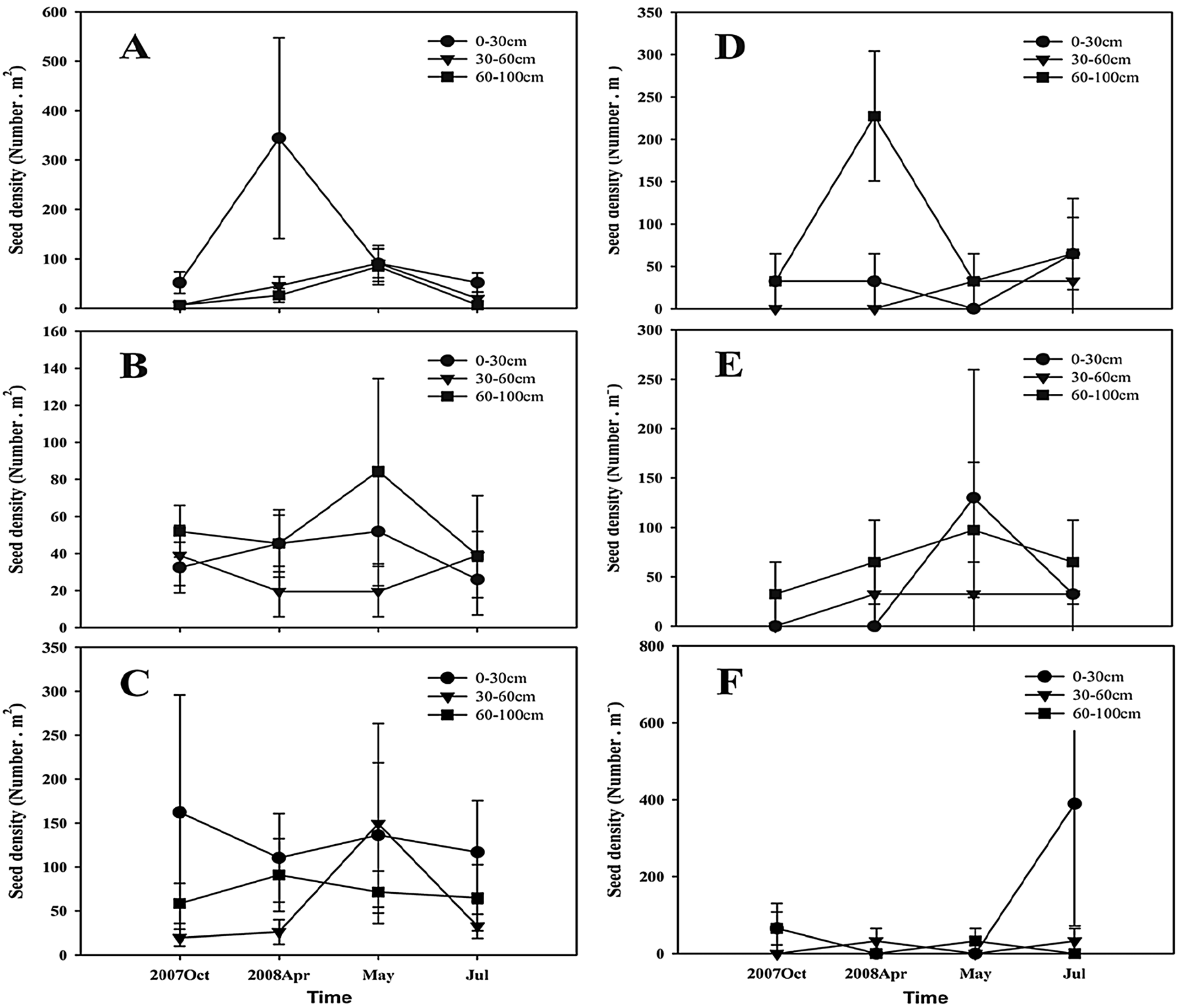

Figure 5. Seasonal changes in seed bank density with regard to depth and position of the active sand dune. (A) The lower windward slope; (B) the middle windward slope; (C) the upper windward slope; (D) the upper leeward slope; (E) the middle leeward slope; (F) the lower leeward slope. Winter: October to April; windy season: April to May; rainy season: May to July. Values are means ± SE.

the upper windward slope was higher than those on other positions of an active sand dune. In active sand dunes, seeds tend to accumulate on the upper windward slope because the wind carries the seed–sand mixture to the dune crest (Bai *et al.*, 2004). For the vertical distribution of soil seed bank, seed bank density decreased dramatically with soil depth in the stabilized sand dune (Figure 2A), which is consistent with the fact in most soils (Fenner & Thompson, 2005). On the active sand dune, however, despite of a slight decrease in seed density with soil depth, the vertical distribution of seed density was heterogeneous, and a relatively high amount of viable seeds was still found up to 100 cm depth. This vertical pattern of seed density in the active sand dune could be explained by the differences in wind activity intensity that occurs between stabilized and active sand dunes. On the active sand dune, seed density fluctuated with time in different soil layers. The seed density in the top 0–30 cm layer of the lower windward slope and in the 60–100 cm layer of the upper leeward slope of the active sand dune increased in April 2008. Subsequently, the seed density in the top 0–30 cm layer of the middle windward slope and in the 30–60 cm layer of the upper windward slope increased 2 months later, and another increase in the top 0–30 cm layer occurred in July for the lower leeward slope (Figure 5). These data suggest that seeds in active sand dunes are not only transported from the wind erosion-prone zones (i.e. the windward slopes) to the burial-prone zones (i.e. the dune crest and leeward slope) but also that deeply buried seeds could become shallowly buried or even be exposed to soil surface under wind erosion. Even though the seed transport by wind is the main contributing factor to changes in soil seed bank patterns in active sand dunes, seed germination can also occur during the rainy season when conditions are favourable. And, the inhabitation of pioneer species on the active sand dune strongly suggests that deep soil seed banks have the potential to contribute to population regeneration.

Table I. Species list of the stabilized sand dune and active sand dune

Stabilized sand dune			Active sand dune		
Family	Species	Life form	Family	Species	Life form
Chenopodiaceae	*Agriophyllum squarrosum*	AH	Chenopodiaceae	*Agriophyllum squarrosum*	AH
	Chenopodium acuminatum	AH		*Chenopodium acuminatum*	AH
	Chenopodium aristatum	AH		*Chenopodium glaucum*	AH
	Chenopodium glaucum	AH		*Corispermum candelabrum*	AH
	Corispermum candelabrum	AH			
Gramineae	*Chloris virgata*	AH	Gramineae	*Chloris virgata*	AH
				Digitaria ciliaris	AH
	Digitaria ciliaris	AH		*Phragmites communis*	PH
	Eragrostis pilosa	AH		*Setaria viridis*	AH
	Phragmites communis	PH			
	Setaria glauca	AH	Compositae	*Artemisia wudanica*	SS
	Setaria viridis	AH		*Erigeron acer*	ABH
				Eupatorium lindleyanum	AH
Leguminosae	*Caragana microphylla*	S		*Senecio argunensis*	PH
	Glycine soja	AH			
	Hedysarum fruticosum	SS	Apocynaceae	*Apocynum venetum*	PH
	Lespedeza davurica	SS	Asclepiadaceae	*Cynanchum sibiricum*	PH
	Swainsonia salsula	SS	Cyperaceae	*Bolboschoenus compacts*	PH
	Vicia amoena	PH	Leguminosae	*Lespedeza davurica*	SS
			Polygonaceae	*Polygonum thunbergii*	AH
Compositae	*Artemisia wudanica*	SS	Salicaceae	*Salix gordejevii*	S
	Erigeron acer	ABH			
	Eupatorium lindleyanum	AH			
Caryophyllaceae	*Dianthus chinensis*	PH			
Cyperaceae	*Bolboschoenus compacts*	PH			
Polygonaceae	*Polygonum lapathifolium*	AH			
Salicaceae	*Salix gordejevii*	S			
Zygophyllaceae	*Tribulus terrestris*	AH			

AH, annual herbaceous; ABH, annual–biennial herbaceous; PH, perennial herbaceous; SS, semi-shrub; S, shrub.

It was suggested that in sand dunes and some other degraded ecosystems, seed availability might be the key limiting factor of population recruitment and vegetation restoration (Crawford, 1989; Guardia *et al.*, 2000). But, some other studies also demonstrated that the absence of vegetation in disturbed ecosystems, for instance in the typical badland area of southeastern Spain and the Loess Plateau region of China, might be attributed to the limitation of environmental factors on seed germination and seedling survival rather than seed availability (García-Fayos *et al.*, 1995; Cerdà & García-Fayos, 1997; García-Fayos *et al.*, 2000; Wang *et al.*, 2014). In this study, the vertical distribution of soil seed bank (especially the deep soil seed bank) could potentially provide the sustained seed supply for population regeneration and vegetation restoration on the active sand dune. The establishment of some psammophytes via soil seed banks on the active sand dune can facilitate the colonization of other non-psammophytic herbaceous species, such as *B. dasyphylla* O. Kuntze, *C. virgata* Swartz and *S. viridis* Beauv., which will promote the stabilization

Table II. Comparison of species richness between different dune positions and soil depths on the stabilized sand dune and active sand dune

	Species richness			
	Stabilized sand dune		Active sand dune	
Dune position	Lower windward	5·00 ± 0·1 a	Lower windward	1·63 ± 0·23 *a*
			Middle windward	1·53 ± 0·09 *a*
	Middle windward	5·25 ± 0·25 a	Upper windward	1·60 ± 0·11 *a*
			Upper leeward	0·49 ± 0·09 *b*
	Upper windward	4·38 ± 0·18 b	Middle leeward	0·35 ± 0·07 *b*
			Lower leeward	0·35 ± 0·05 *b*
Soil depth (cm)	0–10	5·88 ± 0·13 a	0–30	2·19 ± 0·20 *a*
	10–20	4·50 ± 0·19 b	30–60	1·50 ± 0·10 *b*
	20–30	4·25 ± 0·16 b	60–100	1·99 ± 0·10 *a*
Total species richness	6·75 ± 0·21 *		3·64 ± 0·14	

Values within a column for different dune positions and soil depths followed by the same letter are not significantly different at $p < 0{\cdot}05$ level. Normal: stabilized sand dune; Italic: active sand dune.
*Significant difference in the total species richness between the stabilized and active sand dunes at $p < 0{\cdot}05$ level.

Table III. Relative abundances (%) of the five most abundant species in the soil seed bank of the stabilized sand dune

Species			Relative abundance (%)
Setaria viridis	Dune position	Lower windward	7 ± 1 b
		Middle windward	13 ± 2 ab
		Upper windward	14 ± 3 a
	Soil depth (cm)	0–10	10 ± 1 a
		10–20	10 ± 1 a
		20–30	13 ± 2 a
Chenopodium acuminatum	Dune position	Lower windward	75 ± 4 a
		Middle windward	60 ± 4 b
		Upper windward	52 ± 5 b
	Soil depth (cm)	0–10	62 ± 3 a
		10–20	65 ± 4 a
		20–30	66 ± 4 a
Chenopodium glaucum	Dune position	Lower windward	7 ± 1 a
		Middle windward	11 ± 2 a
		Upper windward	13 ± 3 a
	Soil depth (cm)	0–10	10 ± 2 a
		10–20	10 ± 2 a
		20–30	8 ± 2 a
Corispermum candelabrum	Dune position	Lower windward	7 ± 3 a
		Middle windward	10 ± 3 a
		Upper windward	12 ± 3 a
	Soil depth (cm)	0–10	11 ± 3 a
		10–20	7 ± 2 a
		20–30	8 ± 2 a
Digitaria ciliaris	Dune position	Lower windward	1 ± 0 a
		Middle windward	2 ± 0 a
		Upper windward	2 ± 1 a
	Soil depth (cm)	0–10	1 ± 1 a
		10–20	1 ± 1 a
		20–30	1 ± 1 a

Values within a column for different dune positions and soil depths followed by the same letter are not significantly different at $p < 0{\cdot}05$ level.

of active sand dunes and thus control desertification and sand storms effectively (Li *et al.*, 2007). In this case, the deep soil seed bank should be taken into account in implementing vegetation restoration on active sand dunes.

On the other hand, active sand dunes could provide specific habitats for some pioneer species and endemic species, such as *A. squarrosum* and *A. wudanica*, which often have a persistent soil seed bank (Liu *et al.*, 2007). Our study demonstrated the role of deep soil seed banks in the population maintenance of those species on active sand dunes. Seeds may be deeply buried and form a persistent soil seed bank under sand burial, while those seeds

Table IV. Relative abundances of the two most abundant species in the soil seed bank of the active sand dune

Species		Relative abundance (%)	
Agriophyllum squarrosum	Dune position	Lower windward	24 ± 4 b
		Middle windward	39 ± 6 ab
		Upper windward	65 ± 8 a
		Upper leeward	56 ± 16 ab
		Middle leeward	29 ± 12 ab
		Lower leeward	60 ± 12 ab
	Soil depth (cm)	0–30	34 ± 5 a
		30–60	36 ± 8 a
		60–100	31 ± 5 a
Artemisia wudanica	Dune position	Lower windward	10 ± 5 ab
		Middle windward	19 ± 2 ab
		Upper windward	7 ± 2 ab
		Upper leeward	4 ± 3 b
		Middle leeward	24 ± 11 a
		Lower leeward	15 ± 9 ab
	Soil depth (cm)	0–30	10 ± 4 a
		30–60	9 ± 3 a
		60–100	15 ± 4 a

Values within a column for different dune positions and soil depths followed by the same letter are not significantly different at $p < 0{\cdot}05$ level.

buried deeply will be shallowly buried and contribute to population recruitment under wind erosion. Our study indicates that the deep soil seed bank might be one of the important adaptations of species in response to wind activities on the active sand dune. After the stabilization of active sand dunes, these pioneer species and endemic species will be replaced by some non-psammophytic herbaceous species (Li *et al.*, 2007). Therefore, the deep soil seed bank might play an important role in the conservation for some pioneer and endemic species.

The species richness of the soil seed bank on the stabilized sand dune was significantly higher than that of the active sand dune (Table II), which could be attributed to the relatively dense vegetation and high species richness of the aboveground plant community on the stabilized sand dune (de Villiers *et al.*, 2003). Our results also show that annual non-psammophytic species accounted for the majority of the soil seed bank on the stabilized sand dune, while pioneer psammophytes contributed more to the soil seed bank of the active sand dune. The change in species composition of the soil seed bank from a stabilized sand dune to an active sand dune is consistent with the vegetation processes, which show that the richness and abundance of annuals increased significantly after sand dune stabilization (Li *et al.*, 2007). We assume that under the adverse conditions on the active sand dune, only pioneer species (psammophytes) can complete their life cycles and produce seeds and rely on their distinct spatiotemporal patterns of soil seed bank to recruit themselves, while after dune stabilization, non-psammophytic annuals start to establish and contribute to the soil seed bank.

Seedling emergence might be a key factor influencing seed density in the topsoil layers of the stabilized sand dune during the rainy season. This was shown in this study by the seasonal change in seed banks at different positions (Figure 4). Seeds in the surface layers germinated shortly after effective rainfalls occurred, resulting in a decrease in seed density during the rainy season from May to July (Figure 4). At other sampling times, the wind is the main force responsible for seed movement both within the stabilized sand dune and from other sand dunes. As a result, seed accumulation was observed on the windward slope and transported away from the lower windward slope where wind erosion is usually stronger than at any other position of the stabilized sand dune (Zhu & Chen, 1994). On the stabilized sand dune, seeds in the 10–20 and 20–30 cm layers of the whole windward slope were unlikely to contribute to the aboveground population recruitment because of germination limitation that occurs at those depths even during precipitation events. Inhibition of seed germination by the micro-environmental conditions surrounding the seed bank in the deep soil of sand dunes has been well described by Tobe *et al.* (2005), Liu *et al.* (2011) and Redondo-Gomez *et al.* (2011). In our study, this was shown by a lack of variation over time in seed density recorded in those layers on the stabilized sand dune (Figure 4). However, on the active sand dune, under the effects of wind activities, seeds can either be blown away or buried, according to the season and dune position. The data indicate that seeds stored in deep soil might be shallowly buried or exposed to soil surface under strong wind forces on the active sand dune. In this case, seeds in deep soil also have the potential to be used for population recruitment and vegetation restoration on active sand dunes.

In conclusion, there is a relatively consistent seed density across the sand profile, and seeds in deep soil layers account for a large proportion of the whole soil seed bank on the active sand dune. Under the effects of wind activities, seeds in the deep soil could be shallowly buried and have the potential to be used for population recruitment and vegetation restoration. Therefore, further studies on the soil seed bank and vegetation restoration measures of the active sand dune ecosystem should pay more attention to deep soil seed banks and their ecological implications.

ACKNOWLEDGEMENTS

This work was financially supported by the Key Project of Chinese National Programs for Fundamental Research and Development (2013CB429905) and the National Nature Science Foundation of China (41271529). We thank all our colleagues at Wulanaodu Station for their assistance during field investigation. We also should be grateful for the comments from two anonymous reviewers.

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